Arafat Abdel Hamed Abdel Latef *Editor*

Sustainable Remedies for Abiotic Stress in Cereals

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Arafat Abdel Hamed Abdel Latef is a professor at the Department of Botany and Microbiology, Faculty of Science, South Valley University, Egypt. He has published more than 80 research articles in peer-reviewed journals and 12 book chapters in international books. He served as editor of one published international book. He serves as an editorial member of several reputed journals. Furthermore, he is an expert reviewer for about 110 international journals. Recently, he received Top Peer Reviewer Award 2019 Powered by Publons. He has received several awards, such as the Egypt State Award of Excellence in Agricultural Sciences 2021, South Valley University Award of Scientific Excellence 2019 and South Valley University Award of Scientific Publication for the years from 2010 to 2021.

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Part I

Cereals and Abiotic Stress

Cereals Under Abiotic Stress: An Overview

1

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Abstract

The changing climate poses the threat to yield stability of the major food crops around the world. Drought, salinity, cold or freezing temperatures, air pollution, intense light, pesticide pollution, light fluctuations, UV-B irradiation, wounding, ozone exposure, osmotic shock, heavy metals, etc. have become serious threats to agriculture production due to increased severity. The combination of abiotic stress and interactions with biotic stresses makes the situation worse and more complex to solve. In all stress conditions, photosynthesis is a highly affected activity. This, of course, eventually significantly affects crop production and quality. Comprehensive knowledge of the biochemical and physiological disorders related to each stress needs to be studied in detail. Perception of the stresses at the cellular level activates a cascade of signaling networks associated with stress tolerance. Phytohormones play a central role in these signaling cascades and maintain a balance between the allocation of the flux of resources

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for growth and stress tolerance. Phytohormones work in a synergistic or antagonistic manner to regulate abiotic stress tolerance of cereals and may cross talk with one another to converge multiple abiotic stress tolerance pathways. Since the abundance of these response metabolites inherently varies from crop to crop depending upon the phylogenetic and evolutionary position of the species, it is expected that the mechanism of overall response may also vary across or within the species. Therefore, to throw light on the stress tolerance mechanism, one has to consider different plant systems to obtain a better understanding of the role of various metabolites in stress avoidance and mitigation. In the present chapter, we focus on the individual stress types and their combinations across the major cereal crops.

Keywords

Abiotic stress · Cereals · Wheat · Drought · Cold · Stress tolerance

1.1 Introduction

The majority of cereal plants are being cultivated in adverse conditions in many parts of the world. In the past several years, the severity of abiotic stresses such as extremely high temperatures, intense light, drought, salinity, environmental pollution, etc. along with the inappropriate agricultural practices has increased dramatically, especially in the summer period at midday (Balfagón et al. 2019). As commonly observed, almost all the abiotic stresses are related to water consumption, and almost all abiotic stresses are experienced severely in the summer period, particularly in the daytime. Since water movement and consumption have been affected, this is finally reflected in photosynthesis efficacy. During abiotic or biotic stress, reactive oxygen species (ROS) or reactive nitrogen species (RNS) is formed. These free radicals can impair many metabolic functions, and in severe cases, they are also able to damage the nuclear membranes and DNA molecules causing single- or double-strand breaks.

Plants have evolved several mechanisms to shape their metabolisms to sustain their growth and development. The stress management strategies of plants are highly complex and may involve a change in physiological, metabolic, or cellular processes. The stress signals are perceived by plants at the cell surface by specific receptors which activate a cascade of signaling networks involved in transcriptional reprogramming of the stress-related genes and transcription factors. Plants generally face multiple stresses in their environment, and the cellular response to one stress may further severe the symptoms caused by other stresses (Atkinson and Urwin 2012). The simultaneous occurrence of heat and drought stress may present added complexity as the opening of stomata to relieve the heat stress may lead to further loss of water which is harmful to plants facing drought stress (Rizhsky et al. 2004). Similarly, abiotic and biotic stresses may interact positively or negatively with each other adding another dimension to the management of these stresses. For instance, the induction of salinity stress was found to enhance resistance to powdery mildew in barley (Wiese et al. 2004). The stress responses primarily may involve the counterbalance of stimuli without net penalty on growth and development of the plant system, which may be economic or biological yield for practical consideration. The aim of this chapter here is to underline the mechanism of such responses in relation to their effects on plant machinery. The chapter also outlines certain mitigation strategies which can only be conceptualized after there lies a proper understanding of the mechanism behind and beyond the interface between the crop system and the environment.

1.2 Major Abiotic Stresses in Cereals

Cereals are the staple food for the major parts of the world. Since they are field crops, they are often planted in large areas. Worldwide production of cereals has reached to 2817 million tons (FAO 2021). However, they are continuously exposed to a variety of stress factors in their natural environments. The growth and development of cereals are damaged at biochemical, physiological, and molecular levels due to several abiotic stressors along with the biotic ones, and this situation results in significant yield losses (Dresselhaus and Hückelhoven 2018). Plants have complex and complicated mechanisms to deal with the environmental stressors; however, cereals may be deprived of these adaptation mechanisms as they are hybridized by artificial breeding studies (Hurni et al. 2014; McIntosh et al. 2011; Nasir et al. 2019); therefore, they are under serious threat. Although improvements are made for the quality and quantity of cereals and tolerance to abiotic stress factors, duration, severity, and combination of abiotic stress factors make the breeding programs quite different, and their interactions with biotic stress factors make the case remain to be unsolved (Dikilitas et al. 2020, 2021a, b).

Abiotic stresses trigger a wide range of plant physiological and structural adjustments in cereals. Abiotic stress has a wide range of stress conditions. It includes drought, temperature extremes, waterlogging, salinity, light fluctuations, UV-B irradiation, wounding, ozone exposure, osmotic shock, heavy metals, etc. The physiology of essential processes such as photosynthesis, respiration, and nutrient acquisition is hampered in cereals under abiotic stress conditions. These stress factors are hostile to plant growth and development. Quite a several research articles have been published on abiotic stress factors in cereals. However, the recent status of abiotic stress factors appears as more severe with prolonged periods. New approaches to deal with the abiotic stress factors have to be made to sustain the increasing world population.

The breeding process of cereals has made them polyploid throughout history (Feuillet et al. 2008). Because of this, they have an extremely complex genome. While breeding cereals with favorable traits, we, unfortunately, make cereals susceptible to many abiotic and biotic stress factors (Hurni et al. 2014; McIntosh et al. 2011; Nasir et al. 2019). Many traits have been lost, e.g., regarding multiple defense mechanisms while we improve or try to increase the defense mechanism for a particular stress response.

1.2.1 Drought Stress

So far drought stress has been recognized as one of the most important stress factors among abiotic stressors for cereals. Drought and water scarcity stress are sometimes mixed, interrelated, and confused. As they often occur simultaneously in nature, the confusion between drought and water scarcity terms can be negligible. However, there is an important difference between them. To continue from the literature definitions, the explanation of drought is a natural hazard caused by climate variability on a broad scale. Drought cannot be controlled by agricultural practices and water management in nature. On the other side, water scarcity or water deficit refers to the long-term unfavorable use of water resources, which can be influenced by human activities (Van-Loon and Van-Lanen 2013). Drought stress is one of the most common yield-limiting abiotic stress factors for cereals such as maize (Daryanto et al. 2016; Gammans et al. 2017), wheat (Itam et al. 2020; Khadka et al. 2020; Shokat et al. 2021), rice (Melandri et al. 2020; Piveta et al. 2021), and sorghum (Gano et al. 2021). During drought conditions, the water content of plant tissues decreases, cells shrink, and the general turgor pressure decreases. Although most plants have developed various adaptations to drought conditions, drought is one of the most dangerous abiotic stresses for cereals. It primarily affects cereals by changing their key biochemical and morpho-physiological processes, and as a consequence of drought-induced osmotic stress, reduced nutrient uptake and yield are inevitable (Abid et al. 2018; Hussain et al. 2019; Zhang et al. 2018). When cell volume decreases, concentrates of solutes in cells cytoplasms increase. A reduction in the water content of the leaf can indirectly cause solute loss from the guard cells. Leaf expansion and root elongation are the most affected plant processes by turgor decrease (Liu et al. 2015). A thicker cuticle, which limits water loss from the epidermis, is a frequent development response to water stress (Bi et al. 2017). One of the most common consequences of drought is overaccumulation of reactive oxygen species (ROS) which cause oxidative stress in plants. In the case of homeostasis, all plants produce ROS; however, in osmotic stress or water deficit conditions, oxidative damage and the level of lipid peroxidation in membranes significantly increases (Cruz and Carvalho 2008; Jaleel et al. 2008; Todorova et al. 2021). Drought disrupts the balance between the synthesis of ROS and the antioxidant defense mechanism. It is important to manage abiotic stress in cereals because it also triggers susceptibility to other stress factors such as biotic stressors. During vegetation periods, cereals are not only exposed to one kind of abiotic stress; multiple abiotic and biotic stresses may also limit cereal production simultaneously (Kissoudis et al. 2016; Suzuki et al. 2014). The aggravation of the damages of other stresses makes drought stress a major yield-limiting factor for cereals (Cruz and Carvalho 2008).

1.2.2 Salinity Stress

Salinity stress is another abiotic factor for cereals. It has been reported by many studies that cereals are sensitive to saline conditions (Iqbal et al. 2021; Majeed et al. 2019; Dikilitas et al. 2021a, b). Salinity stresses are caused by the same impaired conditions as drought stress: lack of precipitation and irrigation (Abdelraheem et al. 2019). Many recent studies have examined both drought and salinity stress in cereals (Dugasa et al. 2019; Tang et al. 2019; Yaghoubi-Khanghahi et al. 2020). Considering global climate change, drought and salinity can be considered the two most important abiotic stress factors for cereals in the future. Studies showed that climate change and groundwater salinity will have negative effects on cereal yields in the near future (Akbari et al. 2020). A recent study on the tolerance of different cereal species against salinity stress and other soil constraints reported that cereal yield was affected by different ranges depending on cereal species (Page et al. 2021). Salinity stress occurs when the concentration of Na^+ and Cl^- in soils exceeds, principally interfering with potassium uptake which disturbs stomatal undulations causing severe water loss and necrosis in cereals (Ahanger and Agarwal 2017; Gul et al. 2019; Munns and Tester 2008). Salinity stress is difficult to deal with because of the genetic and physiological complexities of the salt tolerance trait (Abdelraheem et al. 2019; Almeida et al. 2017; Rasool et al. 2020). Soil salinity may be also caused by uncontrolled or excessive irrigation (Feng et al. 2017).

Salinity hampers the growth of cereal plants and affects photosynthesis and induces oxidative damage to plant cells with overproduction of ROS (Arif et al. 2020; De Azevedo Neto et al. 2006; Mahlooji et al. 2018). Excessive accumulation of sodium and chloride ions in the rhizosphere of salt-affected soils leads to severe nutritional imbalances in cereals. Excessive Na^+ concentrations in the rhizosphere also decrease the soluble matter ratio in plant tissues (Almeida et al. 2017). Salinity not only affects the vegetative and generative stages of cereals but also imports the germination process in cereals via disturbing hormonal balance during germination. For example, Liu et al. (2018) stated that gibberellic acid contents significantly decreased during the germination of rice seeds under saline conditions.

1.2.3 Heat Stress

Cereals are vulnerable to heat stress or high temperature stress, especially in growth and reproductive stages, including flowering and early grain filling stages (Ali et al. 2019). When we consider climate change, it is clear that heat stress will upset many cereal producers in the future. When compared to different climatic factors, an increase in temperature is considered to be a primary abiotic factor of plants (Ortiz-Bobea et al. 2019). Heat stress is well-known to reduce *Oryza sativa* yields during the grain filling stage causing yield loss, but the investigation of the mechanisms of heat stress has emerged recently (Ren et al. 2021). Recent studies demonstrate transcriptional regulatory networks modulate seed development and heat stress responses at rice different reproductive stages. High temperature stress at different growth stages results in grain yield losses in most cereal species. Individual and simultaneous implications of drought and heat stress significantly alter water contents, osmolytes, sugars, and soluble proteins along with the activated antioxidant defensive system in cereals (Cairns et al. 2013; El-Esawi et al. 2019; Sattar et al. 2020). As expected, the effects of heat and drought stress are more devastating in cereals (Sattar et al. 2020). Even without the combination, heat stress is quite destructive and significantly reduces photosynthetic efficiency, water-use efficiency, leaf area, and stomatal conductance of cereals, i.e., rice and maize (Li et al. 2020; Mbava et al. 2020; Singh et al. 2020; Wang et al. 2021c; Zhen et al. 2020). Heat stress also damages chloroplast ultrastructure and photosystem II in cereals (Bahadur-Poudel 2020; Chaudhary et al. 2021; Li et al. 2020). Among cereals, maize and sorghum were found as more water-use efficient than wheat, barley, and millet (Mbava et al. 2020).

1.2.4 Chilling, Cold, or Low Temperature Stress

Cold stress hampers production by affecting seedling growth and seed germination, especially in early vegetation periods (Guan et al. 2019; Hassan et al. 2021; Li et al. 2019). Cold-induced severe membrane damage, mechanical injury, and metabolic dysfunction through ice crystallization are the primary factors causing the stress (Yadav 2010). Cold stress is primarily perceived by the receptors at the cell membrane, and then some signal transductions regulate the transcription factors and cold-responsive genes mediating stress tolerance (Yadav 2010). Biomass accumulations and photosynthesis are the most important physiological processes and major sources of grain yield in cereals. These vital processes in cereals are highly vulnerable to cold stress (Liu et al. 2019; Wang et al. 2019a; Xiaochuang et al. 2017). Cold stress induces a series of imbalances in biochemical, molecular, and biological functions of the cereals (Hsu and Hsu 2019; Zhao et al. 2019). Decreased respiration rate, reduced enzymatic activity, oxidative stress, and deterioration of grains are the major outcomes of cold stress (Golizadeh and Kumleh 2019). Some cereals are highly susceptible to cold stress, while others tend to survive and continue their life cycle by increasing their tolerance ability via molecular and biochemical adaptations (Jeyasri et al. 2021).

1.2.5 Waterlogging

Natural flooding or water stagnation can cause hypoxia and ROS damage in cereals (Hofmann et al. 2020). Flooding decreases the oxygen level of the environment, and this situation is named hypoxia or anoxia. Plant hypoxia may occur as a result of excessive rain, waterlogging, and over-irrigation that hamper different physiological and metabolic activities (Loreti and Perata 2020). As a result of the stress condition, CO_2 assimilation rate, stomatal conductance, photosynthesis rate, and nutritional imbalance decrease resulting in crop yield loss (Hasanuzzaman et al. 2017). During the spike growth period, waterlogging significantly causes a reduction in grain number per plant up to 70% in wheat and 60% in barley (Celedonio et al. 2018). Different cereal species show different responses to waterlogging stress (Ploschuk et al. 2020). Researchers have studied the impact of waterlogging on yield and its components in wheat, barley, rice, and maize (Ciancio et al. 2021; Mei et al. 2017; Tian et al. 2019).

1.2.6 Light Flux

Plants require light to survive since it is the source of energy for photosynthesis, which has a significant influence on plant development. Since affecting leaf protein composition and shape, light quality and intensity are two of the most essential variables (Schumann et al. 2017). However, photoinhibition occurs when the absorbed light energy exceeds the pace of the photochemical process in plants (Takagi et al. 2019). When two plants growing at high light and low light conditions are compared, the following differences are striking; more cell layers and bigger cells in the leaves, resulting in a thicker leaf, increased number of chloroplasts per cell, Higher Chl a/b ratio and increased β-carotene and xanthophyll cycle pigment levels, higher photosystem II (PSII)/PSI ratio and smaller PSII antenna size, higher electron transport rates, higher CO_2 assimilation rates and higher light compensation points, and higher energy dissipation capacity (Schumann et al. 2017). Investigations were performed to clarify the high light stress effects on photosystem II efficiency in intact leaves of different rice (*Oryza sativa* L.) cultivars, and some chlorophyll a fluorescence parameters were affected only after a short time to high light exposure (Faseela and Puthur 2017).

1.2.7 Heavy Metal Stress

Metal toxicity exists in nature as soil constituents such as lead, chromium, arsenic, zinc, cadmium, copper, and nickel, and also they have been found in soil as a result of agricultural activities (Yang et al. 2018). Heavy metal contamination found in the soil not only reduces wheat crop yield but also poses a health risk to humans and animals. Heavy metal stress is a well-known abiotic stress factor for cereals, and today its many mechanisms have been unearthed (Devanna et al. 2021; Rizwan et al. 2018). Cereal response to heavy metal stress may vary; however, alterations in membrane permeability, water regime, impaired root growth and germination, hormonal status, impaired mineral nutrition uptake, decrease in photosynthesis, transpiration, DNA synthesis, and increased generation of reactive oxygen species (ROS) are the most common outcomes of the stress (Shafiq et al. 2019).

The effect of abiotic stressors on cereals and their combinations is discussed in Table 1.1. Also, the role of beneficial microorganisms or some chemicals in ameliorating the effects of abiotic stresses in cereals is summarized in Table 1.2.

Table 1.1 Various abiotic stresses in cereal crops and their manifestation

Abiotic stress types	Cereal species	Physiological and biochemical disorders	References
Drought stress or water deficit stress	*Triticum aestivum* L.	Increase in leaf monodehydroascorbate reductase (MDHAR)	Shokat et al. (2020)
	Triticum aestivum L.	Reduced trans-zeatin concentration in leaves along with salicylic acid concentration in spikes	Shokat et al. (2021)
	Drought-susceptible rice	Reduced chlorophyll content, water balance, antioxidant enzymes activities, and mineral contents (K$^+$, Ca^{2+} and Mg^{2+})	Sohag et al. (2020)
	Oryza sativa L.		
	Zea mays L.	Contents of non-enzymatic antioxidants and activities of antioxidant enzymes increased while the plant growth reduced and an increase in lipid peroxidation	Ali et al. (2020)
	Zea mays L.	Decrease in total yield and grain characteristics such as total protein, ash, total sugars, nitrogen, phosphorus, potassium, and iron contents	Abbas et al. (2021)
	Hordeum vulgare L.	Significantly decrease in nutrient uptake	Askarnejad et al. (2021)
	Hordeum vulgare L.	Decreased biomass, reduced stomatal conductance by 94%, decreased the shoot-to-root biomass ratio	Bista et al. (2020)
	Zea mays L.	Substantial decline in relative turgidity and chlorophyll contents were observed 13% and 10%, respectively. İncrease in the activities catalase (CAT, 131%), glutathione peroxidase (GPX, 79%), and superoxide dismutase (SOD, 137%)	Usmani et al. (2020)
	Rice (*Oryza sativa* L.)	*The overproduction of ROS in cells is counterbalanced by the antioxidants. Here the strongest known association is the ascorbate-glutathione (AsA-GSH) pathway. It operates inside the chloroplast and is characterized by photo-protection by scavenging hydrogen peroxide. The AsA-GSH cycle involve the following steps:* H_2O_2 *is reduced by APX where AsA acts as electron donor. Later, the oxidized AsA is reduced by the help of reduced GSH. This reduced GSH is produced from GR through oxidized glutathione (GSSG) by utilizing NADPH. These enzymes play vital roles in stress tolerance of plants*	Panda et al. (2021)
Salinity	*Zea mays* L.	Reduced plant growth, increased oxidative stress, and sodium uptake	Ali et al. (2021)

(continued)

Table 1.1 (continued)

Abiotic stress types	Cereal species	Physiological and biochemical disorders	References
	Triticum aestivum L.	Reduced electrolyte leakage and increased production of chlorophyll a, b, and total chlorophyll, and osmolytes, including soluble sugar, proline, amino acids, and antioxidant enzymes	Ilyas et al. (2020)
	Oryza sativa L.	Higher levels of lipid peroxidation and hydrogen peroxide concentrations in plant leaves	Mekawy et al. (2018)
	Sorghum bicolor L. Moench.	Reduced germination percentage, seedling shoot and root length, seedling vigor index, seedling fresh weight, and seedling dry weight. Increase in mean germination time	Dehnavi et al. (2020)
	Hordeum vulgare L.	Increase in proline accumulation and hydrogen peroxide and decrease of chlorophylls	Ferchichi et al. (2018)
	Hordeum vulgare L.	Increase in the malondialdehyde (MDA), proline content, Na and Ca concentrations of the roots and leaves. Decrease in shoot and root dry weight, plant height, membrane stability index, relative water content, survival rate	Ebrahim et al. (2020)
Heat stress	*Oryza sativa* L.	Anther dehiscence inhibition and low pollen shedding onto the stigma during flowering stage. Spikelet degeneration and destroying of floral organ development during panicle initiation stage	Wang et al. (2019a, b)
	Zea mays L.	Premature spore abortion in male reproductive organs, leading to male sterility	Begcy et al. (2019)
		Increase in sucrose as well as a reduction in pyruvate. Increase in unsaturated fatty acids level and decrease in levels of saturated fatty acids	
	Zea mays L.	Decreases in the length and diameter of young ears, floret fertilization rate, total number of florets and number of grains, whereas the length of the undeveloped part at the top of the ear and grain abortion rate increased significantly	Wang et al. (2020)
	Triticum aestivum L.	Increase in evaporation in the leaves cause reduced stomatal conductance with strongly increased transpiration	Balla et al. (2019)
	Sorghum bicolor [L.] Moench	Reduced pollen viability, pollen tube growth, and linear decline in fertility damaged ovarian cells in the susceptible genotype	Chiluwal et al. (2020)

(continued)

Table 1.1 (continued)

Abiotic stress types	Cereal species	Physiological and biochemical disorders	References
	Oryza sativa L.	Increased spikelet fertility and grain quality and decrease in anther dehiscence, number of pollen grains per stigma, number and percentage of germinated pollen grains per stigma	Wu et al. (2020)
Cold, low temperature or chilling stress	*Triticum aestivum* L.	Significantly delayed anthesis stage at elongation and booting stages	Xiao et al. (2021)
	Zea mays L.	Low temperature suppresses nitrogen metabolism and photosynthesis, causing the reduction in dry matter accumulation	Zhang et al. (2020)
	Oryza sativa L.	Significant inhibition in rice shoot growth and developmental traits and a significant reduction in the concentration of chlorophyll	Reddy et al. (2021)
	Hordeum vulgare L.	Hydrogen peroxide and malondialdehyde content increased through freeze and cold stress, increase in lipid peroxidation, decrease in the membrane stability index, increase in electrolyte leakage	Valizadeh-Kamran et al. (2017)
	Sorghum bicolor L. Moench	Significant reduction in the rate of photosynthetic CO_2 uptake	Ortiz et al. (2017)
	Oryza sativa L.	Decrease in chlorophyll biosynthesis, enhanced proline content and soluble sugars like glucose and sucrose accumulation, high production of H_2O_2 and MDA, causing a great impact on the cell membranes in sensitive genotypes, antioxidant enzymes such as SOD, peroxidase (POD), and CAT actively support the cell, alteration in stress-responsive gene expressions	Freitas et al. (2019)
Heavy metal stress	*Triticum aestivum* L.	Heavy metal stress has altered the antioxidant enzyme activity by causing oxidative damage.	Bakir and Agar (2019)
		Decrease in SOD enzyme, while POD enzyme activity and MDA levels were increased	
	Triticum aestivum L.	Heavy metal stress increased the expression of some genes and the activity of key enzymes of the antioxidant defense system along with the increase in cell oxidation levels (MDA, lipoxygenase (LOX))	Navabpour et al. (2020)
	Oryza sativa L.	Damages were observed on growth parameters, protein content, and membrane stability due to heavy metal	Mukta et al. (2019)

(continued)

Table 1.1 (continued)

Abiotic stress types	Cereal species	Physiological and biochemical disorders	References
	Zea mays L.	Different antioxidant enzymes are induced in root and shoot. Mature leaves are found to be more sensitive to heavy metals	AbdElgawad et al. (2020)
Drought + salinity	*Sorghum bicolor* L. Moench.	Reduction in photosynthetic pigments augmented ROS accumulation and osmolyte content, inhibition in plant growth and reduced water retention	Nxele et al. (2017)
	Zea mays L.	Decrease in the leaf area and shoot biomass at silking stage indicating that the photosynthetic leaf apparatus is highly sensitive and that drought has a greater effect than salinity	Romdhane et al. (2019)
	Oryza sativa L.	Increase in the sucrose content in leaf and root tissues and phloem sap	Mathan et al. (2021)
	Hordeum vulgare L.	During stress combination, drought tolerant and susceptible varieties show different manners in the synthesis of some proteins	Ahmed et al. (2020)
Drought + heat stress	*Oryza sativa* L.	Severely affected rice quality by altering the starch structure	Duan et al. (2020)
	Oryza sativa L.	Potential metabolic markers constitutive differences between the cultivars	Lawas et al. (2019)
	Zea mays L.	Grain yield was strongly correlated with ears per plant, ear and plant aspects, days to anthesis and silking	Meseka et al. (2018)
Drought + cold stress	*Zea mays* L.	Decline in photosynthetic capacity and enhanced transcriptional response	Guo et al. (2021)
		Transcription-associated metabolomic alterations, in which raffinose, trehalose-6-phosphate, and proline accumulated and monosaccharide abundance increased	
	Triticum aestivum L.	It's found that 1.3- to 1.8-fold change in 17 protein spots due to the cold treatment, while 1.3- to 3.8-fold change in 19 protein spots due to the drought stress	Labuschagne et al. (2020)
Drought + heavy metal stress	*Zea mays* L.	Water deficit and chromium (Cr) stress combination caused oxidative stress and decreased plant growth	Naz et al. (2021)
	Zea mays L.	Affected the activities of CAT, POD, and SOD, a concentration-dependent increase in MDA content	Song et al. (2014)
Salinity + heat stress	*Triticum aestivum* L.	Increase in germination percentage and amounts of proline and protein content	Song et al. (2005)
	Triticum aestivum L.	The germination percentage of seeds and the fresh weight of seedlings decreased	Lei et al. (2005)

(continued)

Table 1.1 (continued)

Abiotic stress types	Cereal species	Physiological and biochemical disorders	References
		markedly, SOD activity increased, activities of APX and CAT decreased distinctly, and the thiobarbituric acid reactive substances (TBARS) content increased gradually	
	Triticum aestivum L.	Reduced net photosynthesis and increased substomatal CO_2 level, leading to lowered CO_2 assimilation by rubisco	Anjum et al. (2008)

1.3 Combined Stress Responses

Jambunathan et al. (2010) discussed the transcriptome studies on combined stresses in plants where observed higher antioxidant capacity and/or lower accumulation of the reactive oxygen species (ROS) was outlined as a mechanism operative in plants related to combined stresses as was also later advocated by Iyer et al. (2013) and Sales et al. (2013). The unique transcription factors, hormone-responsive genes, and osmolytes are differentially expressed in response to different combined stresses (Rasmussen et al. 2013). The epigenetic modifications in response to stress have been said to be the cause for the trigger of subsequent secondary responses. Mahalingam (2015) has graphically shown the interrelationship of various stresses some of which have been displayed below. It was summarized based on the effect of combined stress on plant growth and development.

	Chilling	Heat	Salinity	Heavy metal
Drought	Negative	Negative	Negative	Negative
Chilling		No interaction	Not known	Positive
Heat			Both	Positive
Salinity				Positive

1.4 Conclusion and Future Prospects

Plants being sessile are exposed to a wide range of abiotic stresses such as waterlogging, salinity, light fluctuations, UV-B irradiation, wounding, ozone exposure, osmotic shock, heavy metals, etc. Plants have evolved intricate mechanisms to cope with such stresses; however, cereals due to extensive artificial selection are deprived of the development of such intricate adaptation mechanisms. Since cereals are a staple diet of the majority of the population worldwide, the improvement of traits related to productivity or nutritional quality has remained a priority. Extensive studies need to be conducted on abiotic stress tolerance in cereals, both solitarily and

Table 1.2 Different organic and inorganic amendments for mitigation of abiotic stresses in cereals

Abiotic stresses	Cereal species	Types of improvement	References
Heat or low temperature	*Oryza sativa* L.	Chitooligosaccharide regulates proline metabolism and cold stress tolerance	Zhang et al. (2019)
		Melatonin pretreatment mitigates the stress-induced inhibitions to photosynthesis and photosystem II activity	Han et al. (2017)
		Pretreatment with exogenous H_2 not only mimicked the above physiological response but also prevented cold-induced growth inhibition	Xu et al. (2016)
	Triticum aestivum L.	Melatonin supplementation enhances photosynthetic carbon absorption and membrane stability in cold-primed plants under cold stress	Sun et al. (2018)
		Increase in activity of SOD, POD, and CAT and content of proline increased significantly, while putrescine, malondialdehyde, and soluble sugar content decreased	Jing et al. (2020)
	Zea mays L.	Diethyl aminoethyl hexanoate ameliorates low temperature stress by improving nitrogen metabolism	Zhang et al. (2020)
		Biochar application improved soil-canopy system, especially soil water-holding capacity. And average grain weight obtained with biochar application	Wang et al. (2021b)
Water deficit or drought	*Triticum aestivum* L.	Foliar application of silicon and selenium	Sattar et al. (2019)
		LQ1230 isolated from *Elymus dahuricus* Turcz inoculation enhanced wheat growth and drought tolerance through regulation of antioxidant enzyme activities and the content of compatible solutes such as soluble sugars and proline	Qiang et al. (2019)
	Oryza sativa L.	Photosynthetic pigments and proline content increased by co-inoculation of *Bacillus altitudinis* FD48 and *B. methylotrophicus* RABA6	Narayanasamy et al. (2020)
		Seed inoculation and foliar spray, the application of *B. megaterium* PB50 significantly improved the plant growth under osmotic stress, protected plants from physical drought through stomatal closure, and improved carotenoid, total soluble sugars, and total protein content	
	Zea mays L.	*E. cloacae* in conjunction with a higher rate of biochar produced a significant improvement in photosynthetic rate, stomatal conductance, chlorophyll a, total chlorophyll and carotenoid contents	Danish et al. (2020)
		Application of humic acid with salicylic acid could be an effective and low-cost approach to ensure the seedling establishment and plant	Bijanzadeh et al. (2019)

(continued)

Table 1.2 (continued)

Abiotic stresses	Cereal species	Types of improvement	References
		growth in fields affected by soil drought in the early season	
Heavy metal stress	*Triticum aestivum* L.	*N*-acetylcysteine enhanced wheat growth exposed to heavy metals by promoting phenolic acids to support antioxidant defense systems	Colak et al. (2019)
		Polyamines (putrescine), as seed soaking to relieve the adverse effects of heavy metals	Taie et al. (2019)
	Zea mays L.	Nitrogen-fixing *Azotobacter chroococcum* alleviates the toxic effects of metals and enhances the performance of maize plants	Rizvi and Khan (2018)
		Exogenous glutathione to alleviate cadmium stress	Wang et al. (2021a)
	Oryza sativa L.	Exogenous citrate and malate alleviate cadmium stress	Sebastian and Prasad (2018)
		Selenite reduced the arsenic uptake and accumulation, enhanced uptake of nutrient elements, increased the phenolic contents, induced oxidative stress	Chauhan et al. (2017)
Salinity stress	*Oryza sativa* L.	Exogenous application of exogenous proline and glycine betaine mediate salt-induced upregulation of antioxidant defense and glyoxalase systems for better protection against salt-induced oxidative stress	Hasanuzzaman et al. (2014)
		External application of brassinosteroid improves growth and biomass content, levels of protein and proline content and antioxidant enzymes activity during salinity stress	Sharma et al. (2013)
		Inoculation of rice with halotolerant *Staphylococcus sciuri* ET101 increased growth rate and stimulated root growth, along with higher transpiration rates, stomatal conductance, and intracellular CO_2 accumulation. Additionally, electrolyte leakage (EL) also decreased in inoculated plants	Taj and Challabathula (2021)
		Bacillus amyloliquefaciens NBRI-SN13 (SN13) confers salt stress tolerance to rice seedlings by the accumulation of proline and total soluble solids (TSS)	Tiwari et al. (2017)
	Triticum aestivum L.	Potassium supplementation improves growth, photosynthetic pigment content, nitrogen and antioxidant metabolism, accumulation of osmolytes comprising free proline, sugars, and amino acids, improvement of the relative water content and yield	Ahanger and Agarwal (2017)
		Photosynthetic rate, pigment synthesis, stomatal conductance, and internal CO_2 concentration improved due to N supplementation under NaCl	Ahanger et al. (2019)

(continued)

Table 1.2 (continued)

Abiotic stresses	Cereal species	Types of improvement	References
		stress. N availability induces synthesis of osmolytes such as proline, free amino acids, glycine betaine and sugars, secondary metabolite accumulation, and redox components under salinity stress	
		Exogenous NO protects chlorophyll and photosynthetic attributes in salt-stressed wheat plants, increases the proline and sugar content, prevents lipid peroxidation and hydrogen peroxide, and improves membrane stability index. Exogenous NO upregulates antioxidant system and improves uptake of N, K, and Ca under salinity stress	Alnusairi et al. (2021)
	Zea mays L.	Application of biochar and plant growth-promoting rhizobacteria (*Azotobacter chroococcum* SARS 10 and *Pseudomonas koreensis* MG209738) mitigated the hazardous impacts of saline water on maize plants and enhanced characteristics like leaf area index, total chlorophyll, carotenoids, total soluble sugar (TSS), relative water content, K^+ and K^+/Na^+	Nehela et al. (2021)

in combination under controlled as well as field conditions. Signal pathways and the precise interplay between components underlying each stress individually and under multiple pathways must be studied in detail.

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Organic Solutes in Cereals Under Abiotic Stress

2

Vaishali Sharma and Neera Garg

Abstract

Cereals are the major source of agricultural grain production worldwide. These cereal crops experience various harsh environmental conditions which reduce their growth and productivity. They respond to these stressful conditions by accumulating various types of organic solutes including amino acids and their derivatives (proline, polyamines), quaternary ammonium compounds (glycine betaine), sugars (trehalose, sucrose, fructans), and sugar alcohols (mannitol, inositol). These organic solutes are highly soluble, nontoxic, and low-molecular-weight compounds that stabilize the membrane structures and other cellular components. Further, they maintain the osmotic potential of the cell, act as signaling molecules, and scavenge reactive oxygen species produced due to osmotic stress. Various cereal crops have been reported to accumulate different compatible solutes under abiotic stress conditions which enhanced the stress tolerance. However, some crops cannot synthesize these solutes in an appropriate amount; thus exogenous applications have been used by various researchers. Further, incorporating genes related to biosynthetic pathway enzymes of organic solutes enhanced their accumulation in various transgenic crops. Therefore, this chapter discusses the main categories of organic solutes and their role in ameliorating the stress in crop plants growing under adverse environmental conditions.

Keywords

Abiotic stress · Cereals · Organic solutes · Osmotic stress

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2.1 Introduction

Cereal crops are one of the main sources of food material and nutritional components for human and fodder for livestock all over the world. The most important cereal crops are rice, wheat, barley, maize, millet, oats, and sorghum. These cereals are a rich source of energy, as well as fiber, protein, vitamins, and nutrients like calcium, iron, zinc, phosphoric acid, potassium, magnesium, etc. (Shewry 2009). The productivity of crop plants is at high risk of worsening environmental conditions due to several abiotic stresses like heat, cold, drought, salinity, heavy metal toxicity, etc. These stress conditions negatively affect plant growth and development, photosynthetic rate, flower production, grain filling, and ultimately crop production (Khare et al. 2015). As a consequence, plants excessively produce reactive oxygen species (ROS) which are the result of incomplete reduction of molecular oxygen. These ROS then cause oxidative damage to lipid membrane, nucleic acids, cellular proteins, and ultimately irreversible malfunctioning of other metabolic structures and then cell death (Petrov et al. 2015). So, for the proper functioning of plants' metabolic processes as well as for the survival of plants, it becomes necessary to reduce these ROS. Therefore, to maintain the redox balance of the cell, plants have developed different repair mechanisms including antioxidant systems (enzymatic and non-enzymatic). Moreover, upon exposure of plants to stress conditions, metabolic alterations occur which result in a change in the level of cellular metabolites. Overproduction of different types of organic solutes (osmolytes) like glycine betaine, proline, sucrose, fructans, trehalose, polyamines, mannitol, inositols, etc. is one of the metabolic consequences of osmotic stress (Chen and Murata 2011; Bisht and Garg 2021). Properties like low molecular weight, high solubility, and less reactive nature make these osmolytes compatible solutes which are nontoxic even at high concentrations. In plants, organic solutes are involved in stress tolerance by regulating the cellular turgor and osmotic potential and by maintaining the redox homeostasis through scavenging excessively produced ROS (Krasensky and Jonak 2012). These organic solutes are mostly localized in the cytosol, chloroplast, and other cytoplasmic compartments of plant cells. Moreover, under abiotic stress, factors like plant species, plant growth conditions, type of stress, and stress severity determine the accumulation and compartmentalization of organic solutes at the cellular level (Kumar 2009). Many crops cannot synthesize some of the organic solutes which are normally accumulated by stress-tolerant plants. For that, various biotechnological approaches have come into account which improve the synthesis and accumulation of these compatible solutes by analyzing and incorporating osmoprotectant-related genes into cultivated crop plants (Zhang et al. 2019). Thus, this chapter summarizes the updated information about the contribution of various organic solutes in imparting abiotic stress tolerance in cereal crops.

2.2 Cereals Under Abiotic Stress

Rice, wheat, maize, barley, etc. are the main cereal crops that account for a large part of the global grain production. They are a good source of carbohydrates, fibers, proteins, minerals, as well as vitamins which are essential for normal human growth. Nutrient quality and grain production of these cereal crops is being negatively affected by various environmental factors such as drought, high and low temperature, salinity, heavy metal toxicity, etc. Moreover, the impact of these abiotic stresses gets enhanced under field conditions, where they accompany and interact with each other. The adverse effects of various abiotic stresses have been reported in different cereals which induce various physiological, biochemical, and molecular changes in plants. For instance, Khalilzadeh et al. (2018) observed that in the maize plant, salinity stress decreased stomatal conductance, relative water content, and photosynthetic efficiency which ultimately resulted in yield loss. Further, by reducing the grain number and lengthening the heading time, salinity stress reduced the grain yield of rice plants (Dramalis et al. 2021). Heat stress also affected plant yield by reducing flowers and spike number of rice plants (Fahad et al. 2016). Other abiotic stresses like cold stress have also been reported to limit plant growth and development by affecting root growth. Rativa et al. (2020) demonstrated that in rice plants, low temperature restricted root proliferation, reduced root hydraulic conductance, and thus decreased water as well as nutrient uptake. Similarly, in maize plants, cold stress reduced the primary root growth which resulted in poor plant growth (Frey et al. 2020). Furthermore, Arsenic (As) accumulation in various parts of the rice plant caused oxidative damage which reduced the photosynthetic rate and ultimately rice growth and yield (Mousavi et al. 2020).

2.3 Organic Solutes

Osmoprotectants or organic solutes are low-molecular-weight, electrically neutral, highly soluble, and nontoxic molecules that act as osmolytes and help plants to endure extreme stress conditions. On the basis of their chemical behaviors, organic solutes are characterized into these main classes, i.e., amino acids and their derivatives (proline, polyamines, etc.), quaternary ammonium compounds (glycine betaine, proline betaine, etc.), sugars (sucrose, trehalose, fructans, etc.), and polyols (mannitol, inositol) (Salama and Mansour 2015). Biosynthesis and accumulation of these osmolytes under different stress conditions is a complex mechanism evolved by plants to maintain cellular integrity. The main function of the osmolytes is to stabilize the cell water relations, and they do so by maintaining the water potential and by keeping the cells turgescent (Wang et al. 2003; Choudhary et al. 2022). In addition to this, they participate in the reduction of various ROS, regulation of redox potential of a cell, stabilization of cellular pH, and maintenance of proteins and membrane structure during environmental stresses (Fig. 2.1).

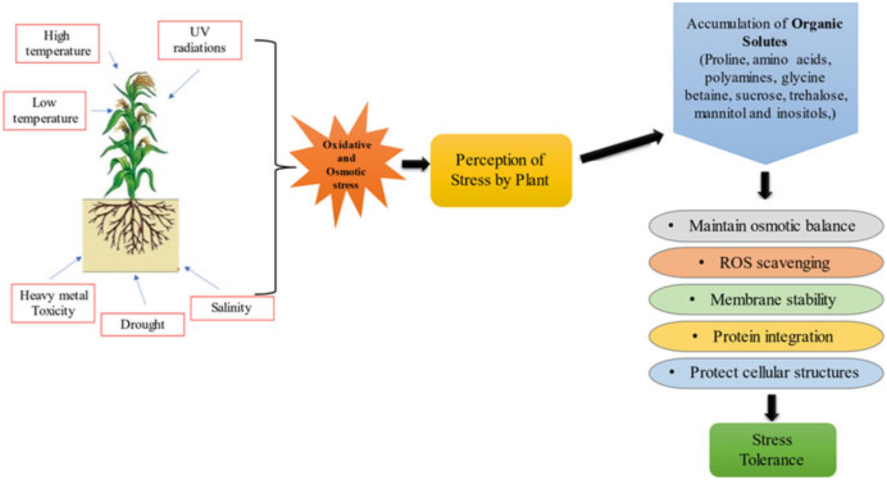

Fig. 2.1 Graphical representation of crop plants under different abiotic stresses and roles of organic solutes in mitigating the negative effects of these stresses. *ROS* reactive oxygen species

2.3.1 Amino Acids and Their Derivatives

Amino acids are the building blocks of proteins and peptides, and they act as a precursor for the biosynthesis of many other biomolecules like nucleic acids, secondary metabolites, etc. They also function as signaling and regulatory molecules in plants under stress conditions (Dondoni and Massi 2006). Several studies have reported the overproduction of amino acids such as proline (Pro), glycine, arginine, alanine, and other derivatives like amides (glutamine and asparagine), amines (polyamines), and nonprotein amino acids (gamma-aminobutyric acid) as well as proteins to counteract different environmental stress conditions (Woodrow et al. 2017). The increase in amino acid biosynthesis and stress-driven breakdown of protein leads to high deposition of amino acids, which was indicative of cell damage as noted in some species.

2.3.1.1 Proline

Pro is one of the important proteinogenic amino acids which plays a significant role in plants' metabolic processes as well as provides osmoprotection against different stresses. It also acts as an antioxidant that scavenges superoxide radicals, maintains the redox potential, and preserves the structure of the cell membrane. Further, as a molecular chaperone, it maintains protein integrity and protects the activity of the enzyme (Suprasanna et al. 2016). High accumulation of Pro has been recorded in different plant species including rice, wheat, barley, maize, tomato, brassica, and *Arabidopsis* experiencing stress conditions such as salinity, drought, heavy metal toxicity, and low and high temperature (Sharma and Dietz 2006; Al Hinai et al. 2022).

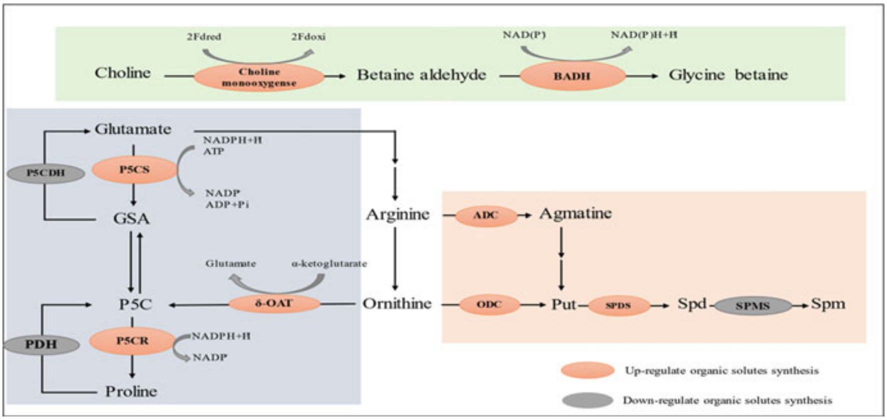

Fig. 2.2 Graphical representation of biosynthetic pathways and enzymes involved in the synthesis of proline, glycine betaine, and polyamines. BADH, betaine aldehyde dehydrogenase; P5C, pyrroline-5-carboxylate; GSA, glutamate-semialdehyde; P5CS, pyrroline-5-carboxylate synthetase; P5CR, pyrroline-5-carboxylate reductase; P5CDH, Δ1-pyrroline-5-carboxylate dehydrogenase; PDH, proline dehydrogenase; δ-OAT, ornithine-δ-aminotransferase; ADC, arginine decarboxylase; ODC, ornithine decarboxylase; Put, putrescine; Spd, spermidine; Spm, spermine; SPDS, spermidine synthase; SPMS, spermine synthase

The level of proline in a cell is regulated by the balance between its synthesis (in cytosol and plastid) and degradation (in mitochondria) (Szabados and Savoure 2010). Plants synthesize Pro mainly by two pathways, i.e., glutamate and ornithine pathway, and out of these, glutamate pathway is more evident under osmotic stress conditions. The catalytic enzymes involved in the glutamate pathway are pyrroline 5-carboxylate synthetase (P5CS) and pyrroline 5-carboxylate reductase (P5CR) whose activity and expression determine the potentiality of Pro production. Firstly, the enzyme P5CS reduces glutamate into glutamate-semialdehyde (GSA) which is immediately transformed into pyrroline-5-carboxylate (P5C), and then enzyme P5CR makes the final product, i.e., Pro, by reducing P5C. Whereas in the ornithine pathway, the first step occurs in mitochondria; the enzyme ornithine-δ-aminotransferase (δ-OAT) converts ornithine into P5C, and further this mitochondrial P5C gets reduced into Pro by the activity of cytosolic P5CR (Dar et al. 2016). Degradation of pro occurs in mitochondria, where enzymes, Pro dehydrogenase (PDH), and Δ1-pyrroline-5-carboxylate dehydrogenase (P5CDH) metabolize glutamate from proline (Fig. 2.2). Biosynthesis, degradation, and transport of the synthesized pro determine the overall pro level in a particular organelle or a cell. It is likely to believe that the synthesis or degradation of pro depends on the plants' condition under stress; synthesis is stimulated during the onset of stress, while degradation is accelerated during restoration from stress. Furthermore, the biosynthesis of enzymes P5CS and P5CR in cytosol and PDH, P5CDH, OAT in mitochondria play an important role to maintain Pro level in stress conditions (Szabados and Savoure 2010).

High accumulation of Pro under various stress environments has been reported in different cereal crops. For instance, Joseph et al. (2015) have noticed a significant increment in Pro synthesizing enzyme, P5CS, in the chloroplast of rice leaves under salt stress, leading to enhanced Pro synthesis. This accumulation of Pro played an important role in providing necessary pressure potential for cell expansion by increasing cellular osmolarity by increasing the influx of water or by reducing its efflux. In another study, Sultana et al. (1999) have observed the accumulation of pro in salinized leaves and grains of rice plants which provides salinity tolerance by improving the osmotic balance. Pre-sowing priming of seeds with Pro has also been reported to amend the negative effects of salt stress in wheat (Kamran et al. 2009). Furthermore, the correlation between overexpression of P5CS gene and accumulation of Pro was also observed in wheat plants under drought stress. This suggested that P5CS is a stress-inducible gene and has the potential to be used in crop plants for the tolerance of different abiotic stresses (Maghsoudi et al. 2018). Rice was transformed with P5CS cDNA of *Vigna aconitifolia*, and the resultant transgenic rice plant accumulated more Pro which resulted in water and salt stress tolerance (Zhu et al. 1998). Furthermore, transgenic wheat and rice cultivars overexpressed P5CS gene and accumulated a considerable amount of Pro which improved the stress tolerance in these plants (Sawahel and Hassan 2002; Vendruscolo et al. 2007). Additionally, the activity of PDH enzyme (Pro catabolic enzyme) gets inhibited in rice under Cd stress, which exhibited the role of PDH gene in the regulation of Pro level in plants at the transcriptional level (Table 2.1) (Paul and Roychoudhury 2018). Improved drought and oxidative stress tolerance in resultant rice cultivars was correlated with increased expression of *OsOAT* gene which suggested the vital role of OAT in stress tolerance (You et al. 2012). A similar increment in the expression of OAT enzyme was reported by Anwar et al. (2021) in wheat plants when incorporated with *AtOAT* gene. The increased expression of OAT enzyme resulted in enhanced proline synthesis which accounted for the salt, drought, as well as heat stress tolerance in transgenic wheat cultivars.

2.3.1.2 Polyamines

Polyamines (PAs) are low-molecular-weight, nitrogenous compounds having two or more two amino groups. They play an important role in plant growth and development by regulating plant metabolic processes. PAs also serve as anti-stress agents by providing membrane stability and osmotic and ionic balance and function as an antioxidant by stabilizing the structure of DNA, RNA, protein, and phospholipids (Kusano et al. 2007). Putrescine (Put), spermidine (Spd), and spermine (Spm) are the extensive forms of polyamines found in higher plants. Biosynthesis of these PAs occurs in cytoplasm where ornithine decarboxylase (ODC) or arginine decarboxylase (ADC) biosynthesizes Put from ornithine or arginine, respectively (Fig. 2.2). Further, the addition of one aminopropyl group to Put synthesizes Spd which is catalyzed by Spd synthase (SPDS), and the insertion of one aminopropyl group to Spd results in the formation of Spm by enzyme Spm synthase (SPMS). The aminopropyl group attached to Spd and Spm came from decarboxylation of

Table 2.1 List of genetically engineered cereal crops under different abiotic stresses

Crop	Gene introduced	Remarks	References
Proline			
Triticum aestivum	P5CS	Increased proline concentration, decreased MDA content, and improved biomass production	Sawahel and Hassan (2002)
Triticum aestivum	P5CS	Enhanced proline concentration, plant biomass, and water stress tolerance	Vendruscolo et al. (2007)
Oryza sativa	OAT	Proline accumulation, improved water retention	You et al. (2012)
Triticum aestivum	P5CS	Increased proline accumulation and drought tolerance	Maghsoudi et al. (2018)
Polyamines			
Oryza sativa	ADC	Increased polyamine concentration and salinity tolerance	Roy and Wu (2001)
Oryza sativa	SAMDC	Enhanced spd and spm concentration and improved salt tolerance	Roy and Wu (2002)
Oryza sativa	ADC	Increased threefold put concentration and induced drought tolerance	Capell et al. (2004)
Glycine betaine			
Zea mays	*betA*	Improved drought tolerance	Quan et al. (2004)
Oryza sativa	*codA*	Enhanced water stress tolerance	Kathuria et al. (2009)
Triticum aestivum	*betA*	Increased drought and heat tolerance	Wang et al. (2010)
Zea mays	BADH	Increased biomass, decreased lipid peroxidation, improved photosynthetic efficiency, and improved salt stress tolerance	Di et al. (2015)
Triticum aestivum	BADH	Increased GB accumulation and photosynthesis; improved salinity tolerance	Tian et al. (2017)
Oryza sativa	BADH	Enhanced Cd stress tolerance	Paul and Roychoudhury (2018)
Trehalose			
Oryza sativa	*otsA and otsB*	3–10-fold trehalose accumulation, salt, drought, and low temperature tolerance	Garg et al. (2002)
Oryza sativa	TPS	Enhanced trehalose production and salinity tolerance	Guo et al. (2014)
Fructan			
Oryza sativa	6-SFT and 1-SST	Enhanced chilling stress tolerance	Kawakami et al. (2008)
Mannitol			
Triticum aestivum	*mtlD*	Increased mannitol production, plant growth and biomass, and salinity tolerance	Abebe et al. (2003)
Oryza sativa	*mtlD*	Improved drought and salinity stress tolerance	Pujni et al. (2007)

S-adenosylmethionine (SAM) by the enzyme *S*-adenosylmethionine decarboxylase (SAMDC).

The increment in the level of PAs has been reported in response to various abiotic stress conditions such as water deficit, salt, metal toxicity, heat, and chilling stress (Tiburcio et al. 2014). They provide extensive tolerance against these stresses by maintaining protein homeostasis, activating antioxidative machinery, detoxifying ROS, enhancing photosynthetic capability, and improving osmotic adjustments. To illustrate, Liu et al. (2000) demonstrated that PAs regulate the opening and closing of guard cells, thus restricting the water loss in plants. They also played a role in determining the size of guard cells as well as regulated the potassium-gated channels. Furthermore, Hassan et al. (2020) observed the ameliorative effects of exogenously applied Spm and Put on wheat plants under drought stress. These PAs protected the wheat plant mainly by increasing catalase activity which reduced ROS and malondialdehyde (MDA) content and thus protected the membrane structure and mesophyll cells under drought stress. Furthermore, foliar application of Put on wheat seedlings mitigated the adverse effects of heat stress by increasing the activity of enzymatic antioxidants (peroxidase and superoxide dismutase) along with non-enzymatic ones (ascorbate and tocopherol) (Asthir et al. 2012). It has been reported that exogenous application of Spd also increased endogenous Spd and Spm level by increasing the expression of genes encoding the biosynthetic enzymes of these polyamines. This increase in polyamine concentration regulated the production of ROS by enhancing the activity of enzymatic antioxidants (CAT, POD, and SOD) (Zhou et al. 2020). In addition to exogenous applications, transgenic approaches demonstrated enhancement in stress tolerance by overexpressing the PAs biosynthetic genes. For example, Capell et al. (2004) observed threefold increment in Put production in *Avena sativa* when introduced with *Datura stramonium* ADC genes (Table 2.1). The resultant transgenic *Avena sativa* plants also accumulated higher level of Spd and Spm which resulted in enhanced tolerance against drought. Furthermore, transgenic rice plants expressing *Tritordeum* cDNA of SAMDC accumulated a higher level of Spm and Spd which conferred enhanced tolerance to salinity (Roy and Wu 2002).

2.3.1.3 Proteins

Accumulation of soluble proteins in response to stressful conditions is one of the adaptive changes that occur in plants. These proteins play a crucial role in mitigating the damage caused by environmental stresses by acting as an osmotic regulator as well as by providing the storage form of nitrogen. Hasegawa et al. (2000) observed that salinity induced the accumulation of various cytoplasmic proteins which helped in maintaining the viscosity of the cytoplasm. A higher concentration of soluble proteins has also been observed in cereal crops such as barley, millet, and rice (Ashraf and Harris 2004). Qayyum et al. (2018) observed the increased synthesis of some of the soluble proteins in wheat plants under drought stress which helped in managing the plant water status by improving water uptake from soil. A similar increase in the total soluble proteins was also observed by Perveen and Hussain (2021) in *Zea mays* under salt stress.

In addition to soluble proteins, plants also respond to stressful conditions by accumulating other defensive proteins such as late embryogenesis-abundant (LEA) protein and heat shock proteins (HSPs). It has been observed that heat stress boosts the accumulation of HSPs which accounted for heat stress tolerance by enhancing photosynthetic efficiency and thermostability of plant cells, proper partitioning of photo-assimilates, and also acting as molecular chaperones (Wahid et al. 2007). Transgenic rice plants have been generated by incorporating HSP 101 gene from *Arabidopsis thaliana* into Pusa Basmati 1 variety of indica rice, and resultant transgenic rice plants displayed better growth and development under heat stress conditions. An upregulation of HSP gene expression was also observed in *Triticum durum* experiencing salt stress (Al Khateeb et al. 2020). Similarly, the natural accumulation of LEA proteins in some drought-tolerant parts of plants such as seeds as well as vegetative parts has also been reported as a drought tolerance response (Liu et al. 2010). In addition to this, enhanced gene expression of other members of the LEA proteins family such as dehydrin has also been reported in wheat plants under low temperature (Kosová et al. 2021).

2.3.2 Quaternary Ammonium Compounds: Glycine Betaine

Betaines are fully methylated amino acids that contain a functional carboxyl group and are categorized as quaternary ammonium compounds. Depending on plant species and environmental stress conditions, plants contain different forms of betaine, including glycine betaine, choline-*o*-sulfate, 3-dimethylsulfoniopropionate, and proline betaine (Nahar et al. 2016). Among these, glycine betaine (GB) is considered as most efficient organic solute because of its low-molecular-weight, high solubility, low viscosity, electrically neutral and dipolar nature (Kurepin et al. 2015). It protects the plants from oxidative damage by accumulating in high amounts under various stresses like drought, salinity, and high and low temperatures (Roychoudhury and Banerjee 2016). The protective mechanisms of GB include regulation of osmotic potential and cytoplasmic pH, maintenance of the structure of lipid membrane and macromolecules, as well as guarding the antioxidant enzymes' activity (Huseynova et al. 2016). Besides this, it maintains cellular Na^+/K^+ balance under salt stress and protects cell membrane and enzymes, such as RUBISCO against heat-induced destabilization (Mäkelä et al. 2000).

Biosynthesis of GB is a two-step process; it starts with the transformation of choline into betaine aldehyde by the enzyme choline monooxygenase, which is then converted into GB by the enzyme betaine aldehyde dehydrogenase (BADH) (Fig. 2.2) (Ashraf and Foolad 2007). Synthesis of GB mainly occurs in chloroplast where it provides protection to the thylakoid membrane and controls the photosynthetic efficiency of the plant under stress (Yokoi et al. 2002). Additionally, Annunziata et al. (2019) have observed the accumulation of GB in young tissues of stressed plants which indicated the role of GB in the protection of young expanding tissues. Increased production of GB in response to stress has been documented in many crop plants such as *Beta vulgaris*, *Hordeum vulgare*, *Sorghum* *bicolor*, *Triticum aestivum*, and *Spinacia oleracea* (Yang et al. 2003). Moreover, the accumulation of GB depends on the plant species; for example, in cereals like barley, maize, and wheat, normal GB accumulation is lower than the threshold value required to mitigate the toxic effects of different abiotic stresses (Kurepin et al. 2015). However, some species like rice, tobacco, and tomato are those that totally cannot synthesize or accumulate GB in normal as well as stress conditions (Kurepin et al. 2015). Therefore, to reduce the adverse effects of abiotic stresses in low-accumulating and non-accumulating plants, the exogenous applications of GB were found effective (Yang and Lu 2005). In wheat plants, exogenous application of GB enhanced the stomatal conductance, net CO_2 assimilation, and photosynthetic efficiency under salt stress (Raza et al. 2007). Further, seed priming of wheat with choline reduced MDA, proline, and glutathione content and enhanced the GB, Ca^{2+}, and K^+ content in shoot as well as root of the plant which resulted in increased salt tolerance (Salama et al. 2011). Ahmed et al. (2021) also reported the ameliorative roles of GB in wheat plants experiencing water stress. They observed that priming of wheat roots with GB improved the overall growth of the plant by detoxifying ROS, increasing antioxidative enzyme activity (POD, SOD), and upregulating the genes related to stress-responsive hormones (SA, ABA, etc.). In recent years, due to the diverse role of GB in various stress-ameliorating mechanisms, genetic engineering of non-betaine accumulating crops with GB biosynthetic genes has also been emphasized (Chen and Murata 2011). Various transgenic plants with GB synthesizing genes have been established for GB accumulation and enhanced stress tolerance (Table 2.1). For example, *betA* gene encoding choline dehydrogenase enzyme from *E. coli* was introduced in maize inbred line DH4866, and resultant maize cultivars produced a high amount of GB which protected against drought stress (Quan et al. 2004). In rice plants, *codA* gene which encodes choline oxidase was incorporated from *Arthrobacter globiformis* which enhanced water stress tolerance (Kathuria et al. 2009). Cd tolerance was also enhanced in rice plants by upregulating the expression of BADH1 gene (Paul and Roychoudhury 2018). Further, rice has also been engineered to accumulate GB under salinity, drought, and chilling stress (Su et al. 2006). Similarly, transgenic lines of wheat and maize plants were reported to have enhanced salt tolerance when transformed with BADH gene from *Atriplex hortensis* and *A. micrantha*, respectively. GB overaccumulation in these transgenic plants resulted in better photosynthetic activity, enhanced antioxidant activity, stability in thylakoid membrane structure, and improved water status (Di et al. 2015; Tian et al. 2017).

2.3.3 Sugars

Sugars are the main source of carbon as well as energy in plants and other living organisms. Plants accumulate soluble sugars such as disaccharides (trehalose, sucrose), fructans, raffinose, and sugar polyols such as mannitol, sorbitol, and inositol in response to various environmental stress conditions (Sami et al. 2016). These sugars regulate the cell osmotic balance, stabilize the membrane structures and cellular proteins, maintain redox homeostasis by scavenging excessively produced ROS, and also participate in stress signaling pathways (Krasensky and Jonak 2012).

2.3.3.1 Disaccharides: Sucrose and Trehalose

Sucrose is a nonreducing disaccharide, composed of one glucose and one fructose molecule which are combined by an α-1, β-2 glycosidic linkage. It is one of the main storage and transport carbohydrates which is primarily biosynthesized from a triose phosphate, i.e., 3-phosphoglycerate in the cytosol. It also acts as a key osmoprotectant that accumulates in response to various adverse stress conditions (Nishizawa-Yokoi et al. 2008). The biosynthesis of sucrose in plants involves two enzymes, viz., sucrose-phosphate synthase (SPS) and sucrose-phosphate phosphatase (SPP). Enzyme SPS catalyzes the first reaction, where it acts upon fructose-6-phosphate and UDP-glucose and synthesizes sucrose-6-P, which is then subsequently converted into sucrose by another enzyme SPP (Fig. 2.3). Under abiotic stress conditions, sucrose prevents plants from dehydration and regulates cellular turgor as well as stabilizes cellular proteins and thus acts as an osmoregulator (Keunen et al. 2013).

Trehalose (Tre) is a highly soluble, chemically inert and non-reducing disaccharide that contains two glucose units linked by α, α-1,1-glycosidic linkage. It plays an important role in plants' normal metabolic processes as well as protects the plant as an osmoprotectant (Lunn et al. 2014). Under stress conditions, Tre plays diverse roles such as it effective in stabilizing lipid membrane, maintaining osmotic balance,

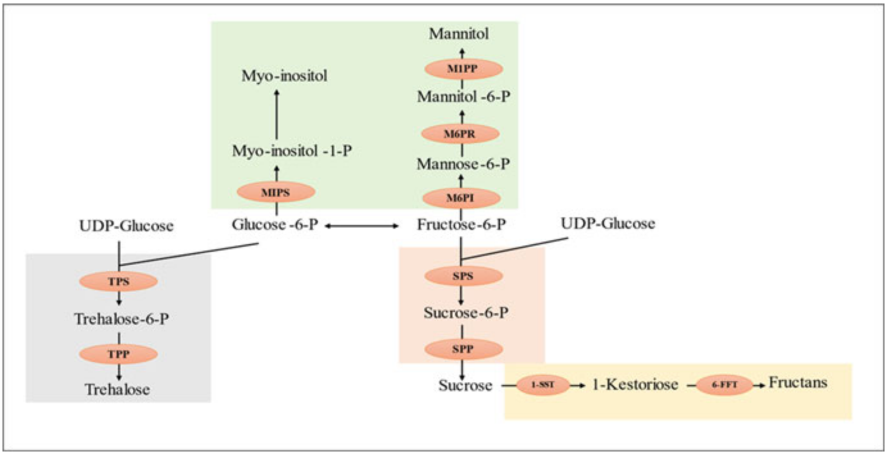

Fig. 2.3 Graphical representation of biosynthetic pathways and enzymes involved in the synthesis of trehalose, fructan, sucrose, mannitol, and myo-inositol. TPS, trehalose phosphate synthetase; TPP, trehalose-6-phosphate phosphatase; SPS, sucrose-phosphate synthase; SPP, sucrose-phosphate phosphatase; 1-SST, sucrose:sucrose 1-fructosyltransferase; 6-FFT, fructan-6-fructosyltransferase; M6PI, mannose-6-P isomerase; M6PR, mannose-6-phosphate reductase; M1PP, mannose-1-phosphate phosphatase; MIPS, myo-inositol-1-P synthase

scavenging excessively produced ROS, and protecting protein-synthesizing machinery (Alam et al. 2014). Additionally, in dehydration conditions, Tre protects membrane or other macromolecules by forming anomalous glass-like structures and by forming a hydrogen bond with a hydrophilic head group of phospholipids (Crowe 2007).

Tre biosynthesis in plants is a two-reaction process; at first, uridinediphospho-glucose (UDP-Glc) and glucose-6-phosphate (Glc-6-P) get converted into trehalose-6-phosphate (T-6-P) and uridine diphosphate (UDP) by the enzyme trehalose phosphate synthetase (TPS). Afterward, T-6-P is dephosphorylated into Tre by the enzyme trehalose-6-phosphate phosphatase (TPP) (Fig. 2.3). Further, hydrolysis of Tre is catalyzed by the enzyme trehalase (Vandesteenea et al. 2010). Under different abiotic stress conditions, a higher accumulation of Tre has been reported in various crop plants (Iordachescu and Imai 2008). For instance, an enhanced level of Tre has been observed in rice under cold stress, where it restored the membrane fluidity by stabilizing the cellular proteins and by restricting the membrane inactivation (Ramon and Rolland 2007). Exogenous application of Tre has also been used in some crops to enhance the internal Tre level and to alleviate the harmful effects of abiotic stresses such as heat, drought, and salinity in wheat and maize plants (Ali and Ashraf 2011; Luo et al. 2010; Ma et al. 2013). It has been reported that under salt stress in wheat, exogenously applied Tre also resulted in an increase in other organic solutes like proline, glucose, total soluble sugars, and free amino acids and thereby decreasing the MDA and H_2O_2 content (Sadak et al. 2019). In another study, the application of Tre along with maltose enhanced the drought stress tolerance in wheat by increasing other osmolytes as well as secondary metabolite content (flavonoids and phenolics) (Ibrahim and Abdellatif 2016). Pre-treatment of Tre also ameliorated high-temperature-induced oxidative injury in wheat seedlings by enhancing the non-photochemical quenching through increasing β-carotene content and decreasing chlorophyll content (Luo et al. 2014). In the past few years, a number of plants have been engineered with genes encoding Tre synthesizing enzymes to enhance Tre accumulation as well as stress tolerance (Table 2.1). For instance, transgenic maize cultivar with rice Tre biosynthetic gene (*OsTPP*) resulted in a high accumulation of Tre and improved drought tolerance (Nuccio et al. 2015). Similarly, rice plant has been genetically engineered to synthesize a high amount of Tre under various stresses like drought, salt, and cold (Garg et al. 2002). Likewise, Guo et al. (2014) cultivated a transgenic rice plant by inserting a gene that encodes for trehalose-6-phosphate synthase (*PyTPS*) enzyme from *Porphyra yezoensis*, and the resultant rice plant exhibited improved salt tolerance.

2.3.3.2 Fructans

Fructans are water-soluble polysaccharides that contain short chains of fructose units and a terminal glucose unit. They serve as reserve carbohydrate molecules in some plants. Fructans are resilient to crystallization and thus get accumulated under severe drought and cold conditions (Krasensky and Jonak 2012). They directly interact with the lipid head group of the membrane and maintain the membrane stability and lipid phase transition under frost and water stress conditions (Ahmad et al. 2020). Fructans are also responsible for the excessive growth and branching of roots in response to water scarcity. Their accumulation under abiotic stress conditions is advantageous due to its properties like being highly water soluble, resistant to crystallization of membrane at very low temperature, and ability of fructan biosynthetic enzymes to function normally even at subzero temperature (Vijn and Smeekens 1999).

Based on the position of glucose unit and glycosidic linkages present between fructose units, fructans are subdivided into five major types: (1) inulin, with 2-1-linked fructosyl residues; (2) inulin neoseries, having 2-1 fructosyl linkage, but glucose moiety is present between two fructose molecules; (3) levan, which has 2-6 linkages between its fructosyl units, and it is mainly present in monocots; (4) levan neoseries, it also contains glucose molecule between two fructose molecules (like inulin neoseries), but fructosyl linkage is 2-6; it has been reported in oat (Livingston et al. 1993); and (5) graminin, is a branched type of fructans in which inulin or levan forms the basic structure with one or more short branches. It has been found in wheat (Bancal et al. 1992).

Fructan is synthesized when photosynthesis surpasses its demand and sucrose level in sink tissue reaches a threshold value. The synthesis starts in the vacuole, where sucrose acts as a precursor and converts into 1-ketoriose by the enzyme, sucrose:sucrose 1-fructosyltransferase (1-SST). Glucose molecule also releases with the formation of this trisaccharide (1-ketoriose). The next step is catalyzed by the enzyme fructan 6-fructosyltransferase (6-FFT) which produces basic linear fructan (inulin) by inserting fructose units into another fructan or sucrose molecule (Fig. 2.3) (Valluru and Van den Ende 2008). Increased activity of these enzymes (6-FFT and 1-SST) was observed in wheat plants under drought stress which resulted in increased scavenging of the hydroxyl radicals, reduced membrane damage, and thus played important role in drought stress tolerance (Nemati et al. 2018). Various researchers studied these fructan biosynthetic enzymes at the genetic level and demonstrated their role in different stress conditions (Table 2.1). For example, Kawakami and Yoshida (2002) isolated sucrose:fructan 6-fructosyltransferase (6-SFT) and sucrose:sucrose 1-fructosyltransferase (1-SST) encoding cDNA, *wft1* and *wft2*, respectively, which were responsible for fructan synthesis in wheat plants. They further noticed that under cold stress, the resistant wheat cultivars transcribed higher levels of these cDNAs, which resulted into high fructan accumulation and enhanced cold stress tolerance. Additionally, Kawakami et al. (2008) developed a transgenic rice cultivar by introducing fructosyltransferase genes from wheat plants, and the resultant transgenic rice cultivar excessively accumulated fructan in mature leaves and displayed improved cold tolerance.

2.3.3.3 Raffinose Family Oligosaccharides (RFOs)

RFOs are non-reducing sucrose molecules with alpha-1,6 galactosyl (Gal) extensions. Generally, in plants, they protect the embryo from desiccation, act as storage and transport carbon, as well as play observed in based on the number of Gal residues, different RFOs are raffinose (Raf), stachyose (Sta), verbascose, ajugose, etc. (Van den Ende 2013). Biosynthesis of these RFOs starts with the conversion of UDP-glucose and myo-inositol into galactinol, and the reaction is catalyzed by galactinol synthase (GolS) (Kannan et al. 2016). Further, galactinol reacts with sucrose to synthesize raffinose, raffinose to synthesize stachyose, and then stachyose to synthesize verbascose, and these reactions are catalyzed by enzymes raffinose synthase (RS), stachyose synthase (STS), and verbascose synthase (VS), respectively. Galactan:galactan galactosyltransferase (GGT) also synthesizes stachyose and verbascose through another pathway (Gangola et al. 2016).

Various crop plants highly synthesize these RFOs under different stress conditions. For example, Saito and Yoshida (2011) observed enhanced accumulation of raffinose and galactinol in rice plant under cold stress. Similarly, Taji et al. (2002) reported a considerable increment in the gene AtGolS which encodes the enzyme GolS and played an important role in water deficit and cold stress tolerance in *Arabidopsis thaliana*. Further, in transgenic cultivars of Arabidopsis, upregulation of the genes encoding enzymes GolS and RS enhanced the synthesis of galactinol and raffinose, respectively, which resulted in increased tolerance to various oxidative stresses (Bolouri-Moghaddam et al. 2010). In another study, AtGolS2 gene from *Arabidopsis* was introduced in rice plants, and overexpression of this gene in transgenic rice plants improved the water stress tolerance (Selvaraj et al. 2017). Shimosaka and Ozawa (2015) also developed a transgenic rice cultivar by overexpressing wheat TaGolS gene to enhance the chilling stress tolerance.

2.3.4 Sugar Alcohols

Sugar alcohols or polyols are organic compounds that are derived from sugars. They contain multiple alcohol (OH) groups attached to every carbon atom. They are low-molecular-weight, non-reactive compounds that can be further categorized into two classes, cyclic and acyclic based on their structures. Mannitol and sorbitol come under the category of cyclic polyols, whereas myo-inositol, pinitol, and ononitol are examples of acyclic polyols (Bhattacharya and Kundu 2020). They perform various functions like maintaining the osmotic balance of the cell, providing membrane stability, and also acting as molecular chaperones in abiotic stress conditions. Under salt stress polyols also facilitate the Na^+ sequestration in the vacuole or apoplast (Li et al. 2011). Furthermore, they protect the macromolecules by forming a sphere of hydration around it and thus prevent their metabolic inactivation under osmotic stress (Schneider 2015). The accumulation of different polyols has been reported in many crop plants under dehydration, salinity, and osmotic stress (Sengupta et al. 2008).

2.3.4.1 Mannitol

Mannitol is an acyclic polyol that contains six-carbon molecules and is extensively accumulated by several species of plants except for halophytes (Salama et al. 2015). It plays a significant role in basic plant processes including photosynthesis, and plant growth also acts as a storage carbon compound. Besides this, mannitol can reduce

ROS production as they are a great quencher of ROS and thus regulate the redox homeostasis of plant cells under stress conditions (Upadhyay et al. 2015).

In plants, fructose-6-P acts as a precursor for the synthesis of mannitol, which gets converted into mannose-6-P by the action of the enzyme mannose-6-P isomerase (M6PI), followed by the conversion of mannose-6-P into mannitol-6-P by the enzyme mannose-6-phosphate reductase (M6PR) (Loescher et al. 1992). Further, mannitol-6-P gets dephosphorylated into mannitol, and the reaction is catalyzed by mannose-1-phosphate phosphatase (M1PP) (Fig. 2.3). Mannitol pool inside a cell is determined by the catabolic enzyme mannitol dehydrogenase (MTD) which is responsible for the conversion of mannitol into mannose. Hameed and Iqbal (2014) studied that pre-treatment of wheat seeds with mannitol and mannose increased the total soluble content in wheat leaves which resulted in providing osmotic adjustment in response to drought stress. Furthermore, in another study, exogenous application of mannitol under salt stress reduced lipid peroxidation and increased the catalase and ascorbate peroxidase activity which enhanced the detoxification of ROS (Seckin et al. 2009). Ameliorative role of mannitol has also been observed in maize plants suffering from Cr toxicity where it restricted the uptake and translocation of Cr in roots as well as leaves and further enhanced the activity of antioxidative enzymes (Habiba et al. 2019). In some plant species, mannitol cannot be synthesized naturally, so in those plants, mannitol-synthesizing genes are being introduced (Table 2.1). For instance, Bhauso et al. (2014) introduced the bacterial *mtl1D* gene in peanut (non-mannitol accumulator), and the resultant transgenic plants exhibited enhanced accumulation of mannitol which aids the drought tolerance. Similarly, in the case of cereals, transgenic rice and wheat varieties were generated which contained *mtl1D* gene of *E. coli.* The resultant transgenic lines exhibited an accumulation of mannitol which led to improved drought and salinity tolerance (Abebe et al. 2003; Pujni et al. 2007).

2.3.4.2 Inositols

Inositol is a cyclic sugar alcohol, which plays a vital role in plants' cellular functions like nucleic acid exportation, protein and macromolecule distribution, signal transduction, and other cellular metabolic activities. Furthermore, under different abiotic stress conditions, it protects plants by acting as an osmoprotectant (Sengupta et al. 2012). Plants accumulate different isomers of inositol such as myo-inositol, pinitol, galactinol, and ononitol in response to stress conditions. These inositols contain glycosidic linkages which make them stable compounds that cannot be easily hydrolyzed. Among different isomers of inositol, myo-inositol is the most abundant one which plays a diverse role in plants including osmoregulation, prevention of DNA fragmentation, etc. under stress (Valluru and Van den Ende 2011). Under abiotic stress, they can function as ROS scavengers and also as water potential regulators (Valluru and Van den Ende 2011). In plants, biosynthesis of inositols starts with the conversion of glucose-6-P into myo-inositol-1-P by the action of the enzyme myo-inositol-1-P synthase (MIPS) (Fig. 2.3). In the next step, myo-inositol-1-P gets dephosphorylated into myo-inositol which further changes into other inositol derivatives containing different compounds like phospholipids (Dastidar et al. 2006).

To increase the biosynthesis of inositol and its derivatives, some crop plants have been genetically engineered, and the resultant transgenic crops could grow well under harsh environmental circumstances. For instance, Sambe et al. (2015) developed a transgenic tobacco plant with the introduction of *Medicago sativa* myo-inositol transporter-like protein (MfINT-like) in tobacco plants and observed increased tolerance to cold stress. Similarly, Nisa et al. (2016) observed enhanced accumulation of myo-inositol along with salt tolerance in *Arabidopsis* plant when transformed with GsMIPS2 biosynthetic gene of *Glycine soja*. In addition to this, Khurana et al. (2017) transferred TaMIPS2 gene from wheat into *Arabidopsis thaliana* and noticed an increase in heat tolerance.

2.4 Conclusion

Production of organic solutes in response to various abiotic stresses is an effective approach developed by plants. Major organic solutes synthesized by plants include proline, polyamines, glycine betaine, trehalose, fructans, mannitol, etc. These organic solutes are capable of imparting stress tolerance as they are highly soluble and chemically inert and have low molecular weight. The main function of these metabolites is to regulate the cell turgor, stabilize the lipid membrane and cellular components, and scavenge excessively produced ROS. Naturally, some plants can synthesize these organic solutes, but it varies from species to species, i.e., some species are high accumulators, some are low accumulators, and some are non-accumulator for some of the solutes. To increase the synthesis and accumulation of these solutes, transgenic crops have been developed which overexpress the organic solute biosynthetic genes. However, a further detailed study is needed to completely understand the mechanism of these organic solutes and to make more transgenic plants that can thrive under adverse environmental conditions.

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3

Oxidative Stress and Antioxidant Enzymes in Cereals Under Abiotic Stress

Kanika Thakur and Neera Garg

Abstract

Cereals are important crops that serve as a major source of calories in the human diet. Environmental changes cause abiotic stress in plants (including cereals) leading to the production of harmful reactive oxygen species (ROS) in the cellular compartments such as chloroplast, mitochondria, and peroxisome. The free radicals produced degenerate the plant membrane system, enzymes, nucleic acids, carbohydrates, etc. To cope with the damaging oxidative burst, plants have an inbuilt system of antioxidant defense that helps them to maintain an equilibrium between the ROS produced and ROS scavenged. The antioxidants involved are (a) enzymatic like catalase, superoxide dismutase, guaiacol peroxidase, glutathione reductase, ascorbate peroxidase, monodehydroascorbate reductase, and dehydroascorbate reductase, and (b) non-enzymatic antioxidants like ascorbic acid, reduced glutathione, carotenoids, α-tocopherol, and flavonoids. This chapter emphasizes various types of ROS, their production sites in the cell, damaging effects, and the potential role of antioxidants in quenching the ROS to ensure cell survival of cereals.

Keywords

Abiotic stress · Oxidative burst · ROS · Scavenged · Antioxidant

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3.1 Introduction

Abiotic stresses such as heat, drought, cold, soil salinity, oxidative stress, and metal toxicity are the general adverse environmental conditions that affect and restrain productivity of the crop worldwide. Abiotic stress can cause various responses in crops, ranging from readjustments of metabolic processes and transport leading to growth inhibition. In general, abiotic stress affects seedling establishment, seed germination, flower fertility, and vegetative growth because of ionic toxicity, oxidative damage, and limited availability of nutrients.

Oxidative stress is a direct result of abiotic stress that includes enhanced production of reactive oxygen species (ROS) which, in turn, negatively affect multiple biological processes. ROS include superoxide radical (O_2^-), hydroxyl radicals (OH^-), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2) in the plant cells which activate some changes in physiological, biochemical, and molecular mechanisms. Oxidative burst is mainly caused due to two reasons: (a) an imbalance between ROS generation and its scavenging (b) de novo ROS biosynthesis involved in signaling during stress and immunity response needed for defense. The plants contain various sites for ROS production such as mitochondria, peroxisomes, chloroplast, and cytosol, which are extremely regulated and tightly coupled to avoid the release of the oxygen radicals. The plants undergoing oxidative stress produce ROS in excessive amounts but cannot detoxify them. High levels of ROS cause damage to cellular components including degradation of nucleic acids, lipids, and proteins. These reactions ultimately lead to alterations in membrane properties like ion transport, fluidity, protein cross-linking, loss of enzyme activity, etc. leading to the death of plant cells. During evolution, plants have acquired sophisticated mechanisms to neutralize the overproduction of ROS by upregulating antioxidant defense machinery.

Antioxidants are compounds that obstruct the oxidation of other molecules by hindering the initiation of oxidizing chain reactions. One antioxidant molecule can neutralize a single free radical by reacting with it through the donation of one of its electrons ultimately ending the carbon stealing reaction. They are the first line of defense against the damage caused by free radicals. Plants contain enzymatic and non-enzymatic antioxidant defense systems which protect them and help to maintain growth and metabolism. Enzymatic antioxidants include catalase, CAT; superoxide dismutase, SOD; ascorbate peroxidase, APX; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione reductase, GR; glutathione peroxidase, GPX; guaiacol peroxidase, GPX, etc., and non-enzymatic antioxidants such as glutathione, GSH; ascorbic acid, AsA; flavonoids; α-tocopherol; carotenoids, etc. Among these, enzymes like superoxide dismutase, peroxidase, and catalase are protective that deal directly with toxic oxidants, whereas monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase are the enzymes that help to conserve the pool of antioxidants in their reduced state. Oxy products such as O_2^- and H_2O_2 with long shelf life are detoxified by high activities of protective enzymes (Pandhair and Sekhon 2006). A protective antioxidant such as SOD is an important quencher of O_2^-; it catalyzes the dismutation reaction of O_2^- anions into O_2 and H_2O_2. Removal of H_2O_2 produced during dismutation becomes essential to avoid the inhibition of enzymes involved in the Calvin cycle. It can be quenched by catalase and a variety of peroxidases. Catalase decomposes H_2O_2 into water and molecular oxygen, whereas peroxidase causes dismutation of H_2O_2 by oxidation of co-substrates such as antioxidants and/or phenolic compounds. Coordinated activities of these antioxidants (enzymatic and non-enzymatic) regulate ROS detoxification and reduce the oxidative load in plants. Though ROS generation is a common occurrence in plants under any kind of stress, it becomes a major concern when it comes to staple food crops, as cereal grains provide more food energy for human consumption than any other type of crop.

The cereal species that are of agricultural significance include wheat, rye, barley, oats, maize, rice, sorghum, and millets. Abiotic stress plays an important role in cultivated crops because it mainly affects the various growth stages which ultimately result in a loss in yield. Physiological processes such as flowering, grain filling, and maturation are highly affected in cereals undergoing oxidative stress. Nevertheless, there is no doubt that a large fraction of potential crop productivity is lost to abiotic stress outcome, i.e., oxidative stress, at multiple levels that include morphology, anatomy, molecular, and whole plant physiology (Witcombe et al. 2008) which needs a practical analysis and understanding.

Thus, this chapter unfolds the processes involved in the generation of ROS, their toxic effects, and their amelioration through the antioxidant defense machinery in cereal crops.

3.2 Oxidative Stress and ROS Generation in Cereal Crops

The partial reduction or activation of oxygen leads to the generation of ROS (Fig. 3.1). The ROS are atoms or groups of atoms having at least one unpaired electron, which contributes to a highly unstable configuration. Therefore, these radicals readily react with other molecules to form more free radicals, as the pairing of electrons is important to get the stable formation of two-electron bonds (Hideg 2005). The production of active oxygen is an inevitable consequence of the photosynthetic electron transport chain in an oxygen atmosphere as ROS are generated in plant cells during normal metabolic processes (photosynthesis and respiration) as well (Garg and Manchanda 2009; Bhalla and Garg 2021). Under oxidative stress, ROS are produced by different mechanisms and are formed in different cell compartments such as the apoplasm, mitochondria, peroxisomes, chloroplasts, and endoplasmic reticulum (ER) (Ashraf 2009). Major generation sites of ROS are the reaction centers of PSI and PSII in chloroplast thylakoids (Asada 2006) with the potential to generate $^1O_2$ and O_2^- (Arora et al. 2002). At complexes I and III of mitochondria, O_2^- is produced as a by-product, and in peroxisomes, O_2^- and H_2O_2 are produced in several key metabolic reactions (del Río et al. 2006). Therefore basically, ROS are produced in the organelles, with highly oxidizing metabolic activity or the ones with an intense rate of electron flow. High levels of ROS can cause carbohydrate oxidation, lipid peroxidation (malondialdehyde (MDA)

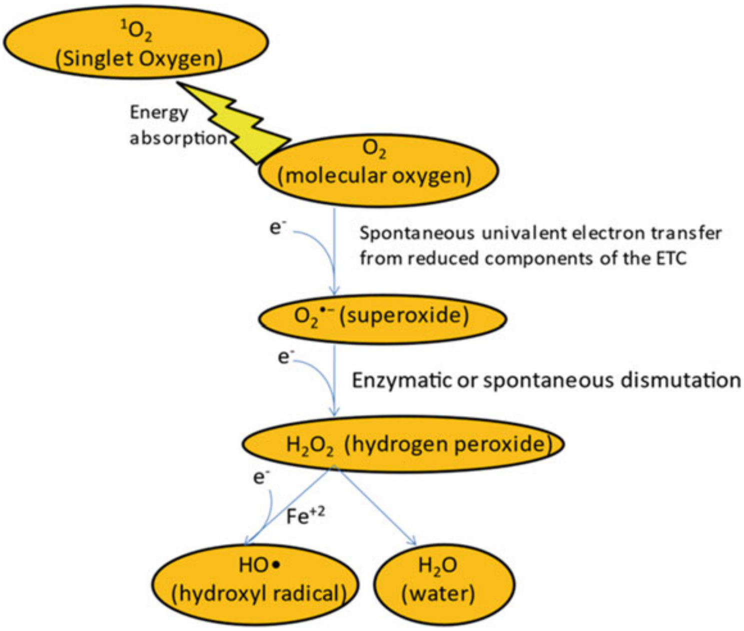

Fig. 3.1 Schematic representation of reactive oxygen species (ROS) generation

formation) in cellular membranes, pigment breakdown, protein denaturation, and DNA damage (Møller et al. 2007). Singh and Roychoudhury (2021) reported that excess fluoride ions in rice seedlings lead to the generation of H_2O_2, causing oxidative stress which ultimately induces the activity of lipoxygenase (LOX), inciting membrane damage, electrolyte leakage, and formation of other cytotoxic metabolites like MDA. Habibi (2012) observed a significant accumulation of MDA and ROS like H_2O_2 in barley plants under drought stress. Furthermore, excessive ROS (H_2O_2 and $HO^\bullet$) accumulation may hurt intracellular ionic homeostasis and induce cytosolic K^+ loss that stimulates protease and endonuclease activity promoting programmed cell death (Demidchik et al. 2010, 2014; Shabala and Pottosin 2014; Hanin et al. 2016) as observed in barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*) under salinity stress by Wang et al. (2018).

3.2.1 Superoxide Radical ($O_2^{\bullet-}$)

Superoxide radical ($O_2^{\bullet-}$) is formed in chloroplast when O_2 is supplied with a single electron and that electron enters one of the π* antibonding orbitals (Halliwell 2006). Under oxidative stress, the $O_2^{\bullet-}$ is produced mainly in the PSI (in thylakoid) during the non-cyclic electron transport chain (ETC). Normally, when cytochrome *c* oxidase interacts with O_2, H_2O is produced but occasionally, O_2 reacts with the different ETC components giving birth to $O_2^{\bullet-}$. It is usually the first ROS to be produced and can also undergo further reactions to form other members of the ROS family (Das and Roychoudhury 2014).

$$O_2^{\bullet -} + Fe^{3+} \rightarrow {}^1O_2 + Fe^{2+}$$

$$2O_2^{\bullet -} + 2H^+ \rightarrow O_2 + H_2O_2Fe^{3+}$$

$$Fe^{2+} + H_2O_2 + Fe^{3+} \rightarrow Fe^{3+} + OH^- + OH^\bullet \text{ (Fenton reaction)}$$

$O_2^{\bullet -}$ can last for nearly 4 μs in water and 100 μs in a polar solvent (Foyer and Harbinson 1994). No extensive damage is caused by $O_2^{\bullet -}$ as it is fairly reactive with a short half-life of 2–4 μs. Instead, it is transformed into more reactive and toxic radicals $OH^\bullet$ and ${}^1O_2$, causing membrane lipid peroxidation (Halliwell 2006). The excitation energy of $O_2^{\bullet -}$ can either be passed to other biological molecules or it can react with them leading to the formation of endoperoxides or hydroperoxides. H_2O_2 that is formed by protonation of $O_2^{\bullet -}$ can cross biological membranes and cause subtraction of hydrogen atoms from lipid hydroperoxides and polyunsaturated fatty acids, thus initiating lipid oxidation (Halliwell and Gutteridge 2015).

3.2.2 Hydrogen Peroxide (H_2O_2)

The production of hydrogen peroxide includes univalent reduction of superoxide occurring both non-enzymatically by being disproportionated into H_2O_2 (at low pH) or by SOD catalyzed reaction.

$$2O_2^{\bullet -} + 2H^+ \rightarrow H_2O_2 + O_2$$

H_2O_2 does not have any free electrons as all of its electrons are paired, which accounts for its moderately reactive nature. Its shelf life is relatively long (half-life of 1 ms) due to which it can diffuse from its generation site. As it is capable to cross biomembranes, it can react with various biomolecules located at different sites. At elevated concentrations, H_2O_2 oxidizes both methionine (–SCH3) and cysteine (–SH) residues, inactivating enzymes of the Calvin cycle, by oxidizing their thiol groups (Halliwell 2006). Most of the H_2O_2 is produced in the electron transport chain of chloroplast, mitochondria, cell membrane, β-oxidation of fatty acid, ER, and photorespiration (Das and Roychoudhury 2014). However, due to its moderate reactivity like $O_2^{\bullet -}$, the damage caused by H_2O_2 is fully realized only when it gets transformed into a more reactive free radical such as highly toxic hydroxyl radicals.

3.2.3 Hydroxyl Radical ($OH^{\bullet}$)

The most reactive and the most damaging form of ROS known is $OH^{\bullet}$ that is produced at neutral pH from a reaction involving H_2O_2 and $O_2^{\bullet-}$. The reaction is catalyzed by transition metals like Fe (Fe^{2+}, Fe^{3+}) (Halliwell and Gutteridge 2015).

$$H_2O_2 + O_2^{\bullet -} \rightarrow OH^- + O_2 + OH^{\bullet}\,(\text{Haber} - \text{Weiss or Fenton reaction})$$

Therefore, in the presence of even small amounts of iron ions, $O_2^{\bullet-}$ and H_2O_2 form damaging $OH^{\bullet}$ that further initiates the oxidation of organic substrates. The half-life of $OH^{\bullet}$ is 1 μs, but it is an extremely damaging ROS, because of its high instability and its ability to react with any cellular component (all biological molecules) present in its vicinity (Vranová et al. 2002). $OH^{\bullet}$ is harmful as it can injure various biomolecules by protein degeneration, lipid peroxidation (LPO), and membrane deterioration. A major problem with $OH^{\bullet}$ is that no enzymatic system is present in plants for scavenging this injurious radical; therefore its overabundance causes severe cellular damage (Pinto et al. 2003) that leads to cell death.

3.2.4 Singlet Oxygen ($^1O_2$)

Singlet oxygen is produced by the reaction of chlorophyll triplet state (^{3}Chl) in the antenna system with O_2. During photosynthesis, insufficient energy dissipation leads to the establishment of a chlorophyll triplet state (^{3}Chl) that transfers its excitation energy onto O_2 (ground-state) to synthesize $^1O_2$ (Holt et al. 2005) which is extremely reactive when compared to O_2.

$$\text{Chl} \rightarrow {}^3\text{Chl}$$

$${}^3\text{Chl} + {}^3O_2 \rightarrow \text{Chl} + {}^1O_2$$

Endoperoxides or hydroperoxides are formed when this excitation energy of $^1O_2$ is transferred to other biological molecules (Halliwell and Gutteridge 2015) causing oxidation of chloroplast molecules triggering cell death (Wagner et al. 2004). $^1O_2$ can last almost 4 and 100 ms in water and a non-polar medium, respectively (Foyer and Harbinson 1994). $^1O_2$ can manage to diffuse some 100 nm and cause damage to a wide range of targets such as pigments, lipids, nucleic acids, and proteins (Wagner et al. 2004; Krieger-Liszkay et al. 2008). Apart from the abovementioned damages, $^1O_2$ is the key ROS involved in the light-induced loss of PSII activity, prompting cell death (Das and Roychoudhury 2014).

3.3 Sites of ROS Production in Plant Cells

The main sites for ROS production in plants include the mitochondria, peroxisomes, and chloroplast. There are secondary sites as well such as the cell membrane, cell wall, endoplasmic reticulum, and the apoplast (Gill and Tuteja 2010).

3.3.1 Chloroplast

In chloroplasts, an extremely organized thylakoid membrane system accommodates all components of the light-capturing photosynthetic machinery and sustains all structural properties for optimal light-harvesting (Pfannschmidt 2003). Under normal conditions, the excited photosystem directs the flow of electron from the centers towards $NADP^+$, which gets reduced to NADPH. It then reduces the final electron acceptor (CO_2), by entering the Calvin cycle. Under oxidative outburst or ETC, overloading $O_2^{\bullet-}$ is generated because a part of the electron flow is diverted from ferredoxin to O_2, reducing it to $O_2^{\bullet-}$ (Elstner 1991).

$$2O_2 + 2Fd_{red} \rightarrow 2O_2^{\bullet-} + 2Fd_{ox}(\text{Mehler reaction})$$

Consequently, at PSI, a membrane-bound SOD converts $O_2^{\bullet-}$ into H_2O_2 (Miller et al. 2010). 2Fe-2S and the 4Fe-4S clusters and Q^A and Q^B electron acceptors of PSI and PSII are the other accomplices of leaking electrons from the ETC, which are the reason for the formation of $O_2^{\bullet-}$. The $O_2^{\bullet-}$ then goes onto transform itself into more deadly ROS like $OH^{\bullet}$ via H_2O_2 as a transitional form, at the Fe-S centers by the Fenton reaction (Das and Roychoudhury 2014). The PSII is also responsible for the production of $^1O_2$ in two ways. Firstly, when there is an imbalance between light-harvesting and energy utilization due to environmental stress, triplet Chl ($^3Chl^*$) is formed, which on reacting with dioxygen ($^3O_2$) releases singlet oxygen ($^1O_2$) (Karuppanapandian et al. 2011). Secondly, over the reduction of ETC induces the light-harvesting complex (LHC) to produce $^1O_2$, at the PSII (Asada 2006). Hence, chloroplasts are the key site of ROS ($O_2^{\bullet-}$, $^1O_2$ and H_2O_2) generation (Fig. 3.2). Therefore, regulating and quenching the ROS in the chloroplast is very essential to ensure the continual survival of plants under oxidative stress.

3.3.2 Mitochondria

ROS are formed in the mitochondria under normal conditions too, but the production of the oxygen radicals is hugely enhanced under abiotic stress conditions (Pastore et al. 2007). In plants, ETC and ATP syntheses are tightly coupled, under normal aerobic conditions; however, various stress factors inhibit and modify its component, which leads to electron carriers over reduction and, hence, ROS formation (Blokhina and Fagerstedt 2010). During stress with the rise in respiratory rate, the ATP synthesis in mitochondria also rises. This is done to make up for the lower rate

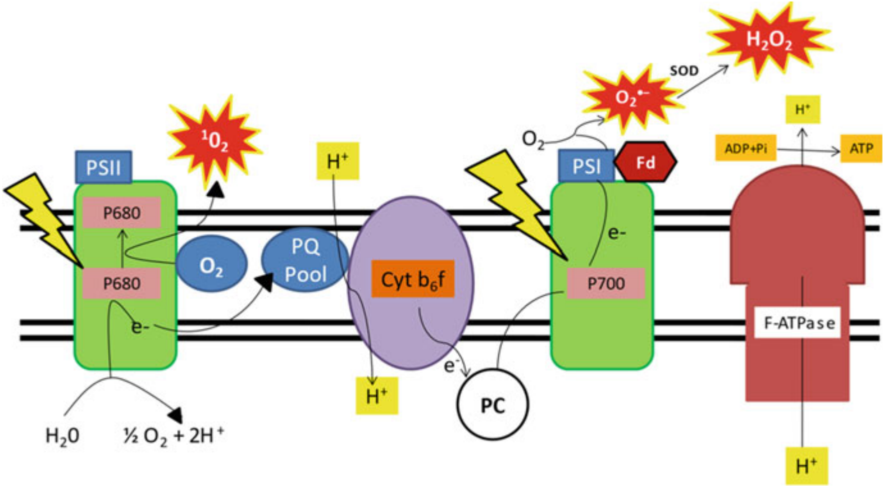

Fig. 3.2 **Reactive oxygen species** (ROS) production chloroplast (Photosystem I and Photosystem II). PQ pool, plastoquinone pool; Cyt b_6f, cytochrome b_6f complex; PC, phycocyanin; PSII, photosystem 2; PSI, photosystem 1; Fd, ferredoxin; SOD, superoxide dismutase; $^1O_2$, singlet oxygen; H_2O_2, hydrogen peroxide; $O_2^{\bullet-}$, superoxide radical

of ATP synthesis in the chloroplast, which ultimately enhances the production of ROS in mitochondria (Atkin and Macherel 2009). Complex I and Complex III (Fig. 3.3) are the two important parts of the mtETC that are responsible for yielding ROS (Møller et al. 2007; Noctor et al. 2007). The Complex I (NADH Dehydrogenase) directly reduces O_2 to $O_2^{\bullet-}$ in its flavoprotein region. The backward flow of electrons, from Complex III to Complex I, due to deficiency of NAD^+-linked substrates, further enhances the ROS production at Complex I, with ATP hydrolysis controlling this reverse flow of electrons (Turren 2003). The fully reduced form of ubiquinone in Complex III transfers an electron to Cytochrome c1 leaving behind ubi semiquinone semi-radical (unstable) which generates $O_2^{\bullet-}$ by favoring leakage of electrons to O_2 (Murphy 2009). Other sources of ROS generation include the enzymes present in the mitochondrial matrix with aconitase being one of them that directly produces ROS. Another enzyme that indirectly forms ROS by supplying electrons to the ETC is 1-Galactono-γ-lactone dehydrogenase (GAL) (Rasmusson et al. 2008). Though the chief ROS in the mitochondria is $O_2^{\bullet-}$, it is transformed by SOD and APX into H_2O_2.

3.3.3 Peroxisomes

Peroxisomes are ubiquitous organelles, chiefly having an oxidative type of metabolism, and are the important sites of ROS production, especially H_2O_2. During stressful conditions, under low water availability and closed stomata, there is a considerable reduction in CO_2 to O_2, which causes an increase in photorespiration

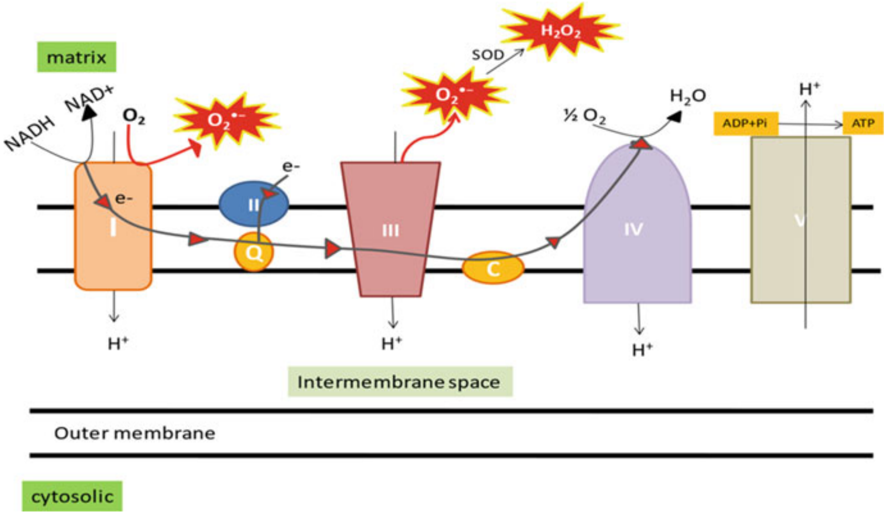

Fig. 3.3 Production of reactive oxygen species (ROS) in the mitochondria (Complex I and Complex III). NADH, mitochondrial complexes 1, II, III, IV, and V; nicotinamide adenine dinucleotide hydrogen; NAD$^+$, nicotinamide adenine dinucleotide; Q, coenzyme Q; C, cytochrome C; H_2O, water; $^1O_2$, singlet oxygen; H_2O_2, hydrogen peroxide; $O_2^{\bullet-}$, superoxide radical; SOD, superoxide dismutase; ADP, adenosine diphosphate; Pi, primary phosphate; ATP, adenosine triphosphate

leading to glycolate formation. Further, this newly formed glycolate is oxidized to release H_2O_2 with the help of glycolate oxidase in the peroxisome, making it a primary manufacturer of H_2O_2 during photorespiration (Noctor et al. 2002). There are two locations of $O_2^{\bullet-}$generation rooted in peroxisomes. The first one is in the organelle matrix, where oxidation of xanthine and hypoxanthine to uric acid is catalyzed by xanthine oxidase (XOD) and $O_2^{\bullet-}$ is generated as a by-product (Fig. 3.4) (Corpas et al. 2001). The second one is localized in the peroxisomal membrane which is a NADPH-dependent small ETC, composed of NADH and Cyt b that utilizes O_2 as the electron acceptor and releases $O_2^{\bullet-}$ into the cytosol (del Río et al. 2002). Other secondary metabolic activities such as the flavin oxidase pathway, β-oxidation of fatty acids, and the dismutation of $O_2^{\bullet-}$radicals also play a part in ROS production inside peroxisomes.

Apart from these three main sources (chloroplast, mitochondria, and peroxisome), there are other cell organelles where ROS are produced.

3.3.4 Other Sources of ROS Generation in Plants

ROS are also generated in the apoplast of plants by germin-like oxalate oxidases and amine oxidases that are pH-dependent cell wall peroxidases (Bolwell and Woftastek 1997). They are stimulated by alkaline pH, which, in the presence of a reductant,

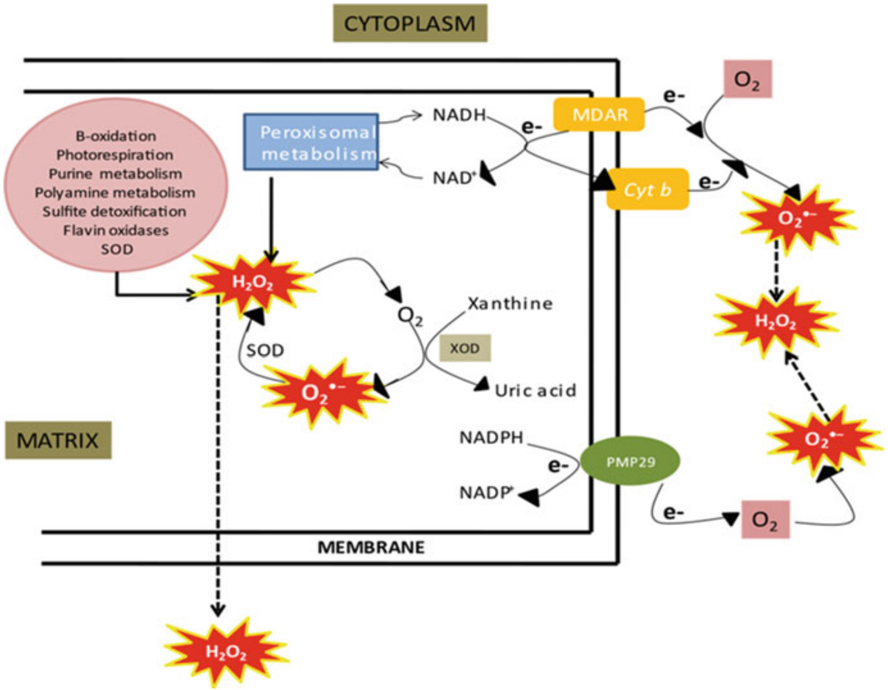

Fig. 3.4 Production of reactive oxygen species (ROS) in peroxisome. NADH**,** nicotinamide adenine dinucleotide hydrogen; NAD^+, nicotinamide adenine dinucleotide; e^-, electron; MDHAR, monodehydroascorbate reductase; Cyt b, cytochrome b; $^1O_2$, singlet oxygen; H_2O_2, hydrogen peroxide; $O_2^{\bullet -}$, superoxide radical; SOD, superoxide dismutase; XOD, xanthine oxidase; NADPH, reduced nicotinamide adenine dinucleotide phosphate; $NADP^+$, oxidized nicotinamide adenine dinucleotide phosphate; PMP29, peroxisomal membrane protein

produces H_2O_2. Diamines or polyamines are utilized by diamine oxidases to generate ROS in the cell wall. $O_2^{\bullet -}$ is produced in the plasma membrane through NADPH oxidase by shifting electrons from NADPH (cytosolic) to O_2, which spontaneously disproportionates to H_2O_2. The cell wall-localized lipoxygenase (LOX) drives the hydroperoxidation of polyunsaturated fatty acids (PUFA) under stress, making it an active source of ROS like $O_2^{\bullet -}$, $^1O_2$, H_2O_2, and $OH^{\bullet}$. On the other hand, NADPH-facilitated electron transport that involves $CytP_{450}$ generates $O_2^{\bullet -}$ in the endoplasmic reticulum (ER) (Mittler 2002). Interaction of organic substrate (RH with the $CytP_{450}$) is followed by reduction with the help of a flavoprotein, to induce a transitional form of free radical intermediate (Cyt P450 R−). This transitional form rapidly reacts with triplet oxygen ($^3O_2$) to give rise to an oxygenated complex (Cyt P450-ROO−). This complex may sometimes disintegrate to Cyt P_{450}-Rh by releasing $O_2^{\bullet -}$ as a by-product (Das and Chaudhary 2014).

3.4 Effects of ROS

Stress factors induce increased production of ROS in cells. ROS that escapes antioxidant facilitated detoxification reacts with cellular molecules such as lipids, proteins, and DNA causing permanent destruction to their structure. These ROS start oxidations of the biomolecules and ultimately deactivate all the cellular functions. The products formed during lipid and protein oxidation are considered important biomarkers in plants undergoing oxidative stress.

3.4.1 Lipid Peroxidation (LPO)

A major portion of the plasma membrane is formed by lipids that include fats, waxes, steroids, phospholipids, hydrocarbons, and free higher fatty acids. Membrane lipids are principally characterized by phospholipids (the more abundant) and sterols (particularly stigmasterol), which are amphipathic, and quickly form bilayers in an aqueous medium (González-López et al. 2011). Above a threshold level, ROS cause a boost in lipid peroxidation in membranes of the cell as well as that of the organelle. Lipid peroxidation produces lipid-derived radicals that react with themselves which aggravates the oxidative stress causing damage to proteins and DNA. One of the final products of unsaturated fatty peroxidation is MDA which is responsible for cell membrane injury (Halliwell and Gutteridge 2015). ROS attacks the phospholipid molecules on two common sites: (1) the unsaturated (double) bond between two carbon atoms and (2) the ester linkage between glycerol and the fatty acid. The polyunsaturated fatty acids (PUFAs) present in membrane phospholipids are particularly sensitive to attack by ROS. Peroxidation of a large number of polyunsaturated fatty acids can be caused just by a single $^{\bullet}OH$ because the reactions involved in this process are part of a cyclic chain reaction. Three different stages are involved in lipid peroxidation, that are initiation, progression, and termination. The initial phase is the rate-limiting step of lipid peroxidation which comprises O_2 activation. Conjugated dienes, lipid peroxy radicals, and hydroperoxides are formed when $O_2^{\bullet-}$ and $^{\bullet}OH$ react with methylene groups of PUFA (Zhao et al. 2001).

$$\mathrm{PUFA}-\mathrm{H}+\mathrm{X}^{\bullet-}\rightarrow\mathrm{PUFA}+\mathrm{X}-\mathrm{H}$$

$$\mathrm{PUFA}+\mathrm{O_2}^{-}\rightarrow\mathrm{PUFA}-\mathrm{OO}^{\bullet}$$

The peroxy radical formed is highly reactive and able to propagate the chain reaction:

$$\mathrm{PUFA}-\mathrm{OO}^{\bullet}+\mathrm{PUFA}-\mathrm{OOH}^{-}\rightarrow\mathrm{PUFA}-\mathrm{OOH}+\mathrm{PUFA}^{\bullet}$$

When these toxic radicals attack the hydrogens of methylene groups, the conjugated diene is formed. This reaction includes the separation of the double bonds and their rearrangement (Recknagal and Glende 1984). According to the following reaction, lipid hydroperoxides that are formed (PUFA-OOH) can suffer reductive cleavage by reduced metals, like Fe^{2+}.

$$\mathrm{Fe}^{2+}\mathrm{complex} + \mathrm{PUFA} - \mathrm{OOH}^{-} \rightarrow \mathrm{Fe}^{3+}\mathrm{complex} + \mathrm{PUFA} - \mathrm{O}^{\bullet}$$

The decomposition of lipid hydroperoxide can lead to the production of several reactive species, namely, aldehydes (malondialdehyde, acrolein and crotonaldehyde), lipid epoxides alkanes, lipid alkoxyl radicals, and alcohols (Davies 2000). Among the abovementioned reactive species, the lipid alkoxy radical ($PUFA\text{-}O^{\bullet}$) can stimulate additional chain reactions:

$$\mathrm{PUFA} - \mathrm{O}^{\bullet} + \mathrm{PUFA} - \mathrm{H}^{-} \rightarrow \mathrm{PUFA} - \mathrm{OH} + \mathrm{PUFA}^{\bullet}$$

The negative impacts of polyunsaturated fatty acid peroxidation include chain breakage which leads to enhanced membrane permeability and fluidity. Rizvi and Khan (2018) observed an elevation in MDA amount in the leaves of maize, grown in soils treated with different concentrations of copper (Cu) and lead (Pb). Aluminum (Al) toxicity could lead to the formation of ROS and cause lipid peroxidation in barley (Sakihama and Yamasaki 2002), wheat (Darko et al. 2004), *Oryza sativa* (Kuo and Kao 2003; Meriga et al. 2004), and maize (Boscolo et al. 2003) Experiment performed by Anjum and co-workers (2017) also revealed that chromium-stressed maize plants were found to have more electrolyte leakage, MDA and H_2O_2 content than the controlled ones. Upadhyay et al. (2020) found that under drought stress, MDA content was enhanced in *Triticum aestivum* plants. Furthermore, MDA and H_2O_2 contents were found to be 2.5 and 2 times higher in barley-sensitive varieties than the tolerant ones under salinity stress (Vasilakoglou et al. 2021).

3.4.2 Oxidative Damage to DNA

The main target of ROS is DNA of plants, which is damaged and degraded during oxidative stress. Since the histones are associated with plant nuclear DNA, they ensure its protection, but mainly DNA of mitochondria and chloroplast undergo the damage of the ROS attack. This is the due fact that mtDNA and ChlDNA lack protective histones as well as have proximity to ROS production machinery. Damage to DNA due to ROS includes nucleotide base modification, deoxyribose sugar residue oxidation, abstraction of a nucleotide, breaks in either DNA strand, and cross-linking of the DNA and proteins. ROS cause the oxidation of both, deoxyribose, and DNA base units. For instance, deoxyribose backbone as well pyrimidine and purine bases can react with hydroxyl radicals. Several mutagenic aberrations such as the liberation of hydrogen from deoxyribose, leading to sugar damage, can be caused through oxidative attacks on DNA. However, when hydrogen atoms are removed from deoxyribose, at C-4 position by ROS, additional radicals are produced that cause single-strand breaks in DNA (Evans and Cooke 2004). Moreover, bases are damaged by OH radicals which results in the formation of the most common product, i.e., 8-hydroxyquinoline, and less common ones such as urea, thymine glycol, dehydro-2-deoxyguanosine, hydroxyl methyl, and thymine and ring-opened adenine. When $OH^\bullet$ reacts with either DNA or associated proteins, it also creates DNA-protein cross-links. DNA-protein cross-links are less abundant as compared to the single-strand breaks and are not readily fixed. If replication or transcription process occurs prior to the fixation, it may be lethal for the plant.

3.4.3 Protein Oxidation

The ROS leads to modification of proteins directly and indirectly. In the direct modification, the protein's activity is modulated through carbonylation, nitrosylation, glutathionylation, and disulfide bond formation, whereas in indirect modification, the protein activity is altered by the products of fatty acid peroxidation through ROS damage (Yamauchi et al. 2008). Due to the profuse amount of ROS formation, site-specific amino acid modification, fragmentation of the peptide chain, accumulation of cross-linked reaction products, and modified electric charge the susceptibility of protein increases towards proteolysis. Oxidation of lysine (Lys), threonine (Thr), proline (Pro), and Arg (arginine) residues by ROS forms carbonyl groups in the side chains of these amino acids (Droge 2002) which hinders or alters their activities and makes them vulnerable to proteolytic attack (Dukan et al. 2000; Dunlop et al. 2002). Carbonylated proteins are generally present at high concentrations inside the tissues injured by oxidative stress, which is mainly used as a marker of protein oxidation (Møller and Kristensen 2004). In a peptide, the amino acids vary in their susceptibility to attack by ROS. Amino acids containing thiol and sulfur group are more sensitive to ROS attack. The H atom from cysteine residues can be abstracted by activated oxygen to form a thiyl radical that can form a disulfide bridge by cross-linking to the second thiyl radical. Furthermore, oxidation by $O_2^{\bullet-}$ can cause irreversible inactivation of the enzymes containing iron-sulfur centers (Choudhary et al. 2020). In these cases, the metal (Fe) binds to a divalent cation-binding site on the protein and forms $^\bullet OH$ through the Fenton reaction. $^\bullet OH$ quickly oxidizes an amino acid residue at or near the cation-binding site of the protein. Oxidized proteins act as better substrates for proteolytic digestion. It has been proposed that protein oxidation could make them prone to ubiquitination, which would further be a target for proteasomal degradation (Cabiscol Català et al. 2000). Bartoli et al. (2004) observed high levels of oxidatively damaged proteins in mitochondria under water-stressed *Triticum aestivum* L.

3.5 Antioxidant Defense

The balance between generation and eradication of ROS must be tightly controlled and/or efficiently metabolized to avoid possible damage caused by ROS to cellular machinery, as well as to overall productivity. This equilibrium between the

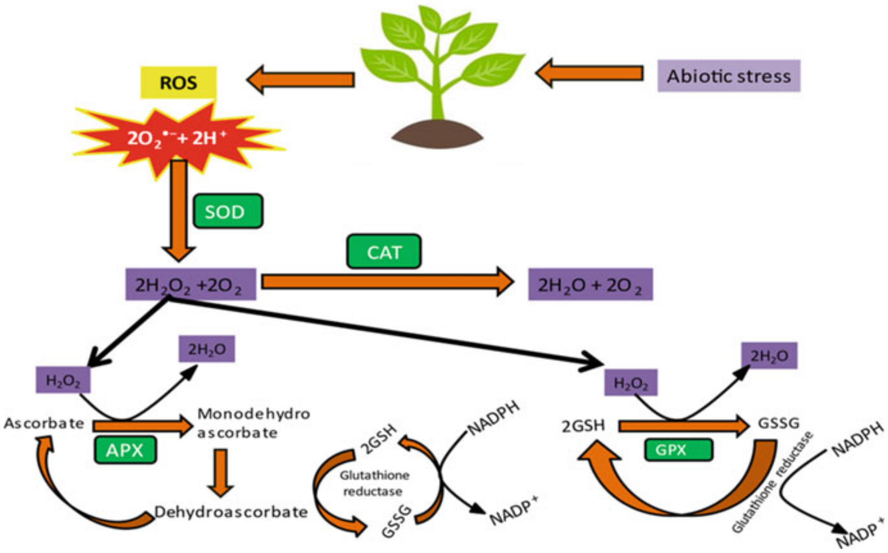

Fig. 3.5 General enzymatic detoxification of reactive oxygen species (ROS). ROS, reactive oxygen species; $O_2^{\bullet-}$, superoxide radical; SOD, superoxide dismutase; H_2O, water; H_2O_2, hydrogen peroxide; APX, ascorbate peroxidase; MDHAR, monodehydroascorbate reductase; GSH, glutathione reduced; GSSG, glutathione oxidized; NADPH, reduced nicotinamide adenine dinucleotide phosphate; $NADP^+$, oxidized nicotinamide adenine dinucleotide phosphate; DHAR, dehydroascorbate reductase; GR, glutathione reductase; GPX, guaiacol peroxidase

production and detoxification of ROS is sustained by enzymatic and nonenzymatic antioxidants (Mittler 2002) (Fig. 3.5).

3.5.1 Enzymatic Antioxidants

3.5.1.1 Superoxide Dismutase (SOD)

The first line of defense against ROS is SOD-catalyzed dismutation and is 10,000 times quicker than spontaneous reactions. The role of SOD in oxidative stress is of great importance as it catalyzes the rapid disproportionation of $O_2^{\bullet-}$ and thus reduces the risk of $^{\bullet}OH$ formation via metal-catalyzed reactions. The SODs remove two molecules of $O_2^{\bullet-}$; one molecule of $O_2^{\bullet-}$ is reduced to H_2O_2 and another is oxidized to O_2.

$$2O_2^{\bullet-} + 2H^+ \rightarrow H_2O_2 + O_2$$

Depending on the metal cofactor existing within the active center, three types of SOD metalloenzymes are present in plants. Cu/Zn-SOD is the foremost abundant isoenzyme found in chloroplast stroma, cytosol, apoplast, and peroxisomes. Another being Mn-SOD, which is located in peroxisomes and mitochondria, but is also present in both cell wall and apoplast, while Fe-SOD is found in less amount in the chloroplast (Caverzan et al. 2016). Plants that are exposed to various abiotic stresses have reported an increase in SOD activity, and elevated activity of SOD is often associated with increased tolerance of the plant against oxidative stress. (Zaefyzadeh et al. 2009). The rise in the production of SOD has been stated in various plants including cereals. The activity of SOD was enhanced under Cd treatment in *Hordeum vulgare* (Guo et al. 2004), *Triticum aestivum* (Khan et al. 2007), and *O. sativa* (Hsu and Kao 2004). Under drought stress increase in SOD activity was noted in *O. sativa* (Sharma and Dubey 2005). Simonovicova et al. (2004) stated that SOD activity increased in *H. vulgare* root tips under Al stress. Mn-SOD overexpression in protoplasts indicated slightly lower oxidative damage and high SOD activity under photooxidative stress (Melchiorre et al. 2009). Furthermore, SOD activity in the embryos of wheat and barley grains was characterized by higher values under UV radiations in an experiment conducted by Kurdziel and co-workers (2018). Zeeshan et al. (2020) compared wheat (salt-tolerant cv. Suntop and -sensitive Sunmate) and barley (salt-tolerant cv. CM72) cultivars and found that SOD had higher activity in salt-tolerant cultivars which helped in mitigating salt-induced oxidative stress. Gholamin and Khayatnezhad (2020) in their study found that drought stress leads to an increase in SOD activity in bread wheat genotype. In tolerant wheat genotypes, the activity of SOD was found to be enhanced under water deficit conditions (Nasirzadeh et al. 2021).

3.5.1.2 Catalase (CAT)

The first enzyme among antioxidants that was discovered and characterized was catalase. It catalyzes the disproportionation of H_2O_2 (two molecules) into water and oxygen (Sharma et al. 2012a).

$$2H_2O_2 \rightarrow 2H_2O + O_2$$

The affinity of catalase for H_2O_2 is high with a turnover rate of 6×10^6 molecules of H_2O_2 to H_2O and $O_2 \text{min}^{-1}$. It is unique among antioxidant enzymes as it does not require any reducing equivalent. Peroxisomes are considered hotspots of H_2O_2 generation due to the processes taking place inside them, such as β-oxidation of fatty acids, purine catabolism, and photorespiration (Mittler 2002). However, it is also reported that CAT is also present in other subcellular compartments like the cytosol (Mhamdi et al. 2010). Three CAT genes have been reported in angiosperms, namely, CAT1, CAT2 and CAT3; CAT1 is expressed in pollen and seeds, expression of CAT2 is mainly in photosynthetic tissues but also roots and seeds, and CAT3 expression is found to be in leaves and vascular tissues. CAT1 and CAT2 are localized in peroxisome and cytosol, while CAT3 is present in mitochondria (Das and Choudhary 2014). A detailed study of CAT isozymes has been done in plants like two in *H. vulgare* (Azevedo et al. 1998). CAT activity has been variably expressed under Cd stress, whereas its activity is enhanced in *O. sativa* (Hsu and Kao 2004) and *T. aestivum* (Khan et al. 2007). Simova-Stoilova et al. (2010) found that the activity of CAT was high in wheat undergoing drought stress, but it was comparatively higher in sensitive varieties. Experiments carried out by Sharma and Dubey (2005) also stated a decline in CAT activity in rice seedlings under drought stress. Under water stress, catalase activity was significantly increased in leaf extracts of barley plants (Hafez and Seleiman 2017). Increased CAT activity was shown in response to various stresses such as heat, drought, salt, etc. in different plants, such as *O. sativa* (Leung 2018). Rohman et al. (2020) found that the activity of CAT was enhanced with the decrease in soil moisture in *H. vulgare*. In response to flooding stress, the activity of catalase was increased in wheat crop (Malik et al. 2022).

3.5.1.3 Enzymes of Ascorbate-Glutathione Cycle

The AsA-GSH cycle also known as the Halliwell-Asada pathway recycles AsA and regenerates GSH also detoxifying H_2O_2 in the meantime. The change in the ratio of AsA (ascorbic acid) to DHA (dehydroascorbate) and GSH (glutathione reduced) to GSSG (glutathione oxidized) is important for the cell to sense and respond to oxidative stress accordingly. The AsA-GSH cycle includes continuous oxidation and reduction of AsA, GSH, and NADPH that are catalyzed by the enzymes such as APX, MDHAR, DHAR, and GR (Fig. 3.6). The AsA-GSH cycle occurs in four locations including the mitochondria, cytosol, peroxisomes, and chloroplast.

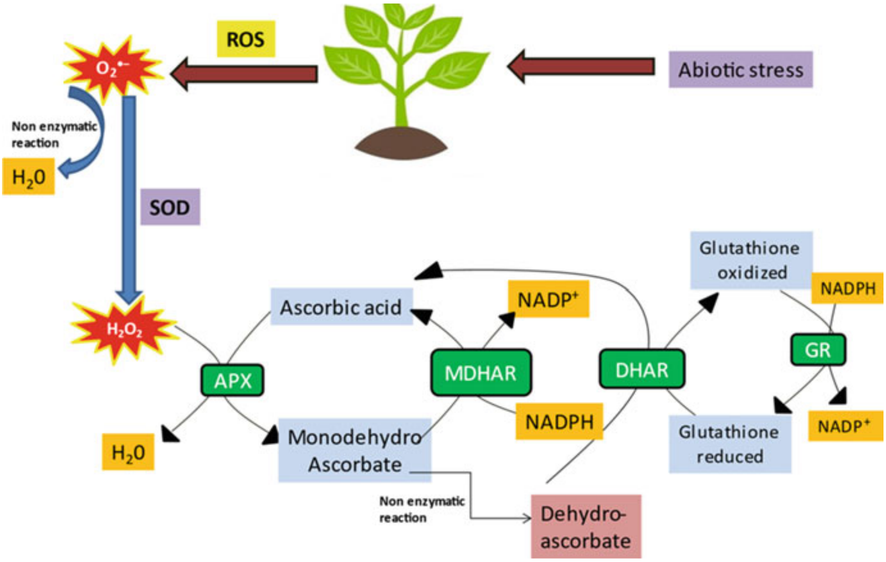

Fig. 3.6 Enzymes (APX, MDHAR, DHAR, GR) involved in detoxification of ROS in Halliwell-Asada pathway. ROS, reactive oxygen species; $O_2^{\bullet-}$, superoxide radical; SOD, superoxide dismutase; H_2O, water; H_2O_2, hydrogen peroxide; APX, ascorbate peroxidase; MDHAR, monodehydroascorbate reductase; NADPH, reduced nicotinamide adenine dinucleotide phosphate; $NADP^+$, oxidized nicotinamide adenine dinucleotide phosphate; DHAR, dehydroascorbate reductase; GR, glutathione reductase

AsA-GSH cycle has a key role in eliminating oxidative stress which is a result of abiotic stress.

3.5.1.3.1 Ascorbate Peroxidase (APX)

APX is an essential constituent of the ascorbate glutathione (ASA-GSH) cycle. While H_2O_2 is mostly quenched by CAT in peroxisomes, APX carries out the scavenging in the chloroplast and cytosol. H_2O_2 is reduced to H_2O and DHA by APX, with ascorbic acid (AsA) acting as a reducing agent.

$$H_2O_2 + AsA \rightarrow 2H_2O + DHA$$

APX is one of the most extensively distributed antioxidants, and its isoforms have more affinity for H_2O_2 than CAT. This makes APXs more effective scavengers of H_2O_2 under oxidative stress. Five chemically and enzymatically different isoenzymes of APX have been discovered based on amino acid sequences, localizing at thylakoidal, stromal, cytosolic, mitochondrial, and peroxisomal sites (Madhusudhan et al. 2003; Sharma and Dubey 2004). H_2O_2 generated in the organelles is quenched by APX present in organelles, while H_2O_2 generated in the apoplast, cytosol, or that diffused from organelles is scavenged by APX present in the cytosol. The cytosolic isoenzymes of APX are less sensitive to depletion of AsA than the chloroplastic isoenzymes (stromal and thylakoid bound enzymes). The expression of APX in plants is enhanced and has been demonstrated in various crops during different stress conditions. Increased activity of APX in leaf under Cd stress was observed in *T. aestivum* (Khan et al. 2007). Hsu and Kao (2007) stated that pretreatment of *O. sativa* seedlings with H_2O_2 resulted in enhanced APX activity and guarded rice seedlings against Cd stress. An increase in APX activity was also reported in *H. vulgare* root tips undergoing Al stress (Simonovicova et al. 2004). In an experiment roots of etiolated *O. sativa* seedlings were analyzed to understand the expression patterns of APX under NaCl stress, and the mRNA levels for four chloroplastic (OsAPX5, OsAPX6, OsAPX7, and OsAPX8), two cytosolic (OsAPX1 and OsAPX2), and two peroxisomal (OsAPX3 and OsAPX4) were quantified. It was observed that 150 and 200 mM NaCl enhanced the expression of OsAPX8 and APX activities, but no effect was detected on the expression of OsAPX1, OsAPX2, OsAPX3, OsAPX4, OsAPX5, OsAPX6, and OsAPX7 in rice roots (Hong et al. 2007). Rahman et al. (2017) reported that in salt-stressed *O. sativa*, the activity of APX was high against overproduced ROS. When two cultivars of *Z. mays* LM-11 (heat-sensitive) and CML-32 (heat-tolerant) were subjected to heat stress, it led to higher APX activity in roots of CML-32 (Khanna et al. 2016). Shan et al. (2018) in their study found out that *T. aestivum* showed higher participation of AsA with higher APX activity in drought conditions for scavenging extra H_2O_2, as well as higher enzymatic activity to run the AsA-GSH pathway systematically. When *Z. mays* seedlings were subjected to waterlogged conditions for 21 h at their root portions, it caused a reduction in AsA content and enhanced the APX activity (Jaiswal and Srivastava 2018). Lower oxidative damage due to higher APX, SOD, and GR activities was observed in tolerant wheat genotype under salt stress (Ouertani et al. 2022).

3.5.1.3.2 Monodehydroascorbate Reductase (MDHAR)

MDHAR is a flavin adenine dinucleotide (FAD) enzyme that is responsible for reviving AsA from MDHA that has a short shelf life. It uses NADPH as a reducing agent and eventually replenishes the cellular AsA pool. As it restores AsA, it is co-localized with the peroxisomal and mitochondrial APX, where it quenches H_2O_2 and causes oxidation of AsA (Mittler 2002).

$$\mathrm{MDHA} + \mathrm{NADPH} \rightarrow \mathrm{AsA} + \mathrm{NADP}^+$$

MDHAR is the only known enzyme that uses an organic radical (MDA) as a substrate. Phenoxyl radicals that are produced by horseradish peroxidase with H_2O_2 are also reduced by MDHAR (Sakihama et al. 2000). Its activity is extensively spread in plants, and isoenzymes of MDHAR have been stated to be expressed in several cellular compartments such as mitochondria and peroxisomes, cytosol, and chloroplasts. In chloroplasts, MDHAR has two functions: the renewal of AsA from MDHA and the facilitation of the photoreduction of dioxygen to $O_2^{\bullet -}$ when the substrate MDHA is not present. Asada (1999) observed the multi-step reduction of FAD thoroughly and minutely. The first step includes the reduction of the enzyme-FAD which leads to the formation of a charge-transfer complex. As the enzyme is reduced, it continuously donates electrons to MDHA, forming two molecules of ascorbate through semiquinone form [E-FAD-NADP(P)$^+$]. The dismutation by photo-reduced ferredoxin (redFd) in the thylakoids is of high value because MDHA can be reduced more efficiently by redFd than NADP$^+$. MDHAR only functions in the presence of NAD(P)H, whereas redFd does not have any such requirement. Several studies have been documented that state the increase of MDHAR in cereals such as rice, which is subjected to abiotic stresses (Maheshwari and Dubey 2009). Sharma and Dubey (2005) stated that in drought-stressed rice seedlings, the activities of MDHAR, DHAR, and GR were higher. Moreover, salt stress affected MDHAR, DHAR, and GR activities in rice seedlings (Mostofa et al. 2015; Rahman et al. 2016). Lou et al. (2018) reported that in flag leaves and spikes of *Triticum aestivum*, the activity of MDHAR was high under drought stress. Lins and Yusuf (2020) observed that the MDHAR activity in rice varieties was enhanced with an increase in NaCl concentrations and exposure time. AbdElgawad et al. (2020) stated that few heavy metals cause an increment in the activity of MDHAR in maize plants.

3.5.1.3.3 Dehydroascorbate Reductase (DHAR)

The reduction of dehydroascorbate (DHA) to AsAby utilizing glutathione (GSH) as an electron donor is carried out by DHAR (Eltayeb et al. 2007). Thus, besides MDHAR, DHAR becomes another agent, which replenishes the AsA pool. Maintenance of the redox state of the plant cell is done by regulating the pool size of AsA in both symplast and apoplast (Chen and Gallie 2006).

$$\text{DHA} + 2\text{GSH} \rightarrow \text{AsA} + \text{GSSG}$$

DHAR, a monomeric thiol enzyme, is profusely present in roots, seeds, and both green and etiolated shoots. The purification of DHAR has been carried out from chloroplast sources (spinach leaves, Hossain and Asada 1984) as well as non-chloroplast sources (potato tuber, Dipierro and Borraccino 1991). Though AsA is straightaway regenerated from MDHA, a certain amount of DHA is always formed, when oxidation of AsAtakes place in leaves and other tissues. DHA has a very short shelf life; therefore, it can either be permanently hydrolyzed into 2,3-diketogulonic acid or can be recycled to AsA by DHAR. The increase in AsA content due to overexpression of DHAR in maize, potato, and tobacco leaves was reported, which suggested that DHAR plays a crucial role in determining the AsA pool size (Chen et al. 2003; Qin et al. 2011). The activities of DHAR, MDHAR, APX, and GR were enhanced in seedling roots of Al-sensitive and A1-tolerant wheat (*Triticum aestivum*) varieties under Al stress (Sun et al. 2015). An increase in DHAR activity was also reported in *Triticum aestivum* under drought stress by Lou et al. (2018).

3.5.1.4 Glutathione Reductase (GR)

GR, a flavoprotein oxidoreductase, utilizes NADPH as a reductant for the reduction of GSSG to GSH. Regeneration of AsA from MDHA and DHA requires reduced glutathione (GSH), and as a result, it gets transformed into its oxidized form, i.e., GSSG. It is a low-molecular-weight compound and is a crucial enzyme of ASA-GSH cycle. GSH maintains an elevated cellular GSH/GSSG ratio by catalyzing the formation of a disulfide bond in glutathione disulfide. It is mainly present in chloroplasts with small amounts found in the mitochondria and cytosol as well. The role of a reductant is played by GSH, to stop the thiol groups from oxidation and their reaction with ROS members like $^1O_2$ and $OH^\bullet$ (Das and Roychoudhury 2014).

$$\text{GSSG} + \text{NADPH} \rightarrow 2\text{GSH} + \text{NADP}^+$$

Two GSH are connected by a disulfide bridge to form GSSG, which can be transformed back to GSH by GR. The catalytic mechanism involves two steps: first, NADPH reduces the flavin moiety, the flavin is oxidized, and a redox active disulfide bridge is reduced to produce a thiolate anion and a cysteine. Second, the reduction of GSSG via thiol-disulfide interchanges reactions. The reduced enzyme can undergo a reversible inactivation if it is not reoxidized by GSSG. Isoforms of GR are present in different cellular compartments, and 80% of its activity in photosynthetic tissues is accounted by chloroplastic isoforms. Two chloroplastic isoforms (*OsGR1* and *OsGR3*) and one GR cytosolic isoform *(OsGR2)* have been identified in rice (Rouhier et al. 2006; Bashir et al. 2007). GR is involved in protecting against oxidative burst as H_2O_2 that is generated in the chloroplast is detoxified by GSH and GR. GSH has a crucial role to play in the cell system, by participating in the ASH-GSH cycle, maintaining the sulfhydryl (–SH) group and a substrate for GSTs (glutathione-*S*-transferases) (Rao et al. 2006). GR and GSH provide tolerance to plants in different stresses (Rao and Reddy 2008). The activity of GR was enhanced under Cd stress in *T. aestivum* (Khan et al. 2007). Sharma and Dubey (2005) noted a significant increase in GR activity in drought-stressed *O. sativa* seedlings. Wu et al. (2013) suggested that salt increased the activity of GR and expression of *OsGR3* in rice plants. A higher GR activity was observed in in root and shoot of *Avena sativa* when exposed to cold conditions showing a better tolerance mechanism (Goyal and Kaur 2018). In maize seedlings, there was a spike in the activity of GR under drought stress as observed by Al-Huqail (2019). The activity of GR was greatly enhanced in *Triticum aestivum* when it was exposed to drought, heat, salt, and arsenic stress (Kaur et al. 2021).

3.5.1.5 Guaiacol Peroxidase (GPX)

GPX is a heme-containing enzyme composed of 40–50 kDa monomers. It removes surplus H_2O_2 during stress by oxidizing aromatic electron donors such as pyrogallol and guaiacol at the cost of H_2O_2.

$$H_2O_2 + GSH \rightarrow H_2O + GSSG$$

GPX is related to many essential biosynthetic processes, including degradation of AsA, biosynthesis of ethylene, wound healing, lignification of cell wall, and defense against abiotic stress (Kobayashi et al. 1996). It is regarded as a crucial enzyme in the disposal of H_2O_2 since it functions intracellularly (cytosol, vacuole) as well as extracellularly (cell wall). GPX can act as an efficient scavenger of intermediary forms of O_2 and peroxy radicals that are formed under stressed conditions. The abiotic stress conditions have stimulated the activity of GPX in rice and maize plants (Verma and Dubey 2003; Moussa and Abdel-Aziz 2008). Radotić et al. (2000) associated the enhanced GPX activity with oxidative response in plants undergoing metal stress and recommended its potential as a biomarker for metal toxicity. The activity of GPX elevated in Cd-stressed plants of *T. aestivum* (Milone et al. 2003). A collateral rise in the activity of GPX under salinity stress was observed in both the root and leaf of *O. sativa* (Yamane et al. 2009). Furthermore, Awaly et al. (2020) observed that the GPX activity increased when wheat varieties were subjected to increasing NaCl concentrations.

3.5.2 Non-enzymatic Antioxidants

3.5.2.1 Ascorbic Acid (AsA)

AsA is the most abundant and is considered a powerful antioxidant as it can provide electrons to a broad spectrum of enzymatic and non-enzymatic reactions. The bulk of AsA in plant cells is produced in mitochondria due to the Smirnoff-Wheeler pathway. This process is catalyzed by L-galactano-γ-lactone dehydrogenase, and the AsA produced is moved to the other cell parts via proton-electrochemical gradient or facilitated diffusion. AsA is also produced through uronic acid intermediates, for example, D-galacturonic acid. During this pathway, galacturonic acid reductase reduces D-galacturonic acid into L-galactonic acid, which gets transformed to L-galactono-1,4-lactone. The L-galactono-1,4-lactone is further oxidized by L-galactono-1,4-lactone dehydrogenase (GALDH) enzyme (Sharma et al. 2012b). Ninety percent of the AsA pool is localized in the cytosol and apoplast, thus making it a major antioxidant in defense against the attack of ROS (Barnes et al. 2002). The key role of AsA is the disposal of H_2O_2 via AsA-GSH cycle. Oxidation of AsA takes place in two continuous steps; that includes, oxidation into MDHA, which if not reduced instantly to ascorbate, dismutases to AsA and DHA. It regenerates α-tocopherol from tocopheroxyl radical by reacting with $OH^•$, $O_2^{•-}$ and H_2O_2, hence guarding the membranes against oxidative injury (Shao et al. 2005). Furthermore, the activities of metal-binding enzymes are also protected and preserved by AsA. It serves as the cofactor of violaxanthin de-epoxidase in its reduced state and controls the dissipation of the surplus excitation energy (Smirnoff 2000). AsA also plays a role in stopping photo-oxidation, by pH-mediated modulation of PSII activity and its downregulation, linked with zeaxanthin production. Demirevska-Kepova et al. (2006) stated that the content of oxidized ascorbate was enhanced under Cd exposure in *H. vulgare*. Baig et al. (2021) concluded that priming wheat seedlings with AsA had positive effects on seedling growth and fresh and dry weights under non-saline and saline conditions. Noreen et al. (2021) observed that under saline conditions, the foliar application of AsA increased the photosynthetic pigments in *Hordeum vulgare* which was due to its role in antioxidant protection mechanism.

3.5.2.2 Reduced Glutathione (GSH)

Glutathione is a thiol tripeptide (γ-glutamyl-cysteinyl-glycine) with low molecular weight and is abundantly found in ER, cytosol, chloroplasts, mitochondria, vacuoles, peroxisomes, and even the apoplast. It has a role to play in processes like cell growth/division, cell differentiation, regulation of sulfate transport, regulation of enzymatic activity, expression of stress-responsive genes, etc. (Mullineaux and Rausch 2005). This versatile nature of GSH is because of its high redox potential. This reducing power of GSH is due to a central cysteine residue that has a nucleophilic character. GSH quenches $O_2^{•-}$, H_2O_2, $OH^•$, and $^1O_2$ and guards the biomolecules by producing adducts (glutathiolated) or by reducing them in the occurrence of ROS and forming GSSG as a by-product. The importance of GSH also lies in its role in restoring AsA to produce GSSG. The generated GSSG is then transformed back to GSH, either through de novo synthesis or enzymatically through GR. This process eventually restores the cellular GSH pool. The synthesis of glutathione involves two steps that are ATP-dependent. First, g-glutamylcysteine is formed from Cys and Glu, which is catalyzed by glutamate-cysteine ligase (GCL). This is thought to be the rate-limiting step of the pathway. In the second step, with the help of glutathione synthetase (GS), addition of Gly to g-glutamylcysteine takes place, which yields GSH. When synthesized, GSH act as a substrate for multiple cellular reactions that produce GSSG (i.e., two glutathione molecules connected by a disulfide bond). For maintaining the cellular redox state, the balance between the

GSH and GSSG is very crucial (Foyer and Noctor 2005) as GSH is necessary to prevent the damaging effects of ROS on cells during the oxidative burst. It is a powerful quencher of $H_2O_{2,}{}^1O_2$, $OH^{\cdot}$ and has a crucial part to play in the antioxidative defense system, as it regenerates another potential antioxidant (water-soluble) like ASH, through the ASH-GSH cycle. Moreover, GSH is involved in the production of phytochelatins via phytochelatin synthase (Roychoudhury et al. 2012), which causes chelation of heavy metal ions and thus quenching another possible source of ROS production in plants. The defensive role of GSH had been documented at low temperature stress in plants like spruce, pine, *O. sativa*, *Z. mays,* and *T. aestivum* (Guo 2006). Increased GSH level and the modified GSH/GSSG ratio were also found in plants suffering heat stress including *T. aestivum* and *Z. mays* (Dash and Mohanty 2002; Nieto-Sotelo and Ho 1986). GSH content considerably increased when barley was subjected to a saline environment, depicting its role in salt tolerance mechanism (Thabet et al. 2021).

3.5.2.3 Tocopherols (Toc)

Tocopherols (α, β, γ, and δ) are a set of lipophilic antioxidants that quench $^1O_2$, oxygen free radicals, and lipid peroxy radicals. The comparative antioxidant activity of the isomers in vivo is $\alpha > \beta > \gamma > \delta$. This variation in the activity is because of the methylation pattern and the number of methyl groups connected to the phenolic ring of the polar head structure. Therefore, α-tocopherol with three methyl groups in its structure has the leading antioxidant activity among the other tocopherols (Kamal-Eldin and Appelqvist 1996). The production of tocopherols is done only by organisms that are photosynthetic, and their occurrence is only limited to green parts of plants. Two compounds, namely, homogentisic acid (HGA) and phytyl diphosphate (PDP), are utilized in their biosynthetic pathway that act as precursors. At least five enzymes 4-hydroxyphenylpyruvate dioxygenase (HPPD), tocopherol cyclase (VTE1), homogentisate phytyl transferases (VTE2), γ-tocopherol methyltransferase (VTE4), and 2-methyl-6-phytyl benzoquinol methyltransferase (VTE3) are involved in the synthesis of tocopherols, except the bypass pathway of phytyl-tail synthesis (Li et al. 2010). Tocopherols are general antioxidants that defend the membrane stability by scavenging ROS such as$^1O_2$. Tocopherols are capable of defending lipids and other membrane components of the chloroplastic machinery. They react with oxygen and scavenge its surplus energy, thus safeguarding both structure and function of PSII. Tocopherol acts as an efficient free radical scavenger by blocking the chain propagation step of the LPO cycle. It reduces lipid radicals such as $RO^{\bullet}$, $ROO^{\bullet}$, and RO^* by reacting with them at the membrane-water interface. Later, it gets transformed into $TOH^{\bullet}$, combines with GSH and AsA, and again gets converted into its reduced form (Igamberdiev et al. 2004). In redox interactions with $^1O_{2,}$ the completely substituted benzoquinone ring and completely reduced phytyl chain of tocopherol serve as antioxidants (Halliwell and Gutteridge 2015). The quenching of $^1O_2$ by tocopherols is very effective, and it is predicted that up to 220 $^1O_2$ molecules can be neutralized in vitro by a single molecule of α-tocopherol before being degraded. α-Tocopherol accumulation has been reported to stimulate resistance toward water deficit, salinity, and chilling in the various plants (Bafeel and Ibrahim 2008; Guo 2006). Transgenic rice plants having Os-VTE1 RNA interference (OsVTE1-RNAi) were extra prone to saline conditions, while in transgenic plants, overexpressing OsVTE1 (OsVTE1-OX) reported greater resistance against salinity (Ouyang et al. 2011). Less H_2O_2 was accumulated in OsVTE1-OX plants than in control plants. Various reports have been documented to indicate the function of Toc in metal toxicity tolerance. Nickel (Ni) treatment in wheat seedlings led to an increase in Toc content in shoots (Gajewska and Skłodowska, 2007). Foliar application of α Toc not only led to the increase in Chl a, Chl b, and carotenoids but also showed a positive impact on yield attributes in *Triticum aestivum* under water stress conditions (Ali et al. 2019). Water stress caused an increase in the accumulation of Toc in leaves root, stem, and leaf of maize genotypes, indicating their role as an antioxidant during stressful conditions (Ali et al. 2020).

3.5.2.4 Carotenoids (Car)

Several mechanisms have been evolved by plants for getting rid of surplus energy in photosynthetic membranes, some of which include isoprenoid compounds. Carotenoids are pigments that are found in microorganisms and plants and are composed of eight isoprene units. Carotenoids (b-carotene and zeaxanthin) and tocopherols are involved in a photoprotective role in all photosynthetic organisms, either by removing excess excitation energy as heat or by quenching ROS and suppressing LPO. They are lipid-soluble antioxidants that play various roles in plant metabolism including oxidative stress resistance. Car performs three important functions in plants that include (1) an accessory light-harvesting role by absorbing the light at a wavelength between 400 and 550 nm and transferring it to Chl; (2) an antioxidant function by protecting the photosynthetic machinery by scavenging a triplet sensitizer (*Chl3), $^1O_{2,}$ and other harmful free radicals which are formed naturally during the process of photosynthesis (Collins 2001); and (3) a structural role by being involved in the assembly of PSI and stabilization of light-harvesting complex proteins along with thylakoid membrane (Gill et al. 2011). Carotenoids also act as precursors to signaling molecules that further play a role in abiotic stress responses and the development of the plants (Li et al. 2008). Carotenoids contain a chain of isoprene residues that provide them the ability to quench, halt, or lessen the formation of triplet chlorophyll. This is because of the presence of several conjugated double bonds in the isoprene units. These bonds allow a quick uptake of energy from excited molecules and their dissipation as heat (Mittler 2002). Under Cd-stress Car content of *H. vulgare* seedlings declined (Demirevska-Kepova et al. 2006). In wheat leaves an increase in α tocopherol and β-carotene by 2.5-fold was observed under drought (Bartoli et al. 1999). Moreover, it has been stated that monoterpene enhanced thermotolerance at high temperatures, and monoterpene had a defensive role against oxidative burst. Loreto et al. (2004) and Gomathi and Rakkiyapan (2011) observed that sugarcane plants experiencing saline conditions had high carotenoids content that helped in better adaptation. In barley plants Pb (lead) toxicity caused an increase in carotenoid biosynthesis indicating its need for heavy metal toxicity tolerance (Souahi 2021).

3.5.2.5 Phenolic Compounds (Flavonoids)

Phenolics are diverse secondary metabolites that possess antioxidant properties and are extensively present in plant tissues. They include flavonoids, hydroxycinnamate esters, lignin, and tannins (Grace and Logan 2000). Flavonoids are profusely found in plants generally in the floral organs, leaves, and pollen grains. The presence of an aromatic ring with –OH or OCH_3 groups in polyphenols imparts antioxidant action to these phenolic compounds. They have surpassed the antioxidants such as α-tocopherol and AsA, in antioxidant assays due to their strong capacity to provide electrons or hydrogen atoms. Polyphenols can directly quench reactive oxygen species and can prevent lipid peroxidation by trapping the lipid alkoxyl radical. They also decrease the fluidity of the membranes by modifying lipid packing order (Arora et al. 2000). These changes obstruct the diffusion of free radicals and limit peroxidative reactions. Flavonoids can be categorized into four classes based on their structure: flavonols (most abundant), isoflavones, flavones, and anthocyanins. They have various roles in plant fertility, pigmentation in flowers, germination of pollen, etc. Flavonoids are considered as a secondary ROS quenching system in plants that are undergoing photosynthetic machinery damage, due to the surplus excitation energy (Fini et al. 2011). The injury triggered to the chloroplastic membrane's outer envelope can also be alleviated by flavonoids as they have a role in quenching$^1O_2$ (Agati et al. 2012). Moreover, flavonoids act in H_2O_2-scavenging by getting oxidized through peroxidase. The number and arrangement of hydroxyl groups attached to ring structures determine the functioning and activity of the flavonoids. Their ability to serve as antioxidants is based on the redox potentials of their radicals and the accessibility of the radicals. After an inductive light treatment, flavonols aggregate in their glycosylated form and absorb UV-B light (280–320 nm) serving as effective UV filters. Ali et al. (2019) observed that water stress caused a spike in the content of flavonoids and other non-enzymatic antioxidants in leaves of wheat plants. Ali et al. (2020) observed a major rise in the flavonoid content in roots and leaves of *Zea mays* under drought conditions. Sahariya et al. (2021) observed higher phenolic content in *Hordeum vulgare* L. under fluoride stress. Rashid and his co-workers (2021) found that the phenolic contents increased in all wheat varieties under drought stress.

3.6 Conclusion

Therefore, it may be generalized that abiotic stresses result in the production of many reactive oxygen species (O_2^-, OH^-, $^1O_2$, H_2O_2) that lead to an oxidative burst in various cellular compartments. ROS are mainly generated in chloroplasts, peroxisomes, and mitochondria, with O_2^- and H_2O_2 being majorly produced in mitochondria and peroxisomes, respectively. When ROS production exceeds a certain limit, they cause oxidation of lipids, DNA, and proteins leading to cell damage and cell death. So, to neutralize the ROS generated, the antioxidants come into play and cause the dismutation of these harmful free radicals. The antioxidant defense mechanism can be enzymatic (SOD, catalase, glutathione peroxidase, and glutathione reductase) and non-enzymatic (glutathione, α-tocopherol, flavonoids, and carotenoids). These antioxidants help to quench the ROS and alleviate the damage caused to the biomolecules. Therefore, cereals having the ability to quench or limit the level of cellular free radicals/ROS may be helpful in the future to tolerate extreme environmental conditions.

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Part II

Role and Responses Under Abiotic Stress

Maize: Role and Responses Under Abiotic Stress

4

Sidra Shafiq, Nudrat Aisha Akram, Muhammad Ashraf,
and Arafat Abdel Hamed Abdel Latef

Abstract

Abiotic stresses, drought, salinity, temperature (high or low), and heavy metals negatively affect the growth and productivity of maize crop at the global level. Maize is the most demanding cereal crop and has the potential for high production than rice and wheat. It is used for humans and animals as well as for industries, while various environmental stresses, climatic changes, and global warming, are becoming a serious threat to maize development and production. Now, the main focus of maize research is to enhance abiotic stress tolerance potential, but it is difficult to identify genetic mechanisms responsible for stress tolerance. Food demand is increasing with the increase in population, so there is an urgent need to develop/explore as well as introduce stress-resistant maize cultivars/varieties. It can be attained by manipulating the molecular, physiological, and biochemical mechanisms underlying the stress-responsive cultivars. Together with these mechanisms, the identification of negative impacts of stresses can also help in modulating the plant stress tolerance capabilities which can be used in future studies.

Keywords

Maize · Drought · Salinity · Temperature · Heavy metals · Abiotic stresses

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4.1 Introduction

Maize (*Zea mays* L.) is usually produced as a staple food, feed, and industrial crop, supporting a significantly world-growing population. However, unfavorable environmental factors also influence the growth and production of maize (Gong et al. 2014; Li et al. 2017; Ngoune Tandzi and Mutengwa 2020). Frequent changes in weather, as well as the quality and availability of water resources and arable land, can cause different abiotic stresses including extreme temperature, salinity, drought, etc. Worldwide crop production and agronomical yield are seriously affected by these environmental stresses. These abiotic stresses can cause a reduction of over 50% in major crop production globally (Fig. 4.1).

In maize, the seedling stage is more sensitive to abiotic stresses, and stunted growth can be caused by damage to the seedling resulting in reduced crop production and encountering economic costs (Gong et al. 2014; de Zelicourt et al. 2016; Li et al. 2017).

Maize is used as raw material for the industry as well as a cash crop. It is cultivated in almost 160 countries; 36% of grain production is produced in an area of 150 Mha globally. Approximately, 70–80% is used as a feed for total maize grain produced around the globe. Cob powder is used as filler for explosives in the manufacturing of glues, resins, plastics, vinegar, artificial leather, and adhesives. It is also used for the manufacturing of hard boards, paper, and pulp. Maize grain is used for corn flour, oil extraction, corn syrup, starch extraction, and corn flakes (Sah

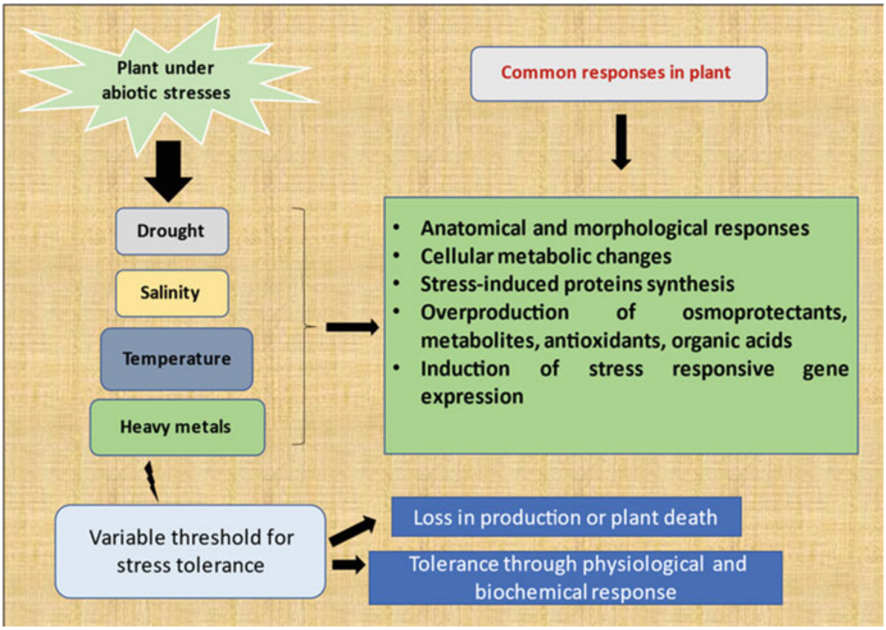

Fig. 4.1 Plant responses to various abiotic stresses

et al. 2020). For higher production, maize requires 500–800 mm water and 28–32 °C temperature range for completing its life cycle. Growth and yield of maize plants not only depend on genotypes, but other environmental factors also influence the growth of plants. During the whole life cycle, plants undergo different phases. In recent years, climate change has become a major challenge for crop production, because temperature and precipitation both are unpredictable (Mao et al. 2015; Bhusal et al. 2021).

In maize production zones of the world, abiotic stresses are becoming a major threat to growth and productivity. The use of maize-resistant cultivars to drought, salinity, and temperature stresses is the most cost-efficient strategy to prevent stress damage. Stress-responsive mechanisms of resistance to temperature, salinity, and drought stress are complex, while revealing the molecular mechanisms of maize to different abiotic stresses is necessary to enable the production of resistant maize varieties and strategies (Li et al. 2017). The production of maize must be doubled to meet the rising requirement of consumption for humans and animals particularly in developing countries.

Effect of drought stress on maize was more severe as compared to salinity, heavy metals, and temperature stresses. In response to stress (s), plants activate signaling pathways including signal transducers, transcription regulators, and plant hormones. As a result, stress-inducible genes are activated to produce enzymes and proteins for stress tolerance metabolism. However, the vulnerability of crop plants to different environmental stresses is a new challenge to maintain high crop production under changing climatic conditions. In the future, stress-tolerant crops may be necessary to maintain crop production (Zandalinas et al. 2018; Bhusal et al. 2021). Here, we summarize the updated findings on the effects of different environmental stresses on morphological, physiological, and biochemical attributes of maize plants. In addition, possible substantial strategies to help the plant to cope with unfavorable stress conditions have also been discussed.

4.2 Drought Stress

Drought stress is a more detrimental factor for crop yield production than any other stress. When plants are grown under drought stress, they attempt to maintain cell homeostasis and water uptake by adaptive mechanisms and osmoregulation and increase protoplasmic resistance to enable them to tolerate, escape, or avoid drought stress (Wang et al. 2019; Ziogas et al. 2021). Combined effect of these strategies includes drought resistance and the ability of plants to cope with dehydration by maintaining turgidity and water balance (Bhusal et al. 2021). Most widely grown cereal crop, with production greater than wheat and rice, maize plants often suffer from drought stress resulting in the reduction of final kernel yield. The growth and productivity of maize are severely affected by water deficiency (Wang et al. 2019). For global food safety measures, ensuring yield under osmotic stress is most valuable, particularly from the perspective of climate change and the increased occurrence of drought events (Su et al. 2019; Shafiq et al. 2019, 2021; Liliane and Charles 2020).

About 80% of areas under maize cultivation are rain-fed where the crop is vulnerable to the unpredictable behavior of rains. Most rainfall occurs at different growth stages and maize crop from pre-flowering to late grain filling stages faces water deficit conditions. These problems affect the reproductive system, phenotype, and seed set of maize plants. Due to erratic water deficit stress (WDS) in rain-fed areas, maize production is decreasing drastically. Usually, WDS occurs from August to September in the wet season and after the first fortnight of February in the dry period of the year. In both seasons, adequate water is accessible to grow the plant to the vegetative stage. From pre-flowering to the grain filling, plants are harshly affected by continued rainfall in the wet season and the scarcity of water in the dry season (Sah et al. 2020).

During the pollination stage, drought stress caused abnormal embryo development and a considerable reduction in kernel numbers. Decreased kernel numbers were also observed in response to drought stress during the early-post and pre-pollination stages. The ear leaf of maize contributes significantly to the accretion of biomass due to photosynthesis and is involved in the development of kernel and ear production (Aslam et al. 2015; Liu et al. 2015; Wang et al. 2019). During the vegetative stage of maize, drought stress reduces plant growth, increases the vegetative growth period, and decreases the period of reproductive growth (Bhusal et al. 2021).

During early growth between seedling and knee-high stage, dry season maize crops show late maturity due to a continued cold season. As a result, more water input is essential for a long duration. In the dry period, loss of production of maize grain is linked to deficiencies of water used for irrigation (Pandit et al. 2017; Waqas et al. 2021). Reduction in grain (30–90%) depends on the duration and degree of WDS and crop stage. Maize stages prone to WDS are silking, vegetative, and grain filling where yield loss may be high as 50%, 25%, and 21%, respectively. In most cereals, damage to phenotypic appearance under WDS is obvious (Pandit et al. 2018). After a serious level of WDS, phenotypic expression is also reduced in maize. The effect of water stress is prominent as a reduction in ear length, plant height, leaf number, kernel per row, kernel rows per ear, seed weight, green-leaf duration, ear length, no. of grains per ear, ears per plant, flowering, and leaf senescence (Sah et al. 2020).

Photosynthesis is a key metabolic pathway that is more sensitive to drought stress and is involved in early responses to drought stress. During stress conditions, water potential and relative water contents decrease resulting in decrease in transpiration cooling and an increase in leaf temperature (Aslam et al. 2015; Bhusal et al. 2021). Decrease in soil moisture causes a similar reduction of leaf water which induces a decline in turgor pressure of guard cells due to stomatal closure. Reduced leaf area, increase in stomatal closure, and subsequent reduction in leaf cooling by evapotranspiration which increases osmotic stress leading to damage to photosynthetic apparatus are major constraints for photosynthesis. Decrease in photosynthesis is attributable to a reduction in CO_2 conduction via stomata and mesophyll restrictions

(Singh and Thakur 2018). Moreover, CO_2 improvement reduced many early responses of maize metabolites and transcripts under drought stress conditions (Sicher and Barnaby 2012; Kapoor et al. 2020). Drought stress severely affects chlorophyll pigments which suppress the light absorption efficiency of plants. In response to drought stress, stomatal closure is a response to amend the adverse effects of drought stress, but CO_2 assimilation reaction and root absorbance reduce as a result of less transpiration rate (Meng et al. 2016; Xie et al. 2017). Drought stress causes damage to Rubisco and other enzymes associated with photosynthesis and is responsible for the loss of photosynthetic pigments. The major cause of chlorophyll degradation is the production of reactive oxygen species (ROS) such as O_2^- and H_2O_2 resulting in lipid peroxidation (Abid et al. 2017; Karimpour 2019).

Drought stress triggers ROS which are scavenged by plant defensive system. Plant defensive mechanism includes enzymatic and non-enzymatic detoxificant moieties which lessen the damage. Antioxidants help to scavenge ROS and decrease electrolyte leakage and lipid peroxidation, maintaining the integrity and viability of cell membrane and organelles. Proportion of ROS and antioxidants regulates cell redox states. Tolerant species have enhanced antioxidants activity than non-tolerant species (Hussain et al. 2019a, b, c). These enzymes are directly or indirectly associated with drought tolerance of maize plants (Anjum et al. 2017). Adebayo and Menkir (2014) reported that the high yield of maize plants was associated with increased activities of antioxidants enzymes.

Water stress reduces soil nutrient accessibility; translocation of nutrients ultimately lessens the ion contents in various plant tissues. Water stress decreases K uptake, eventually reduces the mobility of K, declines transpiration, and weakens the action of root membrane transporters (Kapoor et al. 2020). Drought stress that occurs during the growth period of maize may obstruct water and nitrogen use efficiencies leading to a significant loss in yield production. Drought-associated metabolic and physiological changes might help determine the sensitivity and tolerance under water stress conditions (Anjum et al. 2017).

Maize is a drought-susceptible crop mainly during the seedling stage of development and is grown in a wide range of climatic situations from semi-arid to temperate areas including drought-prone regions of Asia, Africa, Europe, and North and South America (Xie et al. 2017). However, the performance of any maize line varies and depends on its genetic composition and appropriate trait under normal and stress conditions. Various water deficit-tolerant maize lines have been developed, and affected traits were considered as selection criteria for parent selection, while these lines well performed at specific water stress levels and fail to perform best under even a small variation in water level. Water deficit condition is not frequent throughout the plant life cycle. Consequently, proper phenotyping for the recognition of key attributes linked with improvement in yield persists in a main area of investigation. Many studies have been carried out to recognize drought-tolerant cultivars. However, the focus of research has been changed from morphological to the identification of genes responsible for drought stress tolerance (Meng et al. 2016; Hu et al. 2021). Thus, drought stress causes a reduction in germination, growth, photosynthesis, chlorophyll pigments, leaf water contents, alterations in water and nitrogen use efficiency, and transportation of mineral nutrients and leading to reduced yield.

4.3 Salinity Stress

In irrigated and less irrigated areas, high concentrations of salts particularly sodium chloride (NaCl) cause salinity stress. According to worldwide estimation, 50% of irrigated land and 20% of cultivated land are under salinity stress (Munns and Tester 2008; Wang et al. 2017; Yildiz et al. 2020). Due to osmotic stress and ion toxicity in soil, the growth and production of plants reduce under salinity stress. Salinity stress causes degradation to chlorophyll and enzymatic proteins in photosynthetic apparatus. Photosynthetic activity of plants reduces because of a reduction in stomatal opening induced by salinity stress. Moreover, salinity stress causes other stresses like oxidative stress which causes ion toxicity and results in the accumulation of ROS damage plant cell. Photosynthetic pigments, lipids, proteins, and nucleic acids are damaged by ROS. Therefore, photosynthetic capacity and antioxidants are the main fundamentals in salt stress research programs (Chaves et al. 2009; Jiang et al. 2017; Sachdev et al. 2021).

Maize is an important C_4 plant of the Poaceae family that is grown on a wide spectrum of soil and is moderately sensitive to salt stress. However, wide genetic variation for salt resistance occurs in maize. Salinity induces osmotic stress and reduction in growth during the first phase of growth because of ion toxicity in cereals. The sensitivity of maize to salt stress is related to the high accumulation of Na^+ in the leaves. Ion toxicity levels of more than 0.25 M of NaCl damage maize plants and may cause inhibited growth and severe wilting (Farooq et al. 2015; Iqbal et al. 2020). Ion toxicity by sodium and chloride, excessive nutrition due to interfering with the transport, and uptake of crucial nutrients and osmotic stress due to low exterior water potential are three main potential effects of salinity stress on the growth of the plant (Munns and Tester 2008). The toxicity level of sodium in plant organs reduces growth, causes irregular development before plant mortality, and damages subcellar organelles and biological membranes (Hussain et al. 2013; Iqbal et al. 2020).

Various physiological processes such as starch metabolism, photosynthesis, nitrogen fixation, and respiration are affected under salinity stress resulting in reduced crop production (Iqbal et al. 2020). In maize plants, salt stress causes oxidative damage to plant cells by an accumulation of ROS. Salt resistance is the ability of the plant to cope with salinity and produce harvestable yield. In this complex process, the plant undergoes adaptations at the organ, cellular, and subcellular levels including ion homeostasis, osmotic adjustment, hormonal imbalance, stomatal regulation, maintenance of tissue water status level, and activation of antioxidative defense mechanisms under salt stress (Kaya et al. 2010; Jafar et al. 2012).

Germination and early seedling stages are most critical, and the severity caused by salinity stress suspends the primary growth, decreases the rate, and increases the dispersion of germination events during germination establishment. Delay in seed germination is caused by altering protein synthesis, sodium, and chloride toxicity to the embryo and lowering osmotic potential of soil solution to delay water absorption by seeds. Shoots are more sensitive to salt stress than the roots. Salt stress suppresses shoot growth by decreasing internode growth, expansion, and initiation of the leaf as well as increasing leaf abscission in maize plants (Akram et al. 2010; Qu et al. 2012). The decrease in plant growth development by salt stress is primarily caused by the decrease in wall loosening enzymes and apoplastic acidification in maize (Iqbal et al. 2020).

In the first phase of salinity stress, shoot growth is mainly constrained in maize plants. During the first phase of salt stress, assimilation allocation to growing tissue is not restricting, recommending that photosynthesis is not responsible for growth decline in maize. In various maize tissues, uptake and translocation of calcium, potassium, and nitrogen are constraints leading to decreased nitrogen contents and growth under salinity stress. Carbon fixation capacity of maize plants is limited by the reduction in photosynthetic pigments and stomatal conductance, impaired photosynthetic apparatus, and activities of enzymes under salt stress. Inhibition in photosynthesis rate in maize is reduced because of decreased stomatal conductance and carbon fixation as well as reduced leaf expansion, abscission, and development under salinity (Qu et al. 2012).

During the reproductive phase of maize, salt stress reduces the number and weight of grain, resulting in a considerable decrease in grain yield. Salinity-induced reduction in sink limitations, photosynthesis, assimilate translocation and sink limitations are responsible for poor grain filling, setting eventually final grain yield (Iqbal et al. 2020). So, salt stress negatively impacts growth, photosynthetic activity, water relations, nutrient balance, water use efficiency, and final yield of plants.

4.4 Temperature Stress (High and Low)

Maize is the third staple food across the world and faces many environmental constraints including temperature stress (Tiwari and Yadav 2019). Reduction in net photosynthesis rate at leaf was observed in maize plants when temperature rise above 38 °C, and reduction was improved when temperature also increased abruptly (Magar et al. 2019). Photosynthesis and transpiration rates increased with an increase in temperature and stomatal closure. Initiation state of Rubisco is reduced at the temperature range of 32 °C and completely deactivated at 45 °C. Activation of Rubisco adjusted with the rise in leaf temperature and acclimation procedure was related to the expression of newly activated polypeptides. It was concluded that the main restraint for the decrease in photosynthesis rate is the inactivation of Rubisco at high temperatures in maize (Crafts-Brandner and Salvucci 2002). At low temperatures below 15 °C, maize is sensitive to chilling stress and expresses less adaptation. The leaves of maize plants are more sensitive to chilling which induces leaf senescence (Foyer et al. 2002; Bhusal et al. 2021). Different biochemical, physiological, and morphological activities imbalance when temperature range above high than the threshold, resulting in the improvement in plant defense mechanisms. Extreme temperature affects nutrient uptake, biological membranes, and photosynthetic process and limits the functioning of various enzymes in maize plants (Hussain et al. 2019a, b, c; Zafar et al. 2020).

Reduction in photosynthetic rate and inhibited growth causes damage to maize plants. During the growth period especially at the flowering stage of maize plants, morphological and metabolic activities alter under high temperature stress leading to a reduction in yield (Lesk et al. 2016; Shim et al. 2017). At temperatures 10–35 °C, leaf growth of maize increases while it declines at a temperature greater than 35 °C. Crop growth, CO_2 exchange rate, number of grains and grain yield during pre- and post-flowering stages of maize plants decreased at a temperature ranging 33–36 °C (Neiff et al. 2016). During the flowering stage, silk number, floret number, and grain yield of maize were negatively affected under high temperature stress (Neiff et al. 2016; Waqas et al. 2021).

Reduction in ovary fertilization and grain filling is linked with final grain yield under heat stress above 35 °C. Temperature stress reduces the time for pollen shedding and tasseling and increases the anthesis-silking interval to decline the feasibility and pollen amount. Furthermore, maize plants are incapable to convert photosynthates into starch under heat stress. Consequently, reduction in viability, pollen number, and starch biosynthesis involve altering the fertilization procedure (Siebers et al. 2017; Wang et al. 2019). During the reproductive phase, heat stress causes dehydration for pollens, silk, sterility, as well as seed setting leading to final yield reduction. Production loss of maize during the reproductive phase is also related to a reduction in weight and number of grains. Insufficient photosynthates in heat-stressed maize plants are frequently measured as a main limiting factor for yield loss (Tian et al. 2019; Waqas et al. 2021).

Normally, heat stress causes a reduction in endosperm cell division, and amyloplast biogenesis leads to a decrease in grain size. The complex network of enzymes regulates the pathway involved in starch accumulation in growing grains. High temperature impairs starch accumulation and restricts enzyme activities during the filling and hardening process of maize grains (Yamakawa et al. 2007; Shim et al. 2017). Source-sink ratio, radiation use efficiency, and biomass accumulation are the main determinants of final grain yield and harvest index under heat stress. Heat stress adversely affects silks and pollen viability resulting in decreased seed set and economical yield (Waqas et al. 2021).

Maize is cold sensitive and grain yield is less in humid cold regions. The growth period is prolonged when plants are subjected to cold stress-causing weak seedlings and terminating grain filling early at the end of the growth cycle leading to reduced grain production (Thakur et al. 2010; Hussain et al. 2019a, b, c). Damage to cells and tissues in maize at seedling and reproductive stages may vary depending upon the duration and degree of chilling stress. When plants are subjected to a low temperature below 10 °C, plant growth is interrupted from primary seedling to reproductive stages (Farooq et al. 2009). It was reported that growth, seedling, germination, and antioxidative defense system in maize plants are destabilized under cold stress (Chen et al. 2012). It also negatively affects leaf area, seedling emergence, root/shoot ratio, root morphology, chlorophyll pigments, and efficiency of photosystem II (PSII) in maize plants (Hund et al. 2007). It also impacts thylakoid structure, chloroplast, and metabolite transport of the Calvin cycle (Sun et al. 2017). Initiation of anthesis is delayed during growth stages when maize plants are exposed to low temperature stress even for a short duration of 7 days (Hayashi 2016).

Among morphological characteristics, tassel growth, pollination, and grain filling processes are affected by low temperature stress in maize plants. Final yield reduction occurs at low temperature during critical reproductive stages, as plants assign more than 50% of photosynthates to mature grains. Because of the prolonged cell cycle, cold stress reduces plant height, rate of mitosis, and total biomass of maize plants (Hayashi et al. 2015; Liu et al. 2016).

Many biochemical and physiological processes and ailments can be studied in cell membranes, antioxidant activities, and photosynthetic machinery. Chen et al. (2012) studied that cell membrane permeability and malondialdehyde (MDA) contents increased, while water contents, chlorophyll, and proline reduced in maize plants under low temperature stress. Cold stress also caused a reduction in macro-nutrients (P, K, N, Ca and Mg) of shoot and root as well as metabolite transport in maize (Hayashi 2016). In response to chilling stress, maize plants produced signaling molecules such as abscisic acid and nitric oxide as a defense. It also produces ROS and causes damage to membranes, macromolecules, and cellular structures (Hussain et al. 2019a, b, c). In defense mechanism, many enzymes including superoxide dismutase (SOD), peroxidase (POD), as well as catalase (CAT) contents are produced in maize plants (Hussain et al. 2019a, b, c; Hasanuzzaman et al. 2020). Together, low temperature stress alters the photosynthetic rate, germination percentage, growth rate, and final yield of maize plants (Waqas et al. 2021). Collectively, heat and chilling stresses significantly reduced seed germination, growth rate, photosynthesis, and ultimately economic yield of maize.

4.5 Heavy Metal Stress

Heavy metals stress is a major abiotic constraint that adversely affects the quality, quantity, and nutritional value of maize plants (Rizvi and Khan 2018). Collection of heavy metals due to industrial wastes has serious effects on the degradation of soil and severely restrains the plant development and production that leads to agriculture failure as well as danger to human health when entering the food chain through soil, water, and atmosphere and plant continuum. Excessive use of fertilizers is also involved in the accumulation of heavy metals in soil (Youssef and Azooz 2013). Cadmium (Cd) is nonessential for plants, but its presence in soil and atmosphere even in low concentration can disrupt many physio-biochemical and morphological attributes including a reduction in water contents, growth, photosynthetic efficiency, modification in ion homeostasis, ROS production, and alteration in enzymatic and non-enzymatic antioxidants activities/levels (Gul et al. 2016). Copper (Cu) is an important micronutrient for plant growth, while its high concentration causes toxic effects on plants involving inhibition of growth and triggering plant death. High concentration of Cu accumulated in various parts of plant and soil alters nutrient uptake and cell membrane permeability; interrupts photosynthetic machinery, pigments, and proteins; produces ROS; and causes oxidative damage (Gupta and Abdullah 2011; Gul et al. 2016).

Uptake of heavy metals by plant roots depends on soil pH, density, availability of metals in soil nutrients, water-holding capacity, type of charge in soil colloids, and specific soil surface area. Heavy metals can persist in soil and atmosphere for many decades or indefinitely, with other nonessential metals such as lead, cadmium, and mercury (Balkhair and Ashraf 2016; Romdhane et al. 2021). Leaf and root morphology are also distorted by heavy metals. It was reported that heavy metals increased the activities of antioxidant enzymes along with an increase in proline and MDA contents (Rizvi and Khan 2018). Heavy metal toxicity was found to impede normal plant functioning distracting metabolic processes by altering membrane permeability and enzyme activity of cell membranes in higher plants including maize. Heavy metals quickly interact with several biomolecules leading to the accumulation of ROS, eventually disturbing the functions of pigments and enzymes. As a result, growth and productivity reduce and depend on contamination level (Anjum et al. 2016; Ghori et al. 2019).

In maize plants, heavy metals stress triggers variations in morphological, metabolic, and physiological processes with the extent of yield depending on the metal, level of contamination, genetic tolerance level, and combined effect of different metals. Cadmium is more toxic in maize than the other metals, causing severe reductions in growth attributes and field grain yield. In maize plants, the primary effects of Cd stress are stunted growth, perturbation of cell membranes, and cellular damage caused by ROS (Ghani 2010; Rizvi and Khan 2018). The combined effect of different metals such as Pb, Zn, Co, and Cu was found to be effective in decreasing shoot and root biomass and root length. Adaptation strategy in maize under heavy metal stress increased coarse root length and decreased fraction of finer root (Romdhane et al. 2021).

4.6 Management Strategies to Mitigate Stress in Maize

Agronomic practices for a definite cropping system as well as practices that support farmers to acclimate to environmental stresses decrease production loss. Alteration in planting time may help plants to escape the temperature extreme stage at growth stages (Steward et al. 2018). Change in planting time of maize helped to reduce yield loss caused by reducing the adverse effects of heat and chilling stress during grain filling and silk stages (Tian et al. 2019).

In arid and semi-arid regions, harsh climate severely affects maize and ultimately crop failure. To attain adequate grain yield, dry soil planting is highly effective in these regions (Lana et al. 2018). Seeds are sown in dry soil just after the rainy season. Because germination can be started by absorbing moisture contents in dry soil after rain. Such strategies can be supported with mock intelligence more precisely forecasting the rainy season. So, agriculturalists need to acclimate to the future environment by improving the sowing date and maize earliness and choosing maize cultivars with more thermal time necessities according to their limited climate and dry soil planting. Foliar application of plant growth regulators such as proline, salicylic acid (SA), thiourea, etc. can create tolerance against temperature stress (Waqas et al. 2017, 2019).

Various chemicals and organic modifications are used to combat with adverse effects of salt stress for the management of saline soil. These chemicals include potassium, phosphorus, silicon, biochar, salicylic acid, boron, gypsum, and other organic substances. Application of silicon reduces the alterations caused by salt stress in plants by changing the soil factors and plant. Photosynthetic machinery and maintenance of the electron transport chain were improved by silicon application in maize plants under salinity stress (Khan et al. 2017). Silicon also improved defensive machinery, water-use efficiency, photosynthetic apparatus, and lessened oxidative and osmotic stress in maize plants (Khan et al. 2018). Silicon and boron in combination application improved proline and total soluble sugars in maize genotypes (Salim 2014). Potassium application on maize plants alleviated the adverse effects of salinity by decreasing sodium concentration (El-Dissoky et al. 2013). Under water deficit conditions, potassium application improved growth parameters, relative water contents, leaf area, and photosynthetic rate of maize plants (Aslam et al. 2013). Application of biochar and organic matters can also improve maize growth and soil chemical properties (Iqbal et al. 2020).

Plant growth regulators (PGRs) as well as osmoprotectants such as proline and glycine betaine at low concentrations impact plant growth; make defenses by scavenging ROS; stabilize the structure and integrity of proteins and membranes, biosynthesis of osmolytes, and secondary metabolites; increase nutrient uptake; make an expression of antioxidant-related genes; and promote osmotic adjustment (Ahmad et al. 2014; Waqas et al. 2019). Foliar application of PGRs by seed coating and seed priming can contribute to offsetting the adverse effects of temperature extremes on crop productivity. These practices improve germination, seed vigor, quality, physiology, and uniform stand formation under high and low temperature stresses. Seed coating is a conventional technology to elevate the seed performance under environmental stresses (Hussain et al. 2019a, b, c).

Chemicals that normalize plant growth and production including fertilizers, fungicides, plant growth stimulants, and insecticides are employed to save seeds from unfavorable conditions. Foliar application of SA and hydrogen peroxide (H_2O_2) also improved salinity tolerance in maize plants by improving antioxidants activities, leaf area, proline contents, amino acid contents, nutrient uptake, growth, and yield of maize (Gunes et al. 2007; Gondim et al. 2012). Seed priming with SA and H_2O_2 also improved chilling stress in maize plants by promoting hormone metabolism and antioxidant enzymes (Li et al. 2017).

Worldwide, maize plantation with seed coating (SC) technology is also increasing and has become popular. The SC with hydrogen peroxide and chitosan improved protein contents and the emergence rate of maize seedlings (Lizarraga-Paulín et al. 2013). Melatonin is a signaling molecule and powerful antioxidant; its application enhanced heat and cold stress tolerance in plant species and can be used to improve the maize performance under high and low temperature stress (Sharif et al. 2018). To germinate maize seeds under stress conditions, seed priming is an effective pre-sowing treatment (Hussain et al. 2016). Maize seeds priming with natural and synthetic growth promoters improve maize performance under high temperature stress (Hussain et al. 2019a, b, c). Maize seedlings showed improved germination, growth, yield, and nutrient uptake when seeds were primed with micronutrients (Fe, Mn and Zn) under chilling stress (Imran et al. 2013). Seed priming with H_2O_2 and SA alleviated the adverse effects of low temperature stress by improving growth, germination rate, and energy supply; downregulating germination-inhibiting genes; and upregulating the expression of correspondence genes and genes involved in the synthesis of gibberellic acid, α-amylase activity, and antioxidant level (Li et al. 2017). Seed priming with SA, thiourea, AsA, and H_2O_2 improved maize stress tolerance by improving chlorophyll contents, leaf water contents, the integrity of cell membrane, grain quality and yield, and antioxidants activity under heat stress during grain filling and reproductive stages (Ahmad et al. 2017). Seed priming with calcium chloride, potassium chloride, and sodium chloride improved germination, growth, cob number, and final yield of maize crop under saline conditions (Gebreegziabher and Qufa 2017). Maize seedling biomass, growth, and yield were also improved by other seed priming agents such as thiamine, AsA, pyridoxine, and chloroethylphosphonic acid, lessened lipid peroxidation, and improved antioxidants activities under salt stress (Arora et al. 2008; Carvalho et al. 2011).

Natural plant growth promoters such as sugar beet extract, sorghum water extract, and moringa leaf extract also help to mitigate the negative effects of abiotic stresses in the crop. Foliar application of sorghum water and moringa leaf extract improved the growth, physiology, morphology, and antioxidant defense system leading to an increase in grain yield and quality of maize plants under chilling stress (Waqas et al. 2017). Impact of PGRs depends on the application time, dose, as well as variety and species of crop plants. So, farmers should adopt site-specific measures suitable to a place with the guidance of scientists (Waqas et al. 2021).

4.7 Molecular Approaches

Molecular breeding advances, viz., marker-assisted recurrent selection (MARS), marker-assisted backcrossing breeding (MABB), marker-assisted selection (MAS), genomic selection (GS), or genome-wide selection (GWS), offer chances for plant breeders to create high-yielding maize cultivars with resistance to stress conditions. The Cascades of molecular networks are implicated in the modification mechanisms of plants to abiotic stresses. These trigger stress-responsive processes to restore homeostasis and to repair and protect impaired membranes and proteins. Environmental stresses are multigenic and complicated to control or engineer. Therefore, approaches like plant genetic engineering for developing tolerance depend on gene expression engaged in regulating and signaling pathways. Accordingly, engineering genes that sustain and protect the structure and function of cellular components can improve tolerance to stress (Gazal et al. 2018; Hasan et al. 2021).

Molecular breeding method entails initially identifying QTLs for abiotic stress tolerance in plants. After identifying markers linked with genes or QTLs for traits of attention, the genes or candidate QTLs can be introgressed in elite lines through marker-assisted backcrossing (MABC). Until lately, QTLs were discovered through linkage mapping, but now association genetics has begun to increase these attempts in crop plants (Hasan et al. 2015; Gazal et al. 2018). Nested association mapping, which merges the benefits of association mapping and linkage mapping in a single integrated mapping population, is also being applied for genome-wide dissection of complicated traits in maize (Yu et al. 2008).

MABC assists in improving tolerant crops that are adjusted to abiotic stresses such as drought and temperature. One of the complexities of creating superior genotypes for abiotic stresses is that these characteristics are usually regulated by small-effect QTLs or various epistatic QTLs. The assessed genetic advantage by genome-wide selection or MARS is greater than achieved by MABS for transporting genes/alleles for complicated abiotic stress attributes in one genomic background. One of the main limitations for maize production is water restrictions due to insufficient soil moisture, especially during grain filling or flowering stages. Balanced genomic zones correlated with maturity, staying green, flowering, and yield components recognized more than 1080 QTLs (Ribaut et al. 2009; Younis et al. 2020).

In maize, the most significant trait examined under water stress is the expanded interval between anthesis and silking (ASI). A total number of 62 and 83 QTLs for ASI and grain yield were discovered in the bi-parental population under drought stress and normal irrigation (Almeida et al. 2013). In a study 203 QTLs were mapped on chromosomes 1, 3, 4, 5, and 7 and 10 for several drought-related morphological and physiological attributes, and 6 constitutively stated meta-QTLs were mapped onto chromosomes 1, 4, and 5 and 10 for grain yield (Almeida et al. 2014). Out of 354 genes, 52 genes in a B73 inbred line demonstrated considerable variance expression in drought and normal conditions (Li et al. 2016).

Under waterlogging, the study of maize for the assessment of genetic variation in a RIL population resulting from a cross between an elite line (CML311-2-1-3) and waterlogging tolerant line (CAWL-46-3-1) exposed the presence of an important range of difference for grain yield that could be attached to a partial range (Zaidi et al. 2015). Cold stress or low temperature considerably impedes the yield and growth of maize. For early growth and germination, 27 QTLs were mapped onto chromosomes 1, 2, 3, 4, 5, 6, 7, and 8 and 9 in two autonomous RIL populations (Allam et al. 2016). These QTLs for chilling tolerance will be expected to hasten the development of genomics-assisted breeding in maize. In the temperate inbred line of maize, genetic association analysis for cold tolerance, six important QTLs and three primary-effect QTLs for days from planting to emergence and chlorophyll pigments were found (Revilla et al. 2016).

To identify salinity-tolerant QTLs, 15 QTLs were mapped onto chromosomes 1, 2, 4, 5, 6, 7, 8, and 9 and 10 from $F_{2:3}$ population created from a cross among CZ-7 and B73 under the greenhouse environment (Hoque et al. 2015a, b). A *ZmERD2* gene (early responsive to dryness) was later discovered as a heat shock protein that gives heat tolerance (Song et al. 2016). The introgression lines based on Gaspe Flint and B73 were used to recognize three major QTLs for seminal root number in maize. Two known QTLs co-situated with previously well-known mutant genes (*rtcs* and *rum1*) are known to eliminate the induction of seminal roots. The NILs that evolved in the background of B73 can be discovered for useful characterization of genes engaged in the seedling formation and early growth of maize (Salvi et al. 2016).

Likewise, a new genome selection (GS) study on 22 pi-parental tropical maize populations utilizing small mass SNP markers showed that the genomic prediction precision is found to improve with trait heritability, marker density, and population size. Lately, a new procedure has been described for quick cycling GS in a multi-parental maize population. The quick genetic advances attained through the technique along with synchronized management of genetic variety showed it to be on useful approach (Zhang et al. 2017a, b). GS will demonstrate to be significant in the progress of climate-resistant cultivars and thus serve as to maintain and improve food security at the worldwide level. Therefore, QTL breeding suggests chances to plant breeders to improve climate-resistant cultivars via introgression of major/minor QTL for attributes associated with abiotic stress through MARS and MABB methods (Choudhary et al. 2019) (Table 4.1).

4.8 Summary and Future Prospects

Crop plants face different environmental stresses such as salinity, drought, temperature stress, and heavy metals stress during their whole life cycle. These stresses individually or in combination badly affect plant metabolism and normal functioning. In the world, maize is an important cereal crop with a high potential yield. High production of maize is time-demanding due to the increasing population rate and food security. But, changing climatic conditions such as global warming, alterations in rainfall patterns, decrease in soil fertility, and heavy metals in soils due to industries are major constraints for the growth and development of maize plants. These abiotic stresses impact the whole plant life cycle from embryo to maturity phase. Reproductive stages of maize are more vulnerable to drought and heat stresses than other stresses.

Many physiological, morphological, and biochemical adaptations occur in plants to cope with the adverse effects of stress conditions. These include stomatal closure, extended root hairs, accumulation of compatible solutes, increase in the activities of enzymatic and non-enzymatic antioxidants, as well as plant growth regulators. The ROS scavenging by antioxidants, osmoregulation, maintenance of membrane integrity, production of stress-related proteins, compatible solutes, and plant growth regulators are also helpful in generating stress tolerance in plants. In addition, exogenous application of compounds that can promote stress tolerance in maize plants could also be manipulated in a particular environment. Molecular and biotechnological strategies should also be taken into deliberation to produce transgenic plants able to tolerate stress conditions.

Table 4.1 Recently mapped major QTLs in maize for abiotic stress resistance

Stress	Trait	QTL	Chromosome number	PVE %	Markers	References
Drought stress	ASI	qtl	1	19.41	S1_176845338 S1_179724425	Trachsel et al. (2016)
	Plant height	qtl	1	21.08	S1_19133052 S1_19791935	
	Senescence	qtl	2	23.65	S2_188900919 S2_192855248	
	ASI	qtl	2	14.77	pza01755.1 pza01336.1	Almeida et al. (2013)
	Grain yield	qtl	5	17.27	pza01680.3-pza02480.1	
	Senescence	qtl	4	15.76	pza03231.1 pza03409.1	Almeida et al. (2014)
	Normalized differential vegetative index	qtl	5	11.25	S5_82956371 S5_64808654	
	Ears per plant	qtl	5	15.73	pza00963.3-phm3512.186	
	ASI	qtl	10	10.67	Bnlg236-umc1038	
	Plant height	qtl	6	10.87	S6_153880358 S6_153267024	Trachsel et al. (2016)
	Ears per plant	qtl	6	17.64	S6_127200702 S6_61815312	
	Grain yield	qtl	7	17.75	pza03166.1-pza02449.13	Almeida et al. (2013)
	ASI	qtl	9	10.23	pza01096.1-phm4905.6	
Salt stress	Shoot fresh weight	qSFW1s	1	16.7	umc1709-umc1486	Hoque et al. (2015a, b)
	Root fresh weight	qRFW1s	1	15.8	umc1709-umc1486	
	Plant fresh weight	qPFW1s	1	19.2	umc1709-umc1486	
	Root dry weight	qRDW1s	1	16.7	umc1709–1486	
	Root length	qRL2s	2	21.9	umc2403-umc1026	
Heat	Heat susceptibility index for dry grain yield	QHSI: DYa	2	12	SYN22717	Frey et al. (2016)

(continued)

Table 4.1 (continued)

Stress	Trait	QTL	Chromosome number	PVE %	Markers	References
	Quantum efficiency of PSII	qtl	1	10	PZE-101084685	Revilla et al. (2016)
	Days to emergence	qtl	3	11	PUT-163a-78121249-4393	
Cold stress	Vigor	qtl	4	37.8	S_177665741	Allam et al. (2016)
	No. of kernel rows per ear	qtl	5	26.5	S_169975064	
	100 kernel weight	qtl	5	21.2	S_183693045	
	No. of leaves per plant	qtl	6	19.4	S_149209155	
	Plant height	qtl	8	18.2	S_130408047	
	Ear height	qtl	8	43.3	S_132879659	
	Early vigor	qtl	5	14	PZE-105041551	Revilla et al. (2016)

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5

Sorghum: Role and Responses Under Abiotic Stress

Aisha Kamal and Farhan Ahmad

Abstract

Sorghum is an important staple crop that can also be used as an alternative source of energy, human food, animal feed, and other industrial purposes throughout the world. Despite the fact that sorghum is a tolerant crop, extreme environmental conditions and poor agriculture systems reduced the nutritional quality and productivity of the crop. Understanding the effects of stress and plant response is essential for developing more stress-tolerant plants with higher quality. As sorghum has a small genome size, this makes it a model species for genetic and genomic studies to develop tolerant species. In this chapter, we will discuss the use of marker-assisted breeding and other advanced molecular studies to improve sorghum tolerance to drought, salinity, cold, heavy metal stress, etc. The negative impact of abiotic stress on sorghum growth and development, such as osmotic potential, which impedes germination and embryonic structures, and photosynthetic rates, manifested in the form of significant reductions in grain yield and quality will also be discussed.

Keywords

Abiotic stress · Osmoprotectant · Molecular marker

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5.1 Introduction

Sorghum is an important staple crop in the Poaceae family that is widely grown in arid and semi-arid regions of Africa, Asia, and America, including Mexico, Australia, and South Africa (Prasad et al. 2021). It has been ranked as the fifth most important multidimensional crop because it provides several economic benefits such as food, feed, fodder, fibre, fuel (biofuel), and biofertilizers (Tari et al. 2013). In this shifting scenario, the world's population is expected to be 8.7–11.3 billion by 2050, and in order to provide adequate food to this growing population, total global agriculture production must be increased by roughly 60% over current levels (Silva 2018). Sorghum was grown on 43.74 million hectares of land worldwide, yielding 14,198 Hg ha (FAOSTAT 2019). Because sorghum was a major food crop in the European Union and the United States, and it is also used as a fuel in arid areas such as Nigeria, India, Australia, and Mexico, these countries produce the most sorghum, with an average of around 50 megatons per year (Reddy 2019; FAOSTAT 2019) (Fig. 5.1). Sorghum, a C4 plant, has excellent photosynthetic efficiency and is notable for its ability to grow in extreme climate (temperate) conditions due to its unique morphological, anatomical characteristics (thick leaf wax, deep root system) and physiological responses (osmotic adjustment, stay green, quiescence) (Fracasso et al. 2016; Perrier et al. 2017). Although sorghum is a drought-resistant plant, abiotic stresses have proven to be major crop yield-limiting factors by altering biochemical and molecular pathways (Chakrabarti et al. 2020). Crop modeling studies predicted that salinity, severe drought, extreme temperature fluctuations, floods, radiations, and other environmental stresses would hurt crop production and yields (Yang et al. 2020; Abreha et al. 2022; Afzal et al. 2022).

To overcome the negative impact of abiotic stress, various strategies such as hormonal crosstalk regulation, molecular breeding, and molecular and transcriptomic analysis have been used to improve tolerance in sorghum plants (Tawfik and El-Mouhamady 2019; Hossain et al. 2021). Because of the high genetic variability among sorghum genotypes and the small size of its genome, this cereal is

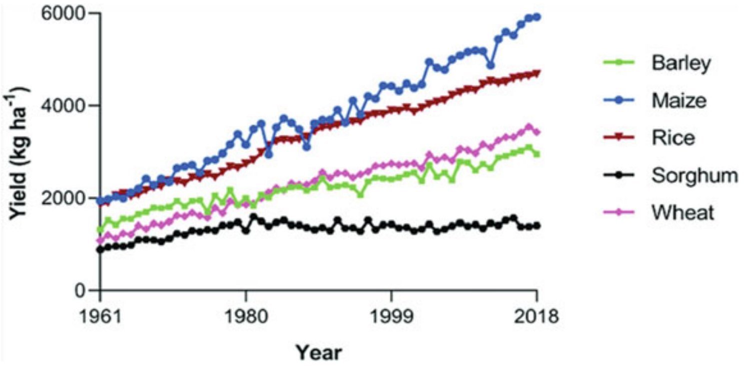

Fig. 5.1 Yield increasing trends of some important crop. (Data obtained from FAO 2019)

an excellent model for identifying drought-related genomic areas and genes that can aid in unravelling the high complexity of tolerance features (Johnson et al. 2014). Recently, it was found that the application of marker-assisted breeding includes several quantitative trait loci (QTL) along with numerous nutrient transporter such as nitrate transporter (NRT), phosphate transporter (PHT), and sulphate transporter (SULTR) were identified to improve tolerance against abiotic stress (Maharajan et al. 2021). Microarray-coupled ontological analyses of 2043 specific transcript were found responsible for transcriptional factor (MYB78 and ATAF1), unique heat shock proteins (HSPs), and polyamine biosynthesis that provide tolerance against combined heat and drought stress (Johnson et al. 2014). Furthermore, plant breeders are primarily concerned with improving quantitative traits that have a high economic cost, such as high yield, resistance to various diseases, tolerance for high salinity, and resistance to water stress. In this study, we will highlight the most recent research on how sorghum plants respond to nutrient deficiency, heavy metal, drought, high salinity, waterlogging, and temperature stress.

5.2 Nutritional Importance of Sorghum

Sorghum has piqued the interest of the food and drug industries for decades due to its superior agronomic properties and health potential. With a growing consumer preference for healthy and plant-based foods, sorghum has enormous potential for producing functional foods as well as other food additives (Xiong et al. 2019). Sorghum grain is gluten-free and a good source of minerals and contains a wide range of bioactive phenolic compounds (de Morais Cardoso et al. 2017). Sorghum's distinct phenolic profile confers a variety of human health benefits, including oxidative stress reduction and cancer prevention (Shen et al. 2018). Sorghum grain is primarily made up of the bran layer (pericarp and testa), endosperm, and germ parts, with some varieties having pigmented testa in between the pericarp and testa. Starch, protein and vitamins, and minerals are the main components of endosperm, while germ parts constitute fat-soluble vitamins, lipids and protein (Yang et al. 2009). Protein is the second important component found in the sorghum and is affected by both genetic and environmental factors (Gerrano et al. 2016) followed by a reduction in amino acid content (threonine and lysine) and total sulphur amount (Virupaksha and Sastry 1968). The quality of proteins found in sorghum is poor as compared to wheat and rice due to the increased contents of tannin and leucine (Kulamarva et al. 2009), and hence it would be beneficial to incorporate other cereal or legume flour to enrich its nutritional quality. Sorghum has high-fat content (3%) than wheat or rice. It is also rich in vitamin B complex and fat-soluble vitamins (D, E, K) but deficient in vitamin C and A (Kulamarva et al. 2009). Because sorghum proteins (kafirins) have high degrees of polymerization and extensive disulphide bridges that are resistant to enzymatic digestion in the digestive tract, sorghum is a promising food source for people suffering from obesity and diabetes (Da Silva et al. 2011). Apart from these advantages, kafirins are used in the food industry in baking and edible-coating microparticles as nutraceutical and drug carriers (Raza et al.

2017). Sorghum grain lipid is primarily made up of unsaturated fatty acids, with polyunsaturated fatty acids being the most abundant.

The phenylpropanoid pathway produces phenolic acids, flavonoids, condensed tannins, stilbenes, and lignins bioactive compounds in sorghum. The leading cause of chronic diseases is oxidative stress, which is caused by an imbalance of free radicals and antioxidants (Shahidi and Ambigaipalan 2015). The antioxidant activity of sorghum phenolic compounds appears to play an important role in the health promotion and disease prevention benefits of sorghum consumption. Aside from direct antioxidant effects, sorghum phenolic compounds have been shown to induce endogenous detoxifying enzymes (phase II enzymes) that are responsible for converting harmful reactive oxygen or nitrogen species into nontoxic compounds, thereby indirectly improving the body's defence against oxidative stress (Svensson et al. 2010). 3-Deoxyanthocyanidins have gotten the greatest attention among the phenolic compounds found in sorghum. Both 3-deoxyanthocyanidins and 3-deoxyanthocyanidin-rich sorghum extract have been shown to inhibit the growth of cancer cells, including colon, hepatoma, esophageal, intestinal epithelial, leukaemia, breast, and stomach cancer cells. These compounds work directly against cancer by inducing cell apoptosis and inhibiting cancer cell proliferation and metastasis, hence showing anticancerous property (Punia et al. 2021). Sorghum has been shown in extensive research to have potential antioxidant, anti-inflammatory, and anticancer activities, as well as the ability to improve glycemic response and insulin-related disorders, prevent dyslipidemia and cardiovascular diseases, influence gut microbiota, and promote colonic health (Burdette et al. 2010; Khayal et al. 2019) (Table 5.1).

Table 5.1 Nutritional value in sorghum

Nutritional components	Content (per 100 g[a])
Carbohydrate	67.68 ± 1.03 g
Protein	9.97 ± 0.43 g
Fat	1.73 ± 0.31 g
Mineral	1.39 ± 0.34 g
Fibre	10.22 ± 0.49 g
Thiamine (B1)	0.35 ± 0.039 g
Riboflavin (B2)	0.14 ± 0.014 g
Niacin (B3)	2.10 ± 0.09 g
Pantothenic acid (B5)	0.27 ± 0.02 g
Total B6	0.28 ± 0.023 g
Biotin (B7)	0.70 ± 0.06 g
Total folates (B9)	39.42 ± 3.13 g
Ergocalciferol (D2)	3.96 ± 0.30 g
Tocopherols	0.04 ± 0.01 g
Phylloquinones	43.82 ± 4.84 g

Source: Indian Food Composition Tables, NIN – 2017 and [a]Nutritive value of Indian foods, NIN – 2007

5.3 Sorghum Response Towards Abiotic Stress

Abiotic stresses limit crop plant development and productivity to varying degrees, depending on the stress's onset, duration, and intensity. It was estimated that only 25% of potential yield is attained due to the negative influence of abiotic stress caused by the environment (Yada et al. 2020). In the twentieth century, crop production was increased by implementing new breeding technologies and biotechnology approaches, and this effort was managed to maintain the needs of the world's growing population. However, rather than focusing on disease resistance, all of these techniques were aimed at increasing yield potential or disease resistance in critical crops such as rice and wheat. Abiotic stress resistance mechanisms are poorly understood, which may explain why progress in abiotic stress breeding has been slow. However, considering the current climatic conditions, there is an urgent need to adapt and expand the physiological trait-based molecular breeding approach for developing abiotic stress-tolerant crops (Ahmar et al. 2020). The selection for secondary traits associated with higher yield under optimal and/or abiotic stress environments is referred to as physiological breeding, also known as analytical breeding (Tong and Nikoloski 2021).

5.3.1 Drought Stress and Tolerance Mechanism of Sorghum

Drought stress, which refers to a lack of water in the root zone and reduces agricultural output, is one of the most serious stresses. In the field, water scarcity may impede embryo growth and seed germination, which can be alleviated by implementing two strategies: the first is to reduce water potential, and the second is to avoid water stress caused by deep and broad root production (Akman et al. 2021). Drought tolerance characteristics can be constitutive (intrinsically expressed qualities) or adaptive (traits that express in response to stress). Drought tolerance mechanisms in sorghum are attributed to morpho-physiological factors, with stay-green traits such as a deep rooting system, improved water utilisation efficiency (WUE), C4 photosynthesis, ability to maintain homeostasis, and high epicuticular wax (EW) regime (Yigit et al. 2016; Tiwari et al. 2021). Both transpiration rate and stomatal conductance will decrease under drought conditions (Yuping et al. 2017). It was discovered that *Sorghum cv. gadambalia* has excellent soil water extraction efficiency, fewer nodal roots per plant, and fewer metaxylem vessels in nodal roots. Other characteristics of the plants include a smaller leaf area and well-developed sclerenchyma in leaf tissues (Salih et al. 1991). A hybrid sweet sorghum variety (BJ0601) has significantly lower water capacity and net photosynthetic rate under extreme water stress, which is strongly related to stomatal conductance. Drought stress increases light compensation point while decreasing light saturation, apparent quantum yield, and dark respiration (Xie et al. 2010).

5.3.2 Effect of Developmental Stages in Drought Tolerance

Sorghum's developmental stages are also important for drought sensitivity. During the early reproductive and vegetative phases, the plant is highly susceptible to dryness; however, the plant's water demand decreases during the late reproductive phase. Depending on whether the stress occurs during the vegetative or reproductive stages, stress reactions are classified as pre-flowering or post-flowering (Emendack et al. 2014). Stress responses vary depending on whether the stimulus occurs during the vegetative or reproductive stages. These two reactions appear to be controlled by separate genetic pathways. Pre-flowering stress reduces biomass, panicle size, grain number, and grain yield (Sanchez et al. 2002), whereas postanthesis drought causes premature leaf and stem senescence, lodging, and reduced seed size, as well as increased susceptibility to biotic stresses like charcoal rot (*Macrophomina phaseolina* (Tassi) Goidanich) and fusarium stalk rot (*Fusarium moniliforme*) (Borrell et al. 2000). It was also reported that in severely drought-stressed sorghum plants RUBISCO, phosphoenolpyruvate carboxylase (PEPcase) and sucrose-phosphate synthatase (SPS) (an enzyme active in source-sink loading) were significantly deactivated, resulting in a decrease in photochemical efficiency of photosystem II (Feller 2016: Ndlovu et al. 2021).

Six distinct genomic regions for early drought tolerance were identified in a sorghum recombinant inbred line (RIL) derived from a cross between Tx7078 (pre-flowering-tolerant, post-flowering-susceptible) and B35 (pre-flowering-tolerant, post-flowering-susceptible) genotypes. Kebede et al. (2001) identified four quantitative trait loci (QTL) associated with pre-flowering drought tolerance in sorghum from RILs derived from the cross, SC 56 and Tx 7000. Sorghum's post-flowering drought tolerance is linked to the stay-green features. The term "stay green" refers to the retaining of green leaf area after maturity (GLAM). Sustaining the stay-green characteristic throughout the grain-filling stage is a key component of drought resistance under soil moisture-deficit stress conditions (Blum 2005). B35 (BTx 642), SC 56, E36-1, and KS19 are three major stay green sorghum sources, with B 35 and KS 19 being two of the most widely utilized (Haussmann et al. 2002). Borrell et al. (2000) found that B 35-derived lines had a larger leaf area at flowering and a normal rate of leaf development, whereas KS 19-derived lines have a smaller leaf area at flowering and a slower rate of senescence.

5.3.3 Qualitative Trait Mapping (QTL) for Drought Resistance

B35 or B35 derivatives are frequently used to map the QTL contributing to the stay-green traits (Tuinstra et al. 1997; Crasta et al. 1999; Xu et al. 2000; Subudhi et al. 2000; Tao et al. 2000). These studies identified four major QTL (Stg1, Stg2, Stg3, and Stg4). QTL Stg1 and Stg2 are located on LG-03, Stg3 on LG-02, and Stg4 on LG-05, respectively, and account for 20, 30, 16, and 10% of the phenotypic variance (Sanchez et al. 2002; Xu et al. 2000) (Table 5.2).

Table 5.2 Studies related to the identification of QTL for the stay-green trait in sorghum

Stay-green parent	Non-stay-green parent	Population	Markers used	References
B35	Tx 7078	RIL	RAPD	Tuinstra et al. (1996)
			RFLP	
B35	Tx 430	RIL	RFLP	Crasta et al. (1999)
B35	Tx 7000	RIL	RAPD	Xu et al. (2000)
			RFLP	
B35	Tx 7000	RIL	RFLP	Subudhi et al. (2000)
			SSR	
QL41	QL39	RIL	RFLP	Tao et al. (2000)
SC56	Tx 7000	RIL	RFLP	Kebede et al. (2001)
E36-1	IS9830 N13	RIL	AFLP	Haussmann et al. (2002)
			RAPD	
			RFLPSSR	

5.3.4 Role of Epicuticular Wax in Drought Tolerance

Epicuticular wax (EW) is thought to have potentially beneficial properties related to stress resistance such as salinity, drought, and disease (Ahmad et al. 2020). A variety of factors influence wax secretion and deposition, including species, organ, developmental stage, and environmental conditions. Although its content and structure vary greatly, EW is mostly hydrophobic (Dalal et al. 2012). Sorghum is unique among cereal crops in that it produces a large amount of epicuticular wax on its abaxial leaf blade and sheath, especially during the early reproductive period. The highest concentration of free fatty acids is found in sorghum wax (16–33 carbons). C28 and C30 make up 78% and 20% of the components, respectively (Jenks et al. 2000). In the BLOOM-CUTICLE (BLMC) region of sorghum, an acylCoA oxidase (a gene involved in lipid and wax production) and seven additional potential transcripts were discovered (Burow et al. 2009). This massive epicuticular wax aids in reducing non-stomatal water loss from plants and improving sorghum water use efficiency by regulating night-time water loss (Burow et al. 2008).

5.3.5 Osmotic Adjustment and Antioxidant Capacity

Drought resistance/tolerance in plants is strongly linked to two characteristics: osmotic adjustment (OA) and antioxidant capacity. The net accumulation of osmolytes such as amino acids (e.g. proline), sugars (e.g. sucrose and fructans), polyols (e.g. mannitol and pinitol), quaternary amines (e.g. glycine betaine), ions (e.g. potassium), and organic acid response to water deficits causes osmotic adjustment, which is an inherited trait (Ahmad and Kamal 2021). In sorghum, osmatic adjustments are controlled by two different main genes (OA1 and OA2), with some minor effects (Basnayake et al. 1995). Glycine-betaine (GB) is a well-known osmoprotectant that plays a role in abiotic stress tolerance. In sorghum, water scarcity was shown to increase the expression of two betaine aldehyde dehydrogenase-expressing genes, BADH1 and BADH15, and this increased expression correlated with GB deposition (Wood et al. 1996). Proline is a compatible osmolyte that builds up during abiotic stresses. P5CS (EC 2.7.2.11), also known as D1-pyrroline-5-carboxylate synthetase, is a key regulator of proline biosynthesis. SbP5CS1 and SbP5CS2, two closely related P5CS genes found on chromosomes 3 and 9, respectively, were isolated from sweet sorghum. When plants were exposed to water-limiting conditions, these genes were found to be upregulated (Su et al. 2011).

More than 28,000 unique genes in sorghum root and shoot tissues were discovered to have transcriptional activities during osmotic stress or ABA treatment. The top five genes upregulated in response to both PEG and ABA were genes coding for late embryogenesis abundant (LEA) proteins; WSI18, a water stress-induced protein; and dehydrins (Dugas et al. 2011). In a recent study, 180 genes were discovered that were differentially regulated in response to drought stress in drought-resistant genotypes; of these, around 70% were upregulated, and 70 were novel genes with unknown functions. A set of drought-regulated genes, including many genes encoding uncharacterized proteins that are associated with drought tolerance at the seedling stage, were also recognized (Abdel-Ghany et al. 2020). Other osmoprotectants such as sugars, K^+ Cl^-, and P were also reported to contribute to osmotic adjustment in sorghum (Wood et al. 1996). Due to methodological constraints, phenotyping for OA trait is difficult; therefore mapping of OA QTL for different osmoprotectants will be for improving osmoprotection in sorghum.

5.4 Waterlogging and Tolerance Mechanism of Sorghum

Heavy rainfall in tropical and subtropical climates, as well as excessive irrigation, can cause crop waterlogging, which has a variety of negative consequences. Waterlogging alters the texture of the soil and causes plant metabolism to be disrupted. Plants with waterlogged leaves produce less biomass, have smaller leaves, and have lower photosynthetic rates, stomatal conductance, and transpiration rates. The age of the seedling determines the severity of the negative effects. Sorghum is more susceptible to flooding during the early vegetative and reproductive stages, but it responds quickly during the grain-filling stage (Promkhambut et al. 2011a, b; Kadam et al. 2017). Although there are genetic differences, flooding for 30 days after it appears has little effect on shoot growth. In root response to waterlogging, several genotypes respond to the development of the root at the base of the stem in submerged soil (Promkhambut et al. 2011b). Sorghum's adaptive response to waterlogging appears to be the formation of additional node roots ((Promkhambut et al. 2011a, b; Hulugalle et al. 2015). The activities of alcohol dehydrogenase (EC 1.1.1.1) and lactate dehydrogenase (EC 1.1.1.27) in the roots of a flood-tolerant sorghum cv. SSG-59-3 are constantly increasing. It also had a higher ethanol content than the sensitive variety S-308, indicating that the flood-tolerant variety has a greater capacity for different fermentative pathways as an alternative means of maintaining ATP synthesis in flooded conditions (Jain et al. 2010). Kadam et al. (2017) discovered 40 aquaporins (AQP) genes in the genomes of *Sorghum bicolor*, which were phylogenetically classified into four subfamilies. Phylogenetic analysis revealed that homologous pairs of AQP proteins from rice, maize, *Arabidopsis*, and sorghum formed a single class. Transcript abundance of PIP2-6, PIP2-7, TIP2-2, TIP4-4, and TIP5-1 showed a differential pattern between plants treated with waterlogging and control plants in an expression profiling of AQP genes in a tissue-type and sampling time-dependent manner.

5.5 Hot and Cold Stress

The crop, which is native to tropical and subtropical regions, is extremely heat tolerant. As a result, cold temperatures during the early stages of growth harm sorghum output. Low temperatures (below 15 °C) harm seed germination, seedling emergence, and plant development (Chiang et al. 2021). Low temperatures reduced photochemical quenching of chlorophyll fluorescence in sweet sorghum plants, resulting in an accumulation of reactive oxygen species (ROS) that are harmful to photosystem II (PSII) and increase membrane stiffness (Zegada-Lizarazu et al. 2016; Guo et al. 2018). Temperatures below 15 °C reduce gas solubility and slow enzymatic activity (Reddy 2019). The osmotic potential, cell wall, and phloem loading of plant cells were also found to be negatively affected by cold stress.

Despite its tropical origins, sorghum exhibits significant genetic variability in cold tolerance. Burow et al. (2011) identified simple sequence repeat (SSR) molecular markers associated with early-season cold resistance. The mapping population consisted of 171 F7-F8 recombinant inbred lines (RILs) derived from a cross between the cold-sensitive RTX430 and cold-tolerant PI610727 lines. PI610727 is also known as Gaigao Liang, a landrace from Chinese germplasm selected for early-season cold tolerance. It has better seedling emergence and vigour under cold conditions than other sorghum cultivars (Franks et al. 2006). These cultivars lack desirable agronomic characteristics. As a result, attempts are being made to integrate beneficial genes from Chinese landraces into elite lineages using marker-assisted selection. A population derived from a cross between the Chinese landrace ShanQui Red (SQR, cold-tolerant) and SRN39 (cold-sensitive) was used for QTL analysis of early-season cold performance in sorghum (Knoll et al. 2008). In early and late field planting, the QTL on linkage group SBI-01 was found to have a strong relationship with seedling emergence and seedling vigour scores. The three QTL were confirmed in two populations (Knoll and Ejeta 2008). Another study used an association mapping approach to discover six SSR markers, Xtxp34, Xtxp88, and Xtxp319, to be associated with seedling emergence, Xtxp211 and Xtxp304 with seedling dry weight, and Xtxp20 with seedling height, to be associated with early-season cold resistance features (Maulana et al. 2017). Multiple chilling tolerance QTL were discovered to be associated with conventional genes for grain tannins (Tan1 and Tan2) and plant height (Dw1 and Dw3), implying that chilling tolerance loci are likely to be associated with these agronomically significant genes and may be useful in improving early season performance of sorghum cultivars using marker-assisted breeding (Marla et al. 2019). The frequency and intensity of extreme heat events are expected to increase in the coming decades due to a variety of environmental factors. The likelihood of yield loss due to high temperature effects will undoubtedly increase over time. High temperatures influenced both vegetative and reproductive growth in sorghum genotypes. It accelerated the rate of development (i.e. the time it took to flower), increased the number of leaves and the rate at which they appeared, but decreased plant height, pollen viability, and seed set (Hammer et al. 2015).

Heat stress reduces sorghum biomass and sugar production by affecting photosynthetic activity, light reactions, and the activity of Calvin cycle enzymes (Yan et al. 2012). High nighttime and daytime temperatures were found to have a negative impact on plant photosynthetic activity. According to reports, hydrogen peroxide flux detected in sorghum leaf tissues exposed to temperatures of 40 °C during the day and 30 °C at night is a sign of the onset of oxidative stress during high temperatures (Mohammed and Tarpley 2010). Plants exposed to high temperatures undergo from thylakoid membrane damage, non-photochemical quenching, and decreased chlorophyll concentration, resulting in increased oxidative stress in the leaves and pollen grains and fewer seed sets (Prasad and Djanaguiraman 2011).

5.6 Salt Stress

Salt is a major biological stressor that affects crop yield and quality. Soil salinity is an issue in both irrigated and dry areas, with irrigation increasing salt content due to poor water quality, poor drainage, and seawater input in coastal areas. High evaporation in dry and semi-arid areas and higher accumulation of salt resulted in ion leaching causes water scarcity near root area of plants (Shabani et al. 2015). Although sorghum is a salt-tolerant crop, genotypic differences exist between cultivars. Plants resist salinity through three mechanisms: (a) exclusion of Na^+ from the cytoplasm due to poor absorption or active ion pumping, (b) sequestration of Na^+ within the vacuole, and (c) preferential accumulation in leaf tissues. However, the genotypes that can sequester Na^+ in leaf cell vacuoles are limited, which affects nutritional value, The yield of salt-sensitive sweet sorghum was found to be significantly reduced by salt stress. Sorghum plants exposed to high levels of salt had lower germination rates and longer germination times (Patanè et al. 2013). There was a significant decrease in net photosynthetic rate, PSII photochemical efficiency, stomatal conductance, and intercellular CO_2 concentration in salt sensitive sweet sorghum species (Sui et al. 2015). The accumulation of harmful ions (Na^+ and Cl^-) slows ion absorption. Salt-tolerant genotypes have excellent K^+/Na^+ discrimination, and tissues with a low Na^+/K^+ ratio are more salt-tolerant (Hasegawa et al. 2000). The salt-tolerant sorghum genotype accumulated less Na^+ in root and shoot tissues than the salt-sensitive genotypes, resulting in a lower Na^+/K^+ ratio (Bavei et al. 2011a). The salt-tolerant genotype has more Ca^{2+} buildup in the leaf and root tissues than the sensitive types (Kimia and Payam), which promotes increased growth and lower sodium absorption (Bavei et al. 2011b). Although sorghum is a more salt-tolerant crop than wheat and maize, the complex genetic mechanism is a major barrier to improving salt tolerance. In a diallel analysis of relative root length in salt-treated and control plants, NaCl has both additive and dominance effects in sorghum (Azhar and McNeilly 1988). Salt stress affects plant chlorophyll concentration and photosynthetic efficiency in both direct and indirect ways. Controlling the levels of activity and expression of enzymes involved in chlorophyll production and photosynthesis has immediate consequences. The indirect effects are achieved through specific regulatory pathways, such as antioxidant enzyme systems. The maximum quantum yield of photosystem II (PSII; Fv/Fm), photochemical quenching coefficient (qP), and electron transport rate (ETR) in sorghum decreased significantly under saline conditions, whereas non-photochemical quenching (qN) increased (Netondo et al. 2004). Swami et al. (2011) discovered that after 96 h of exposure to 200 mM NaCl, the abundance of the ATP synthase a-subunit protein increased in sorghum leaves, indicating that salt stress affected the photosynthetic machinery. Eight of the upregulated proteins were also found to be involved in the detoxification of reactive electrophilic chemicals or the scavenging of ROS (peroxidase (POX) and ascorbate peroxidase (APX)). Other proteins that could be involved in Na^+-induced signalling include lectin-like protein kinase, salt-inducible protein kinase, and serine/threonine-protein kinase. This demonstrates that ammonia absorption is an important mechanism in sorghum grown in high salinity. Sweet sorghum's NADP-malate dehydrogenase (NADP-ME) enzyme has recently been linked to salt tolerance. Salt stress and Sb-activated NADP-ME overexpression in M-81E sweet sorghum, as well as NADP-ME, increased *Arabidopsis* photosynthetic capacity (Guo et al. 2018). Increased NADP-ME levels may result in higher levels of CO_2 and pyruvate, improving CO_2 fixation efficiency. NADPH can also contribute energy to the metabolism of reactive oxygen species (ROS) (Mittler 2002).

5.7 Heavy Metal Stress

Heavy metals (HMs) accumulate in agricultural soils as a result of sewage sludge application, phosphatic fertilizer use, industrial wastes, and improper agricultural watering applications (Radočaj et al. 2020). Heavy metal accumulation causes an increase in the production of reactive oxygen species (ROS), which impede biochemical and physiological processes, denature nucleic acids, inactivate enzymes, and ultimately lead to oxidative stress and cell death (Štolfa et al. 2015; Ahmad et al. 2019). Sorghum, like other plant species, can accumulate large amounts of HMs and thus could be considered a hyperaccumulator. Because it is a metal-tolerant, high-biomass-producing energy crop, it can be used for phytoremediation (Mishra et al. 2021). However, high HMs concentrations reduce plant height, root hair density, shoot biomass, leaf number, chlorophyll, carotenoid, and carbohydrate content. In sorghum, combined exposure to arsenic, nickel, cadmium, lead, and copper reduced morpho-physiological parameters such as total plant biomass, leaf water potential, chloroplast structure alteration, and peroxidation in chloroplast membranes due to ROS generation (Gill et al. 2012; Pandian et al. 2020). When exposed to heavy metal toxicity, sorghum exhibits highly regulated coordination of antioxidant enzyme. Furthermore, increased levels of SOD and CAT may be associated with the production of other active oxygen species or overexpression of SOD encoding genes, as well as a higher H_2O_2 content. GSH levels are kept stable by increased GSH and GR activity. In HMs-treated plants, increased GR activity increases the availability of NADP+, which receives electrons from the electron transport chain, for the smooth operation of biochemical reactions at the cellular level (Sofo et al. 2005; Jawad Hassan et al. 2020). Interestingly, tissue-specific antioxidant changes were also reported, where POX and GST activity increased in shoots but not in roots of sorghum plants when exposed to zinc and cadmium stress (Soudek et al. 2014). The accumulation of appropriate soluble solutes, such as proline, proteins, and increased MDA content, will aid osmoregulation during the adaptation response and allow the plants to tolerate stress (Parida and Das 2005; Ahmad et al. 2020). Even under high-stress conditions, protein content was found to be increased in a dose-dependent manner, indicating that sorghum could withstand a certain level of HM stress (Emamverdian et al. 2015). These changes in protein content in response to abiotic stress could be exploited as possible biomarkers for determining the key processes involved in plant stress responses.

A total of 33 differentially expressed protein spots were analysed using MALDI-TOF/TOF MS cadmium exposed sorghum plant to understand the underlying mechanism of integrated molecular and proteomic studies coupled with two-dimensional gel electrophoresis (Roy et al. 2016). Proteomic analysis revealed Cd-dependent changes in metabolic pathways, as well as translational and transcriptional regulation-related proteins. Cd stress inhibits carbon fixation in general, lowers ATP production, and regulates protein synthesis, according to these findings. Furthermore, it is intriguing to investigate the role of GST enzymes in C4 plant cell Cd toxicity responses. Previous studies on sorghum have primarily focused on its chemical composition, nutritional and medicinal value, response to salinity and drought stress, and the effect of metal distribution and accumulation on photosynthetic efficiency. There is little known about the underlying mechanism of sorghum heavy metal tolerance. Despite this, the availability of the sorghum's complete genome sequence makes it a viable C4 model plant that could be used in conjunction with the C3 plant models *Arabidopsis* and rice to investigate the gene products involved in heavy metal stress adaptation. Proteomics approaches provide high-throughput and large-scale methods for investigating proteins in a specific organism, tissue, or cell at any given time.

5.8 Conclusion and Future Perspective

One of the most difficult issues in agriculture is addressing current and future food security. Environmental stressors, on the other hand, are a major roadblock to achieving this goal. Sorghum is resistant to a variety of abiotic stressors due to its extensive secondary root system, ability to halt development in water-stressed conditions, and accumulation of epicuticular waxes. Sorghum is ready to design a future with its complete genome sequence, vast resources and variety of germplasm, high-density linkage maps, marker-aided drought and heat tolerance, and promise as a bioenergy crop. The sorghum whole genome sequence, in conjunction with the study of abiotic stress-induced transcriptomes, proteomes, and metabolomes, provides an excellent tool for breeders looking to improve the stress tolerance of this critical energy crop. Many useful traits of sorghum's wild progenitors may be discovered and used to increase crop yield. However, the use of these critical traits in crop development is still hampered due to a lack of genetic information on these wild sorghum species and need extensive research.

Conflict of Interest All the authors contributed equally and declared that there are no conflicts of interest.

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Rice: Role and Responses Under Abiotic Stress

6

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Abstract

The effects of abiotic stresses in rice cultivations are drastic and significantly hamper global production. Continued changing environments are accelerating and enhancing the deleterious effects on rice, a staple food crop in many Asian countries. Different biochemical and physiological processes of the rice plants are severely affected due to stresses and, thereby, is threatening the growth, yields, and production. Therefore, it is essential to explore the mechanisms of morphophysiological and biochemical responses of rice plants against different abiotic stresses. With this view, we highlighted and discussed the responses of rice against major abiotic stresses, namely, salinity, ozone, drought, and submergence, in this chapter. These pieces of information can be helpful to figure out the possible mechanisms to minimize the harmful effects of different abiotic stresses on rice, which will ultimately ensure food security.

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Keywords

Rice · Abiotic stresses · Morphophysiological response · Biochemical response · Food security

6.1 Introduction

Rice (*Oryza sativa* L.) belongs to the grass family Gramineae. It is considered one of the most significant cereal foods from an agronomic standpoint, and it serves as a staple food for about half of the world's population (Vetriventhan et al. 2020). Rice is one of the oldest cultivated crops which has been cultivated in India and China for several thousands of years (Talhelm and English 2020). It is a self-pollinating diploid species ($n = 12$) that is categorized in the genus *Oryza* and is a member of the grass family (Poaceae). There are two varieties of farmed rice accessible globally: *Oryza sativa*, which is cultivated and popular in Asia and is referred to as Asian rice, and *Oryza glaberrima*, which is grown in some regions of Africa and is referred to as African rice. *Oryza* has numerous wild relatives, the most notable of which are *Oryza rufipogon*, *Oryza nivara*, and *Oryza barthii* (GRiSP 2013). Rice is one of the most harvested crops (around 162 million ha) and production reached 755 million tons, which is the fourth highest after sugarcane, maize, and wheat (FAOSTAT 2019). Approximately 90% of global rice is grown in China, India, Japan, Korea, Bangladesh, Southeast Asia, and other neighboring regions (USDA 2021). China is the largest rice-producing country, followed by India (2nd) and Bangladesh (4th), and curiously, these three countries, along with Pakistan, generated more than half (about 60%) of world rice production (Fig. 6.1) (FAOSTAT 2019). Rice is accounting for more than 21% of human caloric needs and up to 76% of Southeast Asian caloric intake (Fitzgerald et al. 2009). The world's population is increasing day by day, anticipated to hit 9.1 billion by 2050, but agricultural productivity is declining due to a shortage of agricultural land. Towards zero hunger, worldwide agricultural production needs to be raised by 60–110%, with an extra 2.3 billion people requiring 70% more food by 2050 (FAO 2009).

Abiotic stresses caused by adverse climatic conditions are among the most significant causes contributing to the reduction in agricultural production worldwide. Salinity, ozone, drought, submergence, cold, heat, and nutritional shortage are all important limiting variables in rice production (Padgham 2009). Worldwide land area is affected by different abiotic stresses; drought has affected 64% of the area, submergence (13%), salt (6%), mineral deficiency (9%), and low temperature (57%) (Cramer et al. 2011; Rasheed et al. 2020). It is estimated that salt-affected soils impacted half of the total irrigated global land costing approximately 27.3 billion US dollars (Qadir et al. 2014). The time and progression of stress, different periods of plant development, and biotic and abiotic factors can affect the response to stress conditions (Feller and Vaseva 2014). These environmental difficulties which impacted plant development and production have led to a wide spectrum of responses, including morpho-physiological, biochemical, and molecular alterations

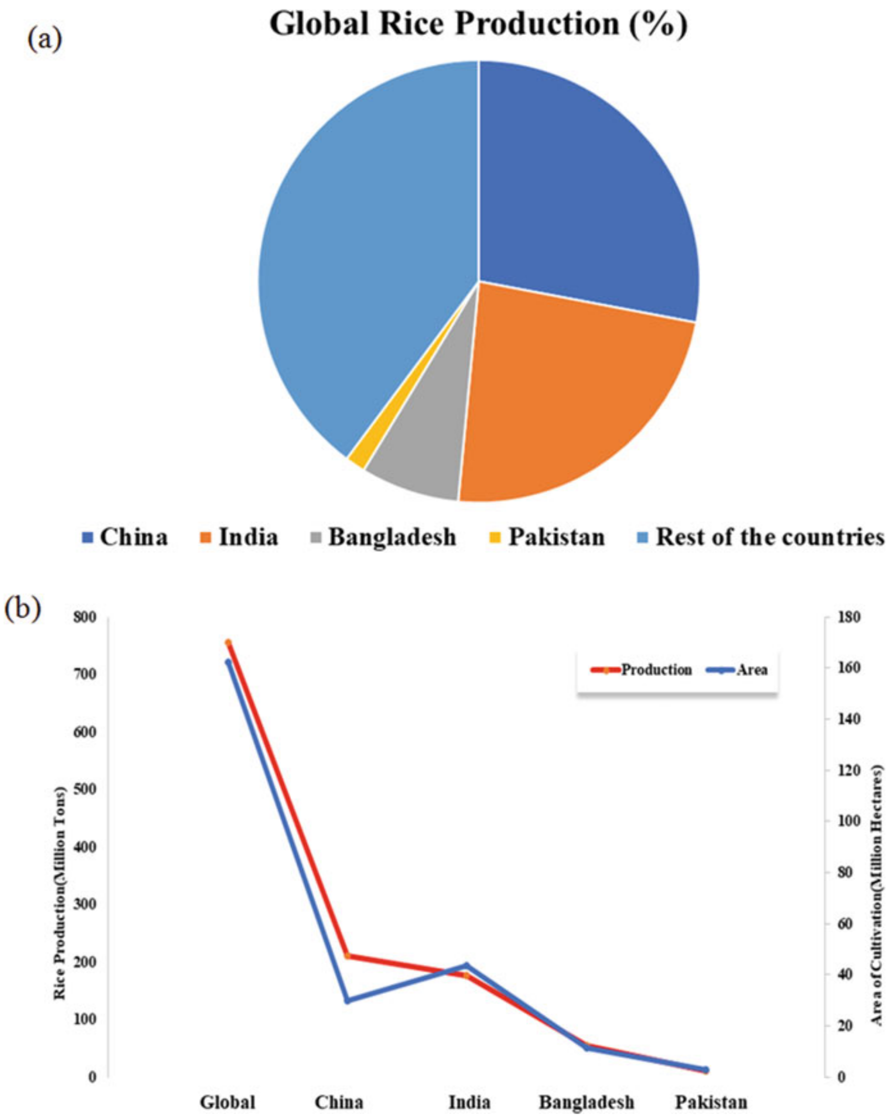


Fig. 6.1 Rice production and cultivation situation of global and major Asian countries. (**a**) Chart indicating rice production percentage of Asian major countries relative to global production. (**b**) Plot area displays rice cultivated area (million hectares) and production (million tons) (FAOSTAT 2019)

(Cvikrová et al. 2013). The time and progression of stress, different periods of plant development, and biotic and abiotic factors can affect the response to stress conditions (Feller and Vaseva 2014).

Plants use different approaches to deal with and respond to stress conditions. These rely on changes in protein levels, either by enhancing or decreasing protein abundance, leading to changes in the proteome, transcriptome, and metabolome levels as a whole (Bohnert et al. 2006; Cho et al. 2008). Abiotic stress conditions may result in the buildup of reactive oxygen species (ROS), such as H_2O_2, which operate as signal transduction molecules, but they may also result in severe cellular damage and photosynthesis suppression (Baxter et al. 2014). Phytohormones are also responsible for plants' complex stress-adaptive signaling cascades in different abiotic stresses (Muñoz-Espinoza et al. 2015). Precisely, the plant hormone abscisic acid (ABA) acts as a crucial regulator in the activation of plant cellular adaptation to salt and drought stress (Danquah et al. 2014). Therefore, this chapter will highlight the different abiotic stresses and how rice responds against those stresses.

6.2 Salt Stress in Rice

6.2.1 Overview

Rice (*Oryza sativa* L.) is one of the most salt-sensitive monocots (Wang et al. 2018). The salt concentration in the rhizosphere affects the responsiveness of rice differently from other cereals. A considerable risk to crop production is posed by saline stress, which will affect around 20% of irrigated land by 2050, and the affected area is likely to increase to 50% of irrigated land by that time (Kibria et al. 2017). Rice exhibits high sensitivity during the vegetative and reproductive phases. High salt levels decrease seed germination, plant growth, and agricultural yield. Salts leaching from the soil has a substantial impact on crop yield (Shrivastava and Kumar 2015). Excessive salt stress has several negative consequences in rice plants, including reduced overall CO_2 absorption, leaf development, leaf cell enlargement, accumulation of dry matter, and relative growth, all of which contribute to lower crop yield and biomass production (Chang et al. 2019).

6.2.2 Causes of Salinity

Salinity refers to the accumulation of salts in soil or water. In most cases, sodium chloride is the dominating salt. The degree of salinity observed in irrigated landscapes is known as irrigation salinity. Increased leakage and recharging of the groundwater increase the water table, leading to water salinity (USDA 2021). Due to rising water tables, plant development, and soil structure, salts might penetrate through the plant root zone. Irrigation and inefficient drainage systems are a significant source of excess leakage, increasing the risk of salt and waterlogging in irrigated areas (Okur and Örçen 2020). Farmers need more irrigation water to get the salts out of the plant's root zone when irrigation uses salty water. The use of salty groundwater can lead to the formation of saline solution. Coastal salinity is another source of salinity. Seawater comprises saltwater brought to the surface by high tides, groundwater inflows, and salt-laden aerosol (Salehin et al. 2018).

6.2.3 Effects of Salinity Stress in Rice Crops

Plant production is usually reduced under salinity stress; though, these impacts vary on salt concentration, environmental variability, and plant species (Kordrostami and Rabiei 2019). Rice susceptibility to salinity stress is determined by the time of exposure and salt concentrations encountered (Ma et al. 2018). During the early stages of salt stress, reduced leaf growth and osmotic stress occur in rice. Although ionic stress causes leaf senescence in rice plants over time, it is more visible in younger leaves (Acosta-Motos et al. 2017). Rice productivity is affected by the reducing rate of CO_2 assimilation in the leaf. The accumulation of dry matter impacts leaf development, leaf cell enlargement, relative growth, induced metabolic changes, decreased ability to water uptake, and nutrients' overall decrease in rice growth rate (Hussain et al. 2017). Poor development of rice spikelets reduces rice grain yield. Panicle sterility, particularly during pollination and fertilization, results in a decreased rate of rice grain development (Lv et al. 2020). High salt in the soil reduces rice yield, affecting plant growth, development, and eventually productivity; the susceptibility of rice to salt stress changes throughout its life cycle. The sensitivity is greater at the seedling (2–3 leaves) and reproductive (pollen development and fertilization) phases (Yadav et al. 2011).

6.2.4 Morphophysiological Responses

Rice plants exhibit morphological changes in traits that are thought to be indicated saline stress (Fig. 6.2). Root and shoot length indicate rice plants' responses to salt stress, suggesting a reduction in root, leaf, and yield (Ologundudu et al. 2014).

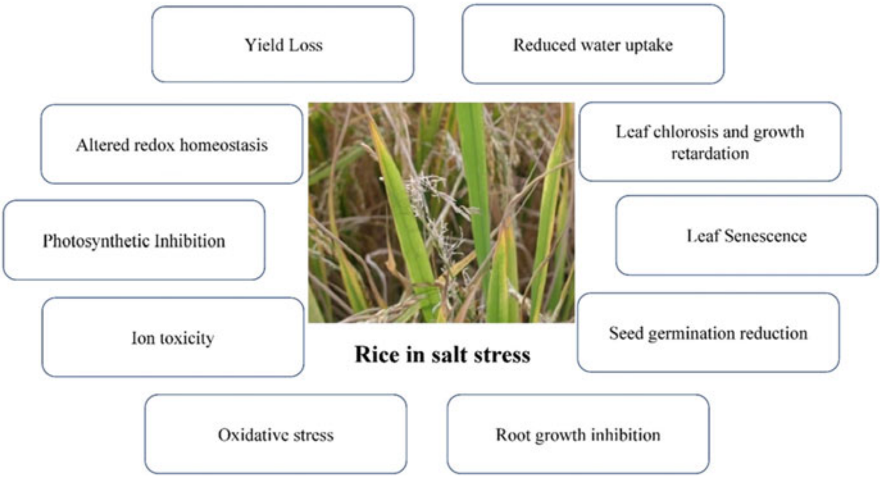


Fig. 6.2 Morphophysiochemical responses of salt stress in rice. (Adapted from Islam et al. 2019 and https://www.plant-phenotyping.org/lw_resource/datapool/_items/item_167/53_singh)

During seed germination, salt stress delays the embryo activation process, which is a complicated phenomenon involving numerous physiological and biochemical variations. In salinity stress, releasing of different hormones solution, α-amylases activity, and K^+ efflux is noticed earlier (Li et al. 2009). It has been experimented to determine the effects of various NaCl (mM) solutions on the seed germination of six distinct kinds of rice genotypes that vary in their salt tolerance. The results from the study have indicated that salt has induced delays in the sprouting of rice seed with a delay of 3–6 days in treatments that include high NaCl (about 200 mM). In a similar kind of study, percentage of delayed germination was adversely impacted by increased salinity from 0 to 150 mM (Shereen et al. 2011; Jamil et al. 2012).

6.2.5 Biochemical Responses

During salt stress, Na^+ and Cl^- plays vital role, and rice plant's growth and development is severely affected due to ion, oxidative, and osmotic stresses (Reddy et al. 2017). Na^+ halts the uptake of Ca^{2+} which induces Ca^{2+} deficiency due to higher Na^+/Ca^{2+} ratios (Gupta and Shaw 2021). Salinity generally changes a broad range of metabolic processes, including ionic content concentration and cellular enzyme activities. Plant cells decrease the growth and elongation of the plants by dehydration and shrinking owing to such changes (Zhao et al. 2021). At low salinity levels, rice plant gets adverse effects because of osmotic stress, nutritional imbalance, and ion toxicity (Ghosh et al. 2016). The accumulation of ions, especially Na^+ and Cl^-, occurs even under mild to severe salinity and nutritional shortage circumstances. As a result, the plant exhibits cyclic morphophysiological and biochemical anomalies because of salinity stress from the advent to maturity phases of development (Riaz et al. 2019). It also decreases photosynthetically active radiation (PAR), degradation of pigment, transpiration rate (Tr), stomatal closure, stomatal conductance (Gs), and relative water content (RWC) (Kole et al. 2015). This stress condition weakens the photochemical efficiency of photosystem I and II in photosynthesis. Chlorophyll and carotenoids content of rice leaves decreased significantly in salt stress (Suriyan et al. 2009). Nutrient imbalance occurs due to the decrease of the N, P, K, Ca, and Mg and it increases Na^+/K^+, Na^+/Ca^{2+}, Ca^{2+}/Mg^{2+}, and Cl^-/NO_3 in plants which also causes stress. When the components (Ca^{2+}, Mn^{2+}, and K^+) are noticed with reduced amounts and uneven ratios in plants, it causes stress due to competition. In several kinds of cereal, including rice, high concentrations of NaCl have lowered the availability of zinc (Zn) and increased cadmium (Cd) toxicity (Amanullah and Inamullah 2016).

In the salt stress of rice, the imbalance in hormone and plant growth regulators (PGRs) production is a common phenomenon. This imbalance shows in abscisic acid (ABA), gibberellins (Gas), cytokinins (CKs) to auxins (IAA), jasmonate (JA), salicylic acid, brassinosteroids (BRs), and triazoles. Osmotic stress induced by high salt levels induces the formation of abscisic acid (ABA), which modulates the ABA-dependent stress response pathway (Ye et al. 2012; Pons et al. 2013; Formentin et al. 2018). In rice, CKs and ABA act as a regulator of assimilating remobilization and leaf senescence. Under salinity stress, gas production is drastically reduced in rice plants (Colebrook et al. 2014). Auxin (IAA) plays a role in cell elongation, apical dominance, and vascular tissue formation. During salt stress, auxin deposition and recognition may be a factor in rice plant that inhibited growth and development (Wang et al. 2001). CKs are involved in cell division, apical dominance, chloroplast biogenesis, vascular tissue and shoot differentiation, leaf withering, anthocyanin formation, and photomorphogenesis in plants. CKs have a beneficial effect on plant tolerance during salt stress and a deleterious effect on plant senescence by extending stomatal closure and leaf senescence (Pospisilova et al. 2005).

JA has a critical role in seed germination, cell and root development, leaf withering, and blooming. As the level of JA in the roots and leaves increased in response to salt stress, rice proteins and JA production genes were promoted (Wasternack and Hause 2013). MYC2 activation by JA may be implicated in the control of salt stress-sensitive genes by ABA (Delgado et al. 2021). JA acts antagonistically to ABA in the rice plant, assisting in reducing Na^+ in the rice root (Kazan and Manners 2012).

BRs have essential roles in seed germination, vegetative development, ethylene production, nucleic acid synthesis, protein synthesis, net photosynthesis (Pn), reproductive growth, and maturity. Carbon absorption, biosynthesis mode, enzyme activation, and stress response are all ways that BRs respond (Fahad et al. 2015.) The osmotic and ABA signalling in rice responses to salt stress has been well documented. The crosstalk between signaling pathways and other hormones, including auxin, gibberellic acid, jasmonic acid, and ethylene, is still unclear and needs further investigation (Yang et al. 2019). Studying the epigenetic regulations of salt tolerance in rice is another important field to dissect. In response to internal and environmental stressors, epigenetic mechanisms govern the expression of stress-responsive genes. Salinity stress impacts rice plant architecture by affecting leaf length, width, area, and internode length or the number of leaves per node which also shows chlorosis, leaf rolling, leaf tillering, leaf burning, etc. (Yaghoubian et al. 2012).

6.3 Ozone Stress in Rice

6.3.1 Overview

Ozone in the Earth's stratosphere is present in modest concentrations, absorbing UV radiation. Ozone mainly evolves in two areas of the Earth's atmosphere: the stratosphere and the troposphere. It is utilized as an oxidant and disinfectant in various industries. Ozone has hazardous effects on crop plants when present in the troposphere. It is a toxic secondary air pollutant produced through the photochemical reaction between primary air pollutants such as nitrogen oxides (Nox), carbon monoxide (CO), and volatile organic compounds (VOCs) (Fowler et al. 2008). Ozone penetrates the plant via opening up the stomata and causes chlorosis, necrosis, and bronzing of the leaves, resulting in decreased crop yield (Ashmore et al. 2006; Mills et al. 2018). Ozone is one of the most critical abiotic stresses severely affecting rice productivity (Ashrafuzzaman et al. 2017; Frei 2015). The process of photosynthesis is strongly influenced by ozone exposure leading to decreased stomatal conductance and sweating rate (Lombardozzi et al. 2013). Ozone is rapidly degraded to apoplast as ROS species. As a result of this ROS, immediate necrosis or apoptosis occurs resulting in several symptoms and signs considering chlorosis, necrosis, spots, tanning, and reddening, all of which result in yield reduction (Kangasjärvi et al. 2005; Krasensky et al. 2017).

6.3.2 Causes of Ozone Stress

Ozone is not created immediately or released into the atmosphere due to any natural or human interaction; indeed, it is produced as a photochemical reaction of a range of the significant pollutants caused by several types of environmental contamination. The most significant pollutants in the environment which are responsible for the formation of ozone are methane, nitrogen oxides (Nox), carbon monoxide, and other volatile organic compounds (VOCs). The main sources of these pollutants are nitrogen oxides and carbon monoxide emissions from fossil fuels. It is also worth noting that nitrogen oxides are formed by biomass burning and lightning, in addition to soils and other sources, while volatile organic compounds (VOCs) are naturally produced (Brauer et al. 2016; Cho et al. 2011). When these gases react with oxygen in the sunlight, they produce ozone. Solar energy is required for ozone synthesis; it is more effective in stationary high-pressure systems during the summer months when temperatures are high. Stratospheric winds also carry ozone. Due to different regular distributions of NOx and VOC emission, the highest levels of downwind ozone are usually seen in urban centers rather than urban regions. It has been discovered that an additional day with an ozone level greater than 120 parts per billion (ppb) can result in a rice yield loss of around 1.12% more when compared to a day with an ozone level of fewer than 60 ppb (Banerjee and Roychoudhury 2019).

6.3.3 Effects of Ozone Stress in Rice

Ozone pollution on plants shows physiological impacts which include reduced photosynthesis, increased antioxidant revolutions, injury to reproductive therapy, increased dark breathing, and reduced carbohydrate movement towards roots (Ainsworth 2008; Ashrafuzzaman et al. 2021; Frei 2015). At the end, physiological abnormalities lead to decreased production. Feng et al. (2003) reported that rice grain production dropped by 49.1% when the concentration of ozone was 200 ppb and declined by 26.1% and 8.2% when exposed to 100 ppb ozone and then 50 ppb ozone. A meta-analysis projected that around 18% of rice yield decrease may occur with 31–50 ppb of ozone, and a 10% extra loss will be seen at 51–75 ppb ozone concentrations (Feng and Kobayashi 2019). In addition, more than 10% of regional loss (Van Dingenen et al. 2009), as well as around 20% of East Asian (Chen et al. 2011) and more than 15% of Indian rice (Debaje 2014; Mills et al. 2018) yield loss is estimated due to ozone pollution in each year. Therefore, it is well documented that ground-level ozone is one of the major limiting factors for rice production.

6.3.4 Physiological Effects on Rice Plants

The formation of rice leaves with brown spots, known as “leaf bronzing,” has been noticed in the plant that has been exposed to ozone (Ashrafuzzaman et al. 2020; Sarkar and Agrawal 2010). The photosynthetic process has a significant impact on ozone exposure because many proteins involved in the light compilation and electron transport system are depleted during the process (Emberson et al. 2018). Stomatal conductance and rate of transpiration diminish, causing decreases in photosynthesis and finally chlorosis. In addition to photosynthetic activity, the yield of grain is decreasing. Even though both of these processes are typically occurring simultaneously in rice plants exposed to ozone, the degree of damage to the leaves, as seen, does not seem to be related to the quantity of the loss of grain yield (Peng et al. 2015). Ozone enters during stomatal opening and is immediately reduced to ROS as superoxide anion (O^{2-}) and apo-plastic containing hydrogen peroxide (H_2O_2). Such ROS may have two effects, cause direct necrotic damage to the tissue or cause scheduled cell death (Krasensky et al. 2017).

6.3.5 Biochemical Effects on Rice Plants

Ozone produces the metabolic reactions of salicylic acid, jasmonic acid, abscisic acid, and ethylene which can play a vital role in the mechanism of plant defense (Alam et al. 2021; Tamaoki 2008). The production of additional enzymes such as superoxide dismutase (SOD), catalases, and ascorbate peroxidase, which are antioxidants, has also increased due to these developments (Ueda et al. 2013). This group of biochemical is interrelated or autonomous in the plant defense mechanism, and they are occasionally antagonistic to one another. Salicylic acid decreases enzyme activity such as catalase and ascorbate peroxidase. When salicylic acid production increases, the antioxidant enzymes catalase and ascorbate peroxidase are inhibited, resulting in the death of cells in the leaf (Khan et al. 2015). A similar synergistic effect between jasmonic acid and ethylene is observed in rice, which is dependent on the rice variety and may either hinder or synergistically affect salicylic acid’s activities. In the metabolism of H_2O_2, catalase and ascorbate peroxidase play a vital function in the plant. During ozone exposure, the synthesis of ethylene causes organ senescence in plants is enhanced. Another plant hormone discovered to have beneficial ozone effects is abscisic acid (ABA). In ozone-exposed plant leaves, treatment of rice plants with ABA resulted in a significant reduction in H_2O_2 levels. Scientists anticipated that ABA-induced ozone tolerance would be more closely related to stomatal mobility than antioxidant enzyme regulation (Finkelstein 2013).

Because of increased lipid peroxidation, ozone stress affects the cell membrane and causes an increase in the accumulation of malondialdehyde (MDA) inside the

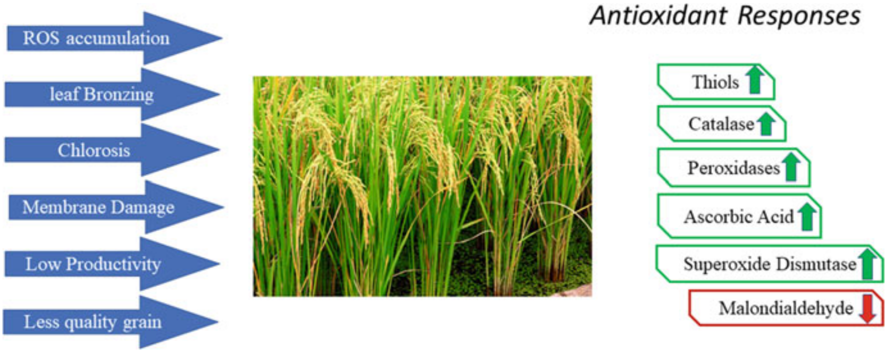


Fig. 6.3 Responses of ozone stress in rice. (Adapted from Banerjee and Roychoudhury 2019)

cell (Ashrafuzzaman et al. 2018). Whenever the levels of ROS and MDA increase, the antioxidant machinery becomes active on both the enzymatic and nonenzymatic levels. Due to the increased activity of SOD and peroxidase related to ozone-induced oxidative stress, cultivar-dependent phenolic buildup develops in the plant. SOD, catalase (CAT), and guaiacol peroxidase (GPX) activity increased by 93.7%, 39.9%, and 312.4% as compared to the control treatment with charcoal-filtered air (Wei-wei et al. 2008). The antioxidant system was highly stimulated in stressed leaves, preventing lipid peroxidation and consequent MDA accumulation. When the ozone level was raised in two tropical rice varieties, the activities of SOD, peroxidase, ascorbate peroxidase (APX), and glutathione reductase (GR) all increased. Nonenzymatic antioxidants such as ascorbic acid (ASA), thiols, and phenolics were also found in the tissues. By decomposing the RuBisCO subunits, ozone decreased the photosynthetic efficiency of the plants (Fig. 6.3) (Banerjee and Roychoudhury 2019).

6.4 Submergence Stress in Rice Plant

6.4.1 Overview

Rice (*Oryza sativa* L.) is grown and consumed predominantly in Asia, and it has a wide range of adaptations, from lowland to highland, rainfed to deep water, and wetland environments. Rice is typically grown by planting rice nursery plants in a puddled area and soaking the land regularly. Submergence is one of rice's most important and distinguishing features, which allows it to endure a high-water supply. Submergence deprives plants of free oxygen in the atmosphere, resulting in a drastic stop in photosynthesis and respiration (Fukao et al. 2019). It has a deleterious impact on most crop plants; however, rice can endure extreme circumstances to some extent (Bailey-Serres et al. 2010).

6.4.2 Causes of Submergence

Flooding produced by river discharge, excessive precipitation, and tidal movements significantly impact the major rice-growing areas. Deepwater and rainfed lowland ecosystems cover around 50 million hectares globally and account for one-third of rice-cultivated land (Bailey-Serres et al. 2010). Rice becomes anaerobic, yet excessive floods, whether complete or partial submersion, can cause various environmental stresses (Phukan et al. 2016). There are two types of flooding, flash flooding and deepwater flooding, which differ in length and depth. When a large amount of rain falls in a short period, this is known as flash flooding, causing shallow water to build and ponding conditions to last for days or weeks. On the other hand, deepwater flooding can linger for months, if not years, with water depths of several meters (Panda and Barik 2021). Rice is affected by submergence, which causes seed germination and growth to be stunted. Lower light exposure, slower exchange of gas, chlorosis, damage of cell wall, and a greater percentage of insect assault are all common side effects of submergence (Panda et al. 2006). Rice plants that have been immersed for 7 days or more may perish due to several causes. Water fills the air holes inside the soil during submerged conditions, causing it to become entirely saturated, perhaps resulting in a shortage of carbon dioxide (CO_2), a reduction in light intensity, and a reduction in rice photosynthesis (Singh et al. 2014). Furthermore, exposure to UV radiation causes the depletion of photosynthetic pigments, growth inhibition, changes in enzyme function, lipid peroxidation, and membrane damage (Pedersen et al. 2013).

6.4.3 Effects of Submergence in Rice

Submergence has an enormous impact on the gaseous exchange (O_2 and CO_2) because of the slow diffusion rate. Plants may survive in hypoxic situations establishing aerenchyma cells, which provide oxygen to submerged plant parts (Steffens et al. 2011). Some researchers believe that radial oxygen loss in the radial zone of the roots is a plant adaptation for surviving in wetlands and submerged circumstances. Submergence negatively affects plant growth and productivity by disrupting source-sink relationships and resource acquisition mechanisms, among other things (Ejiri et al. 2021). Plants suffer from oxidative stress because of changes in physio-biochemical processes (Panda et al. 2006). The physiological, biochemical, cellular, and molecular responses of plants to submergence stress act together towards yield and economic loss.

6.4.4 Physiological Responses

The stomata are open in normal conditions, enabling CO_2 to enter freely and without restriction. However, when plants are submerged, CO_2 cannot penetrate through the stomata because of the water molecules in the surrounding environment (Pedersen

Fig. 6.4 Effects of submergence stress response in rice. (Adapted from Hasanuzzaman et al. 2019 and www.flickr.com/photos/86712369@N00/3968489346/03)

et al. 2013). The cell wall, chloroplast membrane, stroma, and cytoplasm, among other cell tissues and organelles, hinder CO_2 diffusion in a liquid medium, resulting in diminished photosynthesis due to a lack of CO_2 availability chloroplast (Colmer et al. 2011). Photosynthesis in submerged plants is related to the amount of CO_2 and light available in the surrounding water. In submerged situations, reduced light availability not only hinders photosynthesis but also lowers carbon dioxide levels (Pedersen et al. 2009). Terrestrial plants change the shape of their leaves (thin leaves), increase the chloroplast content near the epidermis, and reduce the thickness of their cuticle to increase gaseous diffusion in water (Mommer et al. 2007). Chloroplasts profit from such changes because they can absorb adequate CO_2 from the environment. Submersion prevents gas exchange and promotes the accumulation of ethylene in plants (Iqbal et al. 2017). Submergence causes all oxygen-dependent mechanisms within plant cells to fail, causing anaerobic respiration to take over and the cell to die (Miro and Ismail 2013). The respiration rate increases as the temperature rises, reducing the amount of oxygen available to the cells. Low oxygen levels (anoxic state) cause an energy crisis in the submerged rice plant, limiting its ability to breathe and ultimately killing it (Van Bodegom et al. 2008). Reduced photosynthesis and increased consumption of photo-assimilates in anaerobic respiration (fermentation) result in lower carbohydrates reserves in submerged plants. Such an imbalance and overconsumption of sugars during submersion may result in complete failure of plant growth (Ayi et al. 2016). Submergence reduces photosynthetic rates while decreasing chlorophyll concentrations, resulting in leaf senescence due to the lower chlorophyll content (Krishnan et al. 1999). Water immersion stresses plants because it increases ethylene synthesis and accumulation. Chlorophyll is destroyed as a result, and carbon fixation is diminished (Fig. 6.4). When a plant is submerged in water, it is hypothesized that ethylene synthesis increases gene expression and activates the chlorophyllase enzyme, causing chlorophyll breakdown and, as a result, lower levels of carbon dioxide (CO_2) fixation (Muhammad et al. 2021).

6.4.5 Biochemical Responses

Reduced gas diffusion in submerged environments affects plant metabolism, which is dependent on the availability of oxygen. When the amount of oxygen availability is limited, submerged plants' metabolic activity and survival rate decline. On the other hand, a lack of oxygen within the cells causes the use of stored carbohydrates in plant cells, which can lead to cell death (Sharma et al. 2012). Reduced chlorophyll content in submerged plants frequently suppresses C-fixation, depleting the plants' carbohydrate supply. Submergence has been demonstrated to promote the use of nonstructural carbohydrates and to activate protein hydrolysis in aquatic species (Das et al. 2009). Rice plants have acquired several adaptations to live in submerged circumstances. Many rice types stretch their leaves above the water surface during submergence to absorb atmospheric oxygen. However, in some kinds, the increased energy demand for leaf elongation prevents the plants from recovering the following submergence. The genetic foundation of tolerance against flash flooding was discovered to be quantitative trait loci (QTL) situated on chromosomal number 9, known as the submergence-1 (SUB1) locus. However, the fact that all cultivar does not consist of this SUB1 gene (Singh et al. 2014).

The SUB1 locus consists of three ethylene-responsive factors (ERF) transcriptional regulators (Sub1A, Sub1B, and Sub1C). Sub1A prevents rice shoots from elongation during submersion (Jung et al. 2010). Plants save energy during flash floods by inhibiting the expression of genes encoding sucrose synthase and amylase, enzymes involved in the metabolism of sucrose and starch, respectively. Following submersion, this energy is utilized through a variety of physiological processes. During submersion, alcohol dehydrogenase enzyme activity increases, resulting in ethanol production and NAD^+ regeneration. Due to a lack of gibberellic acid, tolerant cultivars develop slowly during submersion. GA is a cell division-stimulating growth hormone (Gupta and Chakrabarty 2013; Sikdar et al. 2012). Aerenchyma development is essential for the supply of oxygen from the shoot to the terminal region of the roots in submerged environments and the aeration of gases like methane and carbon dioxide. Aerenchyma is formed when ethanol accumulates in submerged plants. Rice roots store oxygen in the aerenchyma during water transport when oxygen is scarce (Nishiuchi et al. 2012).

The development of adventitious roots ensures that the newborn shoots receive a steady supply of nutrients and water. Submersion destroys epidermal tissues, allowing adventitious roots to form. The signal transduction system regulates nodal adventitious root creation, which occurs when submergence causes ethylene accumulation, culminating in the generation of root primordia (Colmer and Greenway 2011). The transcription factors CRL1 and CRL5 mediate ethylene buildup in the formation of root primordia (Mhimdi and Pérez-Pérez 2020). Ethylene boosts the plants' ability to resist low oxygen situations and stimulates the emergence of adventitious roots. The amount of aerenchyma in adventitious roots is greater than that of leaves in submerged plants (Rich et al. 2012). As a result of this adaptation, adventitious roots require less oxygen for respiration than leaves.

6.5 Drought Stress in Rice

6.5.1 Overview

Drought is related to insufficient water availability and cellular dehydration and is a significant factor affecting agricultural production (Kim et al. 2020). It is the most damaging environmental stress and affects several morphological changes which are apparent in the plant's all growth phases (Gaspar et al. 2002; Zhang et al. 2017). As climate change is becoming a major concern for agriculture, the water deficit is a key issue because climate models anticipate an increase in drought intensity and frequency (IPCC 2012; Walter et al. 2011). Over 20 million hectares of rain-fed lowland rice (12% of global rice area and around 20% of global production) are predicted to be impacted by drought, with production losses of up to 81% (Ahmadikhah and Marufinia 2016; FAOSTAT 2019).

6.5.2 Causes of Drought

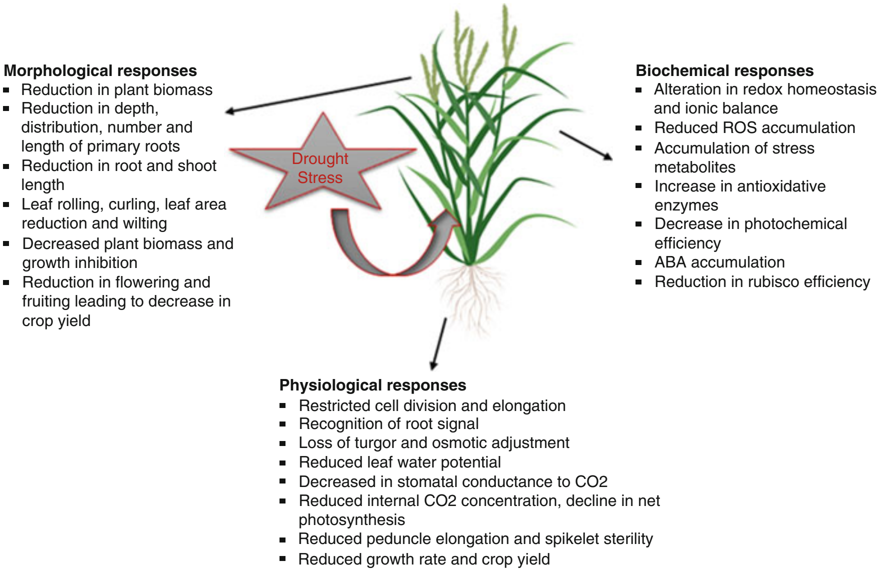
Nowadays, rainfall patterns have changed in most regions because of global climate change, which is leading to an increase in the world's temperature and atmospheric CO_2 levels (Arbona et al. 2013; Mishra and Singh 2011). Climate change is the major cause of drought stress around the world, but there are other causes of droughts. High temperatures increased light intensity, and dry wind all contribute to the evaporation of soil water. Additionally, these factors cause plants to lose more water. As a result, plants become prone to experiencing water stress (Salehi-Lisar and Bakhshayeshan-Agdam 2016; Trenberth et al. 2014).

6.5.3 Effect of Drought Stress on Rice

Rice, more than any other crop, is certainly more susceptible to drought stress (Showler 2016). Under drought circumstances, the earliest phases of growth, such as "seed germination and primary seedling development," are considered to be the most susceptible (Ahmad et al. 2009). Cell development halted under drought stress as a result of the decrease of turgor pressure (Coussement et al. 2021). Drought stress impaired mitosis and cell enlargement in rice, resulting in decreased development and growth yield characteristics (Hussain et al. 2008a, b).

6.5.4 Morphophysiological Responses

In general, the drought stress (DS) response of plants is regulated by a variety of morphological traits that have been shown as accurate indicators of drought stress in multiple studies (Fig. 6.5). These morphological characteristics include "a reduction in the size of the leaf, a reduction in the number of stomata, cutinization of the leaf



Morphological responses

- Reduction in plant biomass
- Reduction in depth, distribution, number and length of primary roots
- Reduction in root and shoot length
- Leaf rolling, curling, leaf area reduction and wilting
- Decreased plant biomass and growth inhibition
- Reduction in flowering and fruiting leading to decrease in crop yield

Biochemical responses

- Alteration in redox homeostasis and ionic balance
- Reduced ROS accumulation
- Accumulation of stress metabolites
- Increase in antioxidative enzymes
- Decrease in photochemical efficiency
- ABA accumulation
- Reduction in rubisco efficiency

Physiological responses

- Restricted cell division and elongation
- Recognition of root signal
- Loss of turgor and osmotic adjustment
- Reduced leaf water potential
- Decreased in stomatal conductance to CO2
- Reduced internal CO2 concentration, decline in net photosynthesis
- Reduced peduncle elongation and spikelet sterility
- Reduced growth rate and crop yield

Fig. 6.5 Morphophysiological and biochemical responses of drought stress in rice. (Adapted from Oladosu et al. 2019)

surface, and thickening of the leaf cell walls" (Anjum et al. 2011; Zaher-Ara et al. 2016; Zokaee-Khosroshahi et al. 2014). Drought stress has a detrimental effect on "mitosis, cell elongation, and expansion, resulting in decreased growth and yield characteristics." Due to the low soil water potential, it lowers "the size, lifespan, and quantity of leaves per plant." Drought stress reduces leaf area, which has a detrimental effect on plants by reducing both fresh and dry biomass output (Hussain et al. 2008b). As drought stress progresses, cell elongation is hampered due to a decrease in cellular turgidity which results in shoot length reduction (Abdullah et al. 2015). Significant decreases in total leaf area due to drought stress were seen in rice and wheat (Kadam et al. 2017). Drought drastically reduces the yield components of *Oryza sativa* L. like "panicle length, branches per panicle, seed setting rate, and grain weight per panicle" (Muthurajan et al. 2011; Wei et al. 2017).

Drought stress alters the physiological characteristics of rice. Some of the physiological characteristics have a substantial effect on plant water relation, which are relative water content (RWC), leaf water potential, stomatal resistance, transpiration rate, and leaf temperature. The relative water content (RWC) of stressed rice is lower than that of non-stressed rice (Fahad et al. 2017; Farooq et al. 2009). Drought stress also affects plants' nitrogen metabolism. Drought stress inhibits nitrate reductase activity in plants. Nitrogen metabolism is critical for photosynthetic response to water stress in rice cultivation at various nitrogen levels (Xu et al. 2015). Photosynthesis is a critical physiological mechanism in plants that is impacted by drought. Drought-induced changes in photosynthesis are mostly related to decreased leaf growth, diminished photosynthetic machinery function, and leaf senescence (Farooq et al. 2009). Drought stress reduces CO_2 availability and makes crops more susceptible to photodamage (Jain et al. 2010). It also affects ATP production and lowers phosphorylation, which is a significant constraint on photosynthesis. DS disrupts ionic equilibrium by reducing mineral absorption (Fahad et al. 2017).

6.5.5 Biochemical Responses

Drought-induced water deficiency changes a variety of metabolic reactions in rice plants (Fig. 6.5). Redox reaction, or electron transfer, occurs naturally in the inner mitochondrial and thylakoid membranes during energy transduction. Oxidative stress is the loss of redox equilibrium due to an excess of prooxidants. Drought-induced redox alteration of cellular components leads in an imbalance in the prooxidant-antioxidant ratios in rice, which causes oxidative stress (Foyer and Noctor 2009). Cellular organelles linked with energy metabolisms, such as mitochondria and chloroplasts, contain the ETC, which is involved in carbon metabolism via NAD(P)H and ATP. Drought stress has been shown to affect carbon and energy metabolism in both of these organelles. Drought stress has the primary impact of accumulating reactive oxygen species in the chloroplast and mitochondria, resulting in oxidative stress (Suzuki et al. 2011). The formation of ROS is one of the early metabolic responses of eukaryotic systems in response to biotic and abiotic stressors. The creation of ROS in plants, referred to as oxidative collapse, is a precursor to the plant's defensive response to drought stress, functioning as a secondary massager to trigger more defense processes. ROS, which include oxygen ions, free radicals, and peroxides, are naturally created as a byproduct of oxygen metabolism and are required for cell signaling. However, when environmental stressors like drought occur, ROS levels drastically increase, resulting in oxidative damage to DNA, proteins, and lipids (Apel and Hirt 2004). As ROS are very reactive, they can cause significant harm to plants by increasing lipid peroxidation, protein degradation, DNA fragmentation, and ultimately cell death. By generating reactive oxygen species, drought stress causes oxidative stress in plants (Farooq et al. 2009). Antioxidants are critical components of crops that scavenge ROS, and their expression enhances rice's drought tolerance (Fahramand et al. 2014). The most prevalent occurrence during drought stress is an imbalance between the production and quenching of ROS (Lum et al. 2014). Plants are protected from the harmful effects of ROS by a sophisticated antioxidant system that includes both enzymatic antioxidants and non-enzymatic compounds. Enzymatic antioxidants are monodehydroascorbate reductase, dehydroascorbate reductase, superoxide dismutase, catalase, glutathione reductase, ascorbate peroxidase, guaiacol peroxidase, and ascorbate-glutathione cycle enzyme; at the same time ascorbate and glutathione act as non-enzymatic antioxidants within the cell (Sahebi et al. 2018). Increased degrees of drought stress increased the activity of enzymatic and non-enzymatic antioxidants in rice. The increasing activity of these antioxidant defense enzymes indicates their beneficial role in mitigating the oxidative damage caused by drought stress (Lum et al. 2014).

6.6 Summary

Different abiotic stresses are becoming the major threat to rice production. Stress-affected lands are increasing due to quick environmental change and global warming. Rapid population and economic growth are the major causes of the shrinkage of cultivable land. Therefore, cultivation of the stress-tolerance crops would be the best alternative to minimize the stress-induced crop yield loss and secure the global food supply. Nevertheless, researchers are continuously working to develop stress-tolerant and/or resistant crop varieties to cultivate in the stress-affected field. Sometimes multiple stresses are evolved together in the actual field condition, which is more challenging to mitigate. Crop production quantity and quality both are important traits for the growers. Thus, there is an enormous scope to elucidate the morphophysiological and biochemical responses of rice plant against different abiotic stresses, which will ultimately help to develop tolerant and/or resistant varieties.

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7

Oats: Role and Responses Under Abiotic Stress

Rahul Kapoor, Harshavardan J. Hilli, and Amandeep

Abstract

Abiotic stresses which include low or high temperature, insufficient or excessive water, high salinity, heavy metals and UV radiation are all detrimental to plant growth and development, resulting in significant crop yield losses around the world, i.e. which can impair crop performance by 50–70%. As these different abiotic stresses frequently occur together in the field, it is becoming increasingly important to equip the crops with multi-stress tolerance nature to relieve the pressure of environmental changes and to meet the demand of population growth and food security. We know that survival strategy is well suited to growth to improve crop sustainability, especially for the forage crop like oats; thus, the attempts are being made worldwide to understand how plants respond to abiotic stresses using modern tools and techniques from all branches of science to manipulate plant performance that is better suited to withstand these stresses. This chapter addresses an overview of different stresses occurring in oat along with various measures to cope with such adverse conditions through various improvement methods beginning from traditional to advanced ones like the acquisition of resistant germplasm sources, marker-assisted breeding, genomic selection, advanced mapping strategies, genetic engineering approaches and various recent approaches.

Keywords

Abiotic stress · Oats · Resistance · Traditional methods · Recent approaches

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7.1 Introduction

Oat (*Avena sativa* L.) is a winter cereal crop that originated in the Mediterranean region and belongs to the genus *Avena* and the family Gramineae (Poaceae). The origin of the present-day oat dates back to its presence as a contaminant in wheat and barley in southwest Asia, especially Mesopotamia. It probably reached Europe when transported with primary crops during the spread of agriculture in the Neolithic age (Murphy and Hoffman 1992; Zhou et al. 1999). It is a self-pollinated crop with limited diversity (Rana et al. 2019) with few commercially produced species: *A. sativa*, *A. nuda and A. byzantina*. Oat ranks sixth in production after wheat, maize, sorghum, rice and barley. The European Union leads the world in oat production with Russia in second place, Canada in third and the United States of America and Australia in fourth and fifth place, respectively (Kumari et al. 2019). The world's oat crop area is 9.26 million ha in 2019–2020 with an average yield of 2.43 metric tons/ha and a production of 22.51 million metric tonnes (FAO 2015). The consumption of oat as human food has increased because of its gaining importance as breakfast cereal. Oat contains the most soluble fibre beta-glucan ranging from 5.0 g (oat meal) to 7.2 g (oat bran) per 100 g serving. Oat also contains more lipids (5–9%) than other cereal crops and is high in unsaturated fats such as linoleic acid. Oat includes avenanthramides, which are unique antioxidants, as well as tocotrienols and tocopherols, which are vitamin E-like substances (Amin 2014). Oat is high in soluble fibre content which helps to lower cholesterol and reduce the risk of heart disease. The protein level of oat is considered to be comparable to that of soya protein and egg protein.

Compared to all stresses that occur in the crops, abiotic components account for 50% of total yield losses (Theilert 2006). High temperatures (40%) are the most common, followed by salinity (20%), drought (17%), cold temperatures (15%) and various types of stress; i.e. only 9% of the world's land is suitable for grain cultivation, whereas 91% is subjected to numerous stresses that restrict crop output and quality. Abiotic stress has a significant impact on the growth and development of crop plants; such adverse environmental conditions can impair crop performance by 50–70%. One of the causes thought to be responsible for the progressive rise in global ambient temperature is the emission of greenhouse gases from various sources (global warming), and this changes the precipitation pattern as a result of global warming resulting in irregular drought or flood stress.

Some physiological responses due to stresses are stomatal closure which greatly reduces CO_2 uptake. As a result, the reduction equivalents for CO_2 fixation via the Calvin cycle (e.g. $NADPH^+$ H^+) drop dramatically. Adaptive responses affect not just the photosynthetic process but also the biosynthetic processes involved in protein, lipid and mineral metabolism. These stresses also have a major impact on carbohydrate, protein, lipid and mineral compositions as a result of these metabolic alterations. Although the impacts of stress on cereal and grain legume yields are generally well recognised, more research on the combined effects of abiotic and biotic stresses, as well as their effects on crop yield and nutritional quality of the product, is needed.

Climate change being a burning threat will have a significant impact on agriculture- affecting crops, soils, livestock and pests directly and indirectly. It requires the development of technologies for adaptation and mitigation, as well as their adoption by farmers. Climate change is expected to have the greatest impact on agricultural production, particularly in low-latitude areas populated by poor countries, due to the negative impacts of increased carbon dioxide and high temperatures which will force researchers to devise adaptation measures. Plants are anchored in their surroundings and must adapt to changing conditions caused by a variety of environmental influences, with severe amounts resulting in abiotic stress (Pereira 2016).

A number of criteria, such as screening procedures, sources and mechanisms of stress tolerance, nature of gene action and heredity and their relationship to agronomic qualities, influence the selection of an appropriate breeding programme to develop resistant cultivars to specific abiotic stress. The relevant timing, duration and intensity of the stress are critical aspects of drought characterization for successful stress tolerance breeding.

Traditional breeding approaches for the development of cultivars that are more resistant to the different abiotic stresses have less importance (Richards 1996). The various reasons for least importance include: (1) the major focus is to get maximum yields despite specific traits; (2) there are a number of problems with the breeding of tolerance traits which are induced by the G × E interactions; and (3) the negligence of use of morphological traits for the measures of stress tolerance have been previously less subject to G × E interactions. Due to problems in properly defining the target environment, complicated interactions of drought tolerance with surrounds and a lack of adequate screening methods, traditional breeding has been tardy in developing high-yielding, drought-tolerant cultivars (Cooper et al. 1999).

To overcome the challenges faced while using traditional breeding approaches, there is a need to use the latest molecular techniques such as genomic selection (GS), marker-assisted selection (MAS) and genome editing techniques like CRISPR/Cas9 approach. The development of SNP markers through genome sequencing has made genomic selection (GS) possible in plants (Dhillon and Chhuneja 2014). As a result, using GS in crops for abiotic resistance becomes a potent breeding strategy. Furthermore, sequencing of the oat genome would give new ideas for plant breeders to develop a large number of different sequence-based markers such as single nucleotide polymorphism (SNPs) to aid in the identification of genes for resistance through linkage disequilibrium mapping and genomic selection. Exploration of newer genome editing techniques would allow for more precise breeding along with an exciting new option. Integrating traditional breeding approaches with modern genomics-assisted breeding to create consensus linkage maps would open up new avenues for identifying and precisely mapping main and minor genes/QTLs influencing stress tolerance.

7.2 Description of Different Abiotic Stresses

7.2.1 Heat Stress

The main abiotic stimuli that cause significant damage to cells in plant species, including crop plants, are heat, drought, cold and salinity that fluctuate yearly depending on climatic nature as they develop and reproduce. These extreme changes in temperature during hot summers, on the other hand, can disrupt the intermolecular connections required for optimal plant development and seed set. The growing threat of climate change is already having a huge influence on agricultural productivity around the world with heatwaves causing considerable yield losses and posing significant risks to global food security in the future (Christensen and Christensen 2007).

Tolerance to heat is characterised by a reduced impact on critical functions like photosynthesis (Prasad et al. 2008). A heat-tolerant variety will typically have higher photosynthetic rates reflected in stay-green leaves, increased membrane-thermostability and successful seed set under high temperatures. However, the main thing is that heat tolerance screening in the field is difficult due to other environmental interactions; hence, genotypes for tolerance should be screened under controlled habitats but make it expensive (Souza et al. 2012). Therefore, unless there is a strong effect on a certain critical process, conventional or modern breeding of a gene or QTL is usually insufficient to generate heat-tolerant lines. Furthermore, achieving the largest genetic increase via traditional methods necessitates a careful selection of the best breeding plan.

7.2.2 Cold Tolerance

Low temperature is a major hindrance to field crop yield, since it can limit germination, slow down vegetative growth by causing metabolic imbalances and delay or inhibit reproductive development. Also here, two terms that need to be noticed are chilling and another one freezing stress. Chilling stress is defined as any temperature below 10–15 °C and as low as 0 °C for the majority of plants, whereas freezing stress is a plant's reaction to a condition in which the temperature of the surroundings as well as the temperature of the plant or its organs falls below 0 °C resulting in a variety of disorders.

A greater area of plant surface in wheat, barley and oat is destroyed by freezing temperatures, and its recovery is reliant on the survival of cells of the crown. Rye is the most freeze-tolerant crop followed by wheat, barley and oat. The necessity to evaluate germplasm lines of all crops across numerous years and locales to identify stable genotypes is indicated by significant year-to-year variability. The researchers believe that separate genes for freezing tolerance existed in each of the progenitor cultivars which were then merged into a single genotype. These germplasm lines will contain genes that allow regeneration cells in the plant crown to withstand ice and cold enough.

7.2.3 Drought

Drought stress is a key stumbling block for many crops' productivity that is caused by several different factors including water deficit. Water deficit can be defined at the cellular level as water content in a tissue or cell that is less than the highest water content seen in the most hydrated state. Drought stress has a variety of effects on plants at different levels of organisation; i.e. cell development decreases and plant growth is slowed when there is a lack of water. Also, drought affects activities including photosynthesis, respiration, translocation, ion uptake and cellular metabolism; i.e. photosynthesis in higher plants declines when the relative water content (RWC) and leaf water potential decreases. It also results in the generation of oxygen free radicals (superoxide, hydrogen peroxide and so on), which causes oxidative damage to cellular membranes.

Plants have developed many different techniques to help them cope with the many aspects of drought stress, and plant responses to water stress vary greatly depending on the duration and severity of the stress as well as the plant species and stage of development. Drought tolerance is achieved through different cellular mechanisms at the physiological, biochemical and molecular levels such as specific gene expression and accumulation of specific proteins. The preservation of a high plant water status is a common goal of drought tolerance. Osmotic adjustment, reduced water loss through the cuticle and avoidance of xylem cavitation are some of the physiological mechanisms that assist plants to maintain their water status during drought. Enhanced uptake of water by roots can be achieved by maintaining the osmotic potential of root cells. Water loss can be checked by regulating stomatal opening and closing. Breeding for enhanced drought tolerance can be roughly defined as heritable changes within a crop to improve drought tolerance (Yordanov et al. 2000). To understand plant adaptation to water stress, detailed research of root response to drought is essential. As a result, in recent years, a growing area of research has been devoted to dissecting root features that may help crops cope with water stress and preserve productivity during drought.

7.2.4 Waterlogging

Waterlogging is one of the most dangerous natural occurrences and is also known as flood, submergence, soil saturation, anoxia and hypoxia. In the field, there are two forms of flooding: one is waterlogging, in which the root and a section of the shoot are submerged, and the other one is total submergence, in which the entire plant is submerged. Due to hindered exchange of gas and subsequent responses of the plant's soil microflora and microbiome, excess water causes complex alterations in various environmental factors. Soil waterlogging causes hypoxia and then anoxia in the root zone as well as enhanced mobilisation of 'phytotoxins' in decreased soils, hence root and shoot growth. Plants have evolved a metabolic mechanism to cope with hypoxic and anoxic environments and the consequent energy deficits as well as structural and morphological changes to promote internal O_2 supply which is now the burning topic of flooding stress research. Rice has been used as a model in flood stress studies because it is a crop with outstanding flooding tolerance and diversity. Other models (Arabidopsis) and the utilisation of selected wild wetland species have also added to our understanding of flood and O_2 deprivation responses, particularly the involvement of ethylene. The breeding of submergence-tolerant cultivars has come from years of interdisciplinary research.

The oat (*Avena sativa* L.) studies were carried out by researchers using 8 commercial genotypes, UPF 14, UPF 16, UFRGS 7, UFRGS 14, UFRGS 16, UFRGS 18, CTC 2 and ORLA 9248, for their stress tolerance studies. Several parameters that they studied were plant height (PH), root length (RL), root dry matter (RDM) and total dry matter (TDM) under flooded conditions for at least 30 days (TDM). Flooding tolerance was shown to be genetically variable across the genotypes examined. Based on the many criteria evaluated by them, the cultivars UPF 16, UFRGS 14 and UFRGS 7 appeared to be more tolerant to soil flooding at the early stages of plant development. Barley breeding projects could benefit from a combination of MAS and traditional field selection. Diversity array technology (DArT) is now thought to be the most effective method for genome profiling. DArT markers can be used to look for waterlogging-tolerant genes or QTLs in grass families, and future studies may be able to compare a DNA sequence to the genome sequences of rice and other species (Claudia et al. 2008).

7.2.5 Nutrient Use Efficiency

The most commonly utilised nutrient source in modern agriculture is nitrogen fertilizer which has considerable environmental and production implications and is essential to maintain a photosynthetically active canopy that ensures grain yield as well as to make grain storage proteins which are required to maintain excellent end-use quality. In the context of various nitrification processes described by many workers, the studies related to such stress give knowledge of physiological, metabolic and genetic factors that influence nitrogen intake and utilisation. NUE can be used to distinguish between genotypes based on their capacity to absorb nutrients for maximum yields. The NUE is based on (a) uptake efficiency, (b) incorporation efficiency and (c) utilisation efficiency. The optimal N application rate is determined by the predicted yield, the mineral N level in the soil in the spring, the organic matter content of the soil and the previous crop. However, due to huge year-to-year changes in growth conditions, particularly temperature and precipitation, anticipated yields are highly unclear. Similarly, Valkama et al. (2013) reported that the average changes in control yields across years for barley, spring wheat and oat were 25%, 22% and 15%, respectively, in a meta-analysis of 61 field experiments in Finland.

To improve nutrient usage efficiency, the features involved particularly nutrient absorption, transport, utilisation and mobilisation should be identified and paired with best management techniques for sustainable agriculture. Many methods can be used to evaluate genetic advances for improved NUE including retrospective analysis of changes in cultivars over time for grain yield and NUE. Also, it is important to know that genes that take part in secondary N metabolism play an important role for NUE than genes involved in primary N assimilation. Apart from genes involved in the N assimilatory pathway, a number of potential candidates are being identified by analysing the NUE of diverse kinds under restricting conditions (Chardon et al. 2010). Biotechnological interventions to improve nitrogen use efficiency (NUE) have mostly focused on manipulating and overexpressing some key candidate genes, as well as utilising knockout mutations to assess the impact on biomass and plant N status and overall yield (Pathak et al. 2008).

7.2.6 Water Use Efficiency

We know that irrigated agriculture consumes the majority of the world's available water resources; i.e. according to FAO (2000), agricultural irrigation consumes over 60% of total water resources in the world. The crops when irrigated can be studied to know the WUE in different lines to know their efficiencies under stress/deficiency. The negative impact of lesser soil moisture on crop yields is dependent on the crop's phenological stage, and the most sensitive stage has been found to differ from area to region. However, the grain-filling period is critical for both yield and WUE. This water scarcity throughout the reproductive phase of development is the most critical limiting factor for winter cereals. However, regardless of the amount of biomass produced during the vegetative phase, the plants must maintain their water requirement during the generative phase if reproductive development is to be successful (Kato et al. 2008).

Higher water intake from the ground and improved drought performance are both associated with a deep root system. However, it's possible that the roots of cultivars grown in a certain area are already fully developed and that no more modifications are required.

7.2.7 Other Stresses

Stress is a factor that has a negative impact on plants and has undesirable consequences that can be either abiotic (climate and soil) or biotic (weeds, diseases, insects and so on). Different types of stress can have varying durations of effect; for example, air temperature can become stressful in a matter of minutes, whereas soil mineral shortage can take months to become stressful. Usually, stress is measured in terms of plant survival, growth and yield, as well as the primary assimilation process which includes photosynthetic rate, nutrient accumulation and growth rate among other things. Human activities such as mining, smelting, intensive agricultural operations, fuel generation and electroplating are the primary causes of heavy metal pollution in soil. Phytoremediation techniques (Salt et al. 1995) that include phytoextraction, phytosequestration, phytodegradation, phytovolatilization, phytohydraulics and rhizodegradation can be used to remove heavy metals from the root zone of soil cost-effectively and efficiently (Tsao et al. 2003).

7.2.8 Traditional Breeding Methods

To hasten the production of stress-tolerant/resistant cultivars with rapid genetic gains in this difficult situation, enhanced conventional breeding procedures are very much necessary along with novel cultivation techniques that are highly cost-effective and efficient to boost the yield and productivity of major crops. Some of the important traditional approaches include selection, introduction, pedigree breeding, backcross breeding, shuttle breeding, etc. However, traditional breeding of crop plants with higher stress tolerances has a limited success (Richards 1996) due to a number of factors including: (1) the focus being on yield, (2) G × E interactions and (3) desired traits which can only be introduced from closely related individuals. Traditional breeding has been slow in generating high-yielding, drought-tolerant rice cultivars, owing to challenges in precisely defining the target environment, complicated interactions of drought tolerance with surroundings and a lack of proper screening methodology (Cooper et al. 1999).

7.3 Genetic Resources of Resistance/Tolerance Genes

Avena sativa has a reasonably narrow gene pool compared to other cereals. According to their inter-fertility with cultivated hexaploid oat, wild *Avena* species are divided into three gene pools, i.e. primary, secondary and tertiary. The primary as well as tertiary gene pools are large and diversified, whereas the secondary gene pool is modest (Harlan and de Wet 1971). All diploid oat spp. and tetraploids (*A. barbata, A. vaviloviana, A. abyssinica, A. agadiriana and A. macrostachya*) are found in the tertiary gene pool.

The genetic diversity within crop species found in a specific ecosystem of habitats is referred to as a crop genetic resource. These genetic resources are a rich source of genetic variation and an important raw material for crop improvement and the development of new value-added products. After wheat, rice, barley, maize, bean, sorghum and soybean, the world’s oat collections are considered to be over 131,000 accessions conserved by 125 institutions in 63 countries, making them the 8th most abundant germplasm collections.

Wild species provide fundamental information on crop plant species relationships and evolution patterns which are very large sources of diversity. In the world’s oat collections, more than 24% of accessions are categorised as wild species. The majority of wild oat species are made up of multiple hexaploid species that are part of the core gene pool. Nearly 30,000 plus accessions of oat wild species are being maintained in 29 oat collections, of which 13 hold more than 20 accessions (Brazil, Canada, China, Germany, Israel, Morocco, Norway, Poland, Russia, Spain, Sweden, UK and USA) (FAO/WIEWS).

7.4 Glimpses on Classical Genetics and Traditional Breeding

Breeding objectives vary among oat-breeding programmes depending on the specific difficulties that are present in each production area. High yield, appropriate maturity, lodging resistance, acceptable grain quality and disease resistance are all objectives shared by most oat breeding efforts. In some projects, fodder and straw production is also given a lot of attention. The traditional strategy makes use of existing genetic variation as well as the sexual cycle to recombine DNA through independent chromosomal assortment and crossing-over. Induced mutations are frequently used in traditional breeding methods as well. Because of the size and complexity of the oat genome as well as the lack of DNA sequence information, molecular genetics research on oat lags far behind that of other cereal crops. However, since O'Donoughue et al. (1995) produced the first linkage-based QTL map in oat, there have been ongoing efforts to increase the density of the map with various types and quantities of markers. Using amplified fragment length polymorphism (AFLP) and restriction fragment length polymorphism (RFLP) markers, several mapping populations were created.

A limited number of genes in oat have been identified in various studies based on their phenotypic effect due to their hexaploid nature. Marshall and Shaner were the most recent authors to summarise these genes (1992). Most genetic aberrations which cause a loss of function in the hexaploid oat would be concealed by genes having similar functions and present on homoeologous chromosomes in the other genomes even if they were homozygous. Most of the single genes found in allohexaploid oat are for disease resistance, particularly crown rust or stem rust resistance; these genes frequently have a dominant effect that is not mirrored by a gene in the other component genome. While significant genetic linkage has previously been discovered within some of these genes, the data was insufficient to create a genetic linkage map for oat. The development of markers that allow for practically infinite variability at the DNA sequence level without relying on phenotypic consequences has made it possible to create oat genetic linkage maps.

7.5 Brief on Diversity Analysis

The degree of differentiation between or within species is usually referred to as diversity, and the crop evolution whether it is natural or induced by humans is essentially based on the population's genetic diversity. All crop improvement programmes are built on the foundation of above-existing intra- and inter-specific differences. Natural variation and differences amongst crop plants have been largely identified and utilised in crop improvement since the beginning of systematic plant breeding. This natural variability has been depleted over time as a result of breeding practices focusing on improving only a few traits: (a) repeated use of a very few selected genotypes as parents and (b) introduction of common superior lines to several countries, resulting in the enhanced genetic similarity between crops. Hence, there is a greater need for the identification of diverse breeding lines, and the creation of genetic diversity and its utilisation in the major breeding programmes is of utmost importance.

7.5.1 Methods of Diversity Analysis

The morphological, cytological, biochemical and molecular characterisations can all be used to assess diversity, viz. morphological markers were first utilised for diversity study which was variations of a certain plant species that occurred spontaneously and are being used today. Similarly, cytological and biochemical distinctions found in a species can be used to determine genetic diversity.

7.5.2 Phenotype-Based Diversity Analysis

The phenotypic diversity study is estimated by raising diverse germplasm lines, purelines, enhanced varieties and so on under a specific experimental design. This entails morphological characterization of various field entries as morphological traits are the most important predictors of plant agronomic value and taxonomy classification. However, it is costly because of the need for enormous expanses of land and human labour over a long time and is also affected by the constraints of environmental sensitivity.

7.5.3 Molecular Markers-Based Diversity Analysis

7.5.3.1 Molecular Markers

It comprises of the investigation of genotype variation at the DNA/RNA level; i.e. various molecular markers have different properties that make them ideal for various applications. Among all markers used, hybridization-based and PCR-based are the two most common types, but in recent days a new generation of markers has been developed based on sequence or array platforms. Because of their great variability, better genomic coverage, high reproducibility, automation ability, neutrality and lack of environmental perturbations, molecular markers are the method of choice for genetic diversity evaluation. Many genetic diversity studies have reported using both morphological and molecular markers at the same time.

7.5.4 Estimation of Genetic Diversity Using Statistical Tools

7.5.4.1 D^2 Statistics

Mahalanobis developed this technique which is also known as Mahalanobis’ generalised distance. By categorising genotypes into various clusters, this approach minimises the number of comparisons between them. The crucial condensation method is used to convert correlated data into uncorrelated variables resulting in D^2 values.

7.5.4.2 Principal Component Analysis (PCA)

Principal components analysis (PCA) is a data reduction technique that can be used with quantitative data which converts multi-correlated data into a new collection of uncorrelated variables. It is based on the decreasing order of variance size of eigenvalues and mutually independent eigenvectors (principal components). Such components produce ideal scatter plots of observations for studying the underlying variability and correlation.

7.5.5 Software for Diversity Analysis

SAS, SPAR, Past, NTSYSpc, GenAlEx, Popgene, Power marker and R package.

7.6 Association Mapping Studies

Association mapping (AM) entails gathering a diverse group of individuals from both natural and breeding populations that can be used for mapping quantitative traits by exploiting the advantage of the linkage disequilibrium (LD) which results from the hybridization between the parents (Gorelick and Laubichler 2004). Association mapping involves several steps like (1) development of association panel, (2) estimation of population structure and relatedness in order to hinder the false LD that might occur between unlinked loci, (3) genotyping, (4) phenotyping and finally (5) association analysis (Fig. 7.1). One of the studies on AM in oat that has been undertaken by Klos et al. (2017) is genome-wide association mapping of oat crown rust (biotic stress) employing 2972 SNPs for genotyping on 631 oat lines for

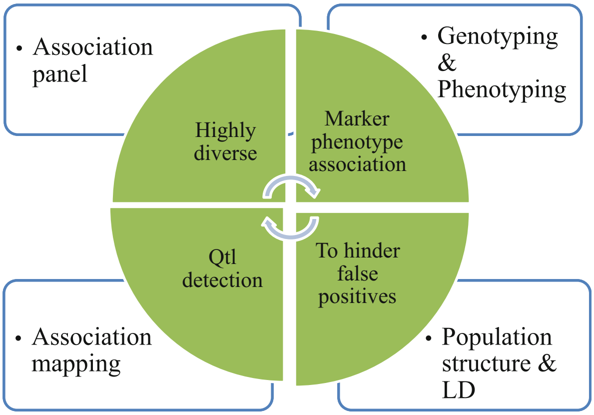

Fig. 7.1 Flow chart for association mapping

association mapping of quantitative trait loci (QTL), but as far as abiotic stress is concerned, it has wide scope in near future with such studies.

Several positiveness from association studies are that this AM method is likely to find markers that are significantly closer to the genes of interest than traditional linkage mapping can. This is to be expected as LD analysis takes into account all of the events occurring during recombination that would have been expected to occur between the gene and the marker in the population used for AM in the past, while linkage mapping, on the other hand, only considers recombination events that occur between the gene and the marker after the two parents have been hybridised (Myles et al. 2009).

The AM also has some drawbacks; i.e. AM results are influenced by many factors such as the history of selection, population structure, kinship and so on, which can lead to false associations between QTLs and markers.

7.7 Brief Account of Molecular Mapping of Resistance/Tolerance Genes and QTLs

Plant breeding has undergone a new technological revolution as a result of the discovery of DNA markers, which has resulted in the production of a vast array of DNA markers that make it easier for breeders to select complex traits that were phenotypically difficult to assess. Marker-assisted breeding (MAB) acts as a boon to breeders since it allows them to conduct effective and quick selection based on DNA markers, and also it may now be utilised for qualities influenced by both qualitative and quantitative genes which helps for the development of a wide range of DNA markers and genetic maps. However, the molecular marker system in oat is less developed than in other cereal crops (rice, wheat, maize, etc.) due to the lack of genomic resources.

Primary and secondary are the two main types of mapping populations usually used for mapping. Hybridization between the two homozygous lines differing in the trait of interest produces primary mapping populations. Whereas, secondary mapping populations are generated by crossing the two lines/individuals which were selected from a mapping population which are developed for fine mapping of the genomic region of interest. The primary mapping populations are (1) F_2, (2) F_2-derived F_3 ($F_{2:3}$), (3) backcross (BC), (4) backcross inbred lines (BILs), (5) doubled haploids (DHs), (6) recombinant inbred lines (RILs), (7) near-isogenic lines (NILs), etc. The important thing that needs to be considered during mapping is that when two genes segregate together, it is necessary to determine if they are segregating independently or connected. The chi-square test is significantly simpler to perform than computing LOD scores, but it only indicates the presence of linkage and provides no additional information. Whereas, LOD score reveals linkage as well as estimates recombination frequency between the two genes. Therefore, LOD scores need to be calculated for various recombination frequencies that range from 0 to 0.5 (Morton 1955). MapMaker/Exp is a command-driven application that analyses multipoint linkage data from experimental crossings and creates primary

Table 7.1 List of the genes/qtl mapped in oats

Gene	Marker	Linked marker/QTL	References
Pc38	RFLP	Cdo673, wg420	Wight et al. (2004)
Pc39	RFLP	Cdo666	Wight et al. (2004)
Pc48	RFLP	cdo337	Wight et al. (2004)
Pc54	RFLP	cdo1435B	Bush and Wise (1996)
Pc58a,b,c	RFLP	PSR637, RZ516D	Hoffman et al. (2006)
Pc59	RFLP	Cdo549B	Bush and Wise (1996)
Pc68	RAPD	ubc269	Penner et al. (1993)
Pc83,84,85	STS	Agx4, Agx9, Agx7	Yu and Wise (2000)
Sr_57130	AFLP	PacgMcga370	Zegeye (2008)

linkage maps (Lander et al. 1987) which simultaneously estimate all the recombination frequencies from even very large datasets for both dominant and co-dominant markers.

O'Donoughue et al. developed the first genetic linkage map in diploid species *A. atlantica* × *A. hirtula*. Acevedo et al. (2010) identified eight QTLs related to MN841801-1 alleles; seven of which had previously been discovered, and a new QTL designated Prq8 was discovered on linkage group MN13 imparting resistance to crown rust disease. Similarly, Gnanesh et al. (2013) generated allele-specific KASP-SNP markers for marker-assisted selection of the crown rust resistance gene Pc91, which is situated on translocated oat chromosome 7C-17A. Yu and Herrmann (2006) used comparative mapping to develop the first report on mapping powdery mildew resistance in hexaploid oat. They discovered that powdery mildew resistance is controlled by a single dominant gene, Eg5. *A. macrostachya* was also discovered to be a new source of resistance in the study. Some of the mapped genes are listed in Table 7.1.

However, the major drawback is that many oat researchers have used the first molecular marker RFLP for comparative mapping for the finding of resistance genes. Also, the difficulties associated with the mapping in a hexaploid genome and complications emerging from multiple chromosomal rearrangements (O'Donoughue et al. 1995) made the oat breeding cumbersome, and thus mapping is carried out usually based on visual selection.

7.8 Marker-Assisted Breeding for Resistance/Tolerance Traits

Genetic markers are crucial tools for analysing variation in the sequences of DNA of various genotypes and thereby avoiding complications caused by environmental factors in the characterisation of genetic resources. Because of their better reproducibility, co-dominant inheritance, simplicity, low cost and usually high polymorphism, microsatellites markers are good markers for molecular research. These can be utilised in several studies, including genotyping and variety protection, germplasm conservation, genetic mapping, QTL analysis, marker-assisted selection breeding and diversification studies. Information on genetic diversity at the molecular level has been reported earlier by many researchers. Few works carried out are Rines et al. (2006) and Kapoor and Batra (2016) on marker-assisted breeding in oat (2016). Also, Fu et al. (2007) used microsatellite markers in their diversity studies.

Some things that need to be taken care of during MAS are discussed by Dreher et al. (2003); i.e. if there is a distance of 5 cM between the marker and gene of interest and the plant is chosen based on the marker pattern, there is a 5% probability of selecting the incorrect plant. This is based on the rule of thumb that 1 cM of genetic distance is about equal to 1% recombination over short distances. The plant breeder will need to evaluate the error rate that is acceptable in the MAS program, keeping in mind that errors are also usually involved in the phenotypic evaluation. One of the recent breeding techniques called advanced backcross—QTL (AB-QTL) analysis—incorporates the various genes which are located in different linkage groups into a single variety by successive backcrosses with the parents that are selected based on the molecular markers (Lambalk et al. 2004). Portyanko et al. (2005) used a total of 230 markers, mainly RFLP and AFLP, and identified 4 major and 3 minor QTLs for partial resistance to *Pca* in oat line MN841801-1.

7.9 Map-Based Cloning of Resistance/Tolerance Genes

A gene must be cloned to understand its functions and explore its potential applications in agriculture, and it needs high-resolution maps which are required to perform chromosomal walking on model crops to extract genes for large genome crops. Heterologous DNA markers that are closely connected to target genes can be utilised as probes to test YAC or BAC libraries derived from model crop genomic DNA. Map-based cloning involves a few steps (Fig. 7.2) like developing a mapping population, genotyping with genome-wide markers for coarse mapping and then going for fine mapping with saturated regions around the markers and its validation by transformation method or any other techniques. *Avena* is poorly studied and possesses huge genomes with a hexaploid oat genome of 11,315 Mb and a diploid

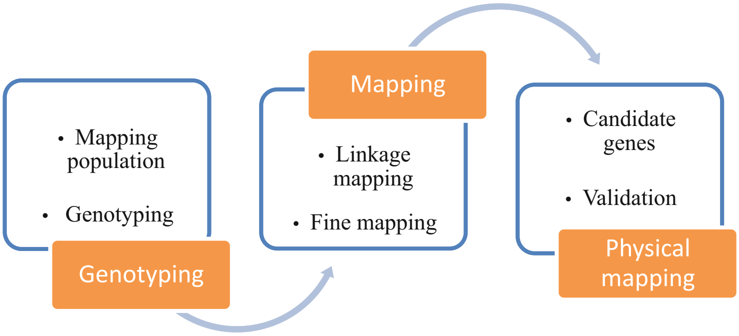

Fig. 7.2 Flow chart of map-based cloning

oat genome of 3770 Mb per haploid genome. A precise syntenic relationship between oat and other species must be constructed in order to exploit the enormous quantity of accessible data from other plant species and to discover the ornithological link among genes in different species. This finding would provide a solid foundation for future *Avena* genetics research.

7.10 Genomics-Aided Breeding for Resistance/Tolerance Traits

Meuwissen et al. (2001) proposed that genomic selection (GS) or genome-wide selection is an alternative to classic MAS that uses all markers which are densely positioned across the genome to predict an individual's total genetic value. GS is essentially a variant of marker-based selection with the exception that markers are not preselected for relevance. This means that no significance testing for markers is done, and the focus is only on determining individual breeding values. Since all markers are included in GS, it can account for more genetic variance, resulting in more accurate breeding value estimations (Solberg et al. 2008). The accuracy of GS is affected by several factors which include marker density, training population size, genetic relationships of training and selection candidates and consistency of LD across populations (Meuwissen et al. 2001; Heffner et al. 2009; Zhong et al. 2009; Habier et al. 2007; Lorenz et al. 2011), and the goals of GS are to estimate accuracy as marker density and training population size increase, to measure accuracies when data is divided over time and to investigate accuracy in the presence of population structure.

The essential steps for putting genomic selection into practice can be summed up in four simple phases: (1) creating training populations with all phenotypic and genotypic data, (2) evaluating marker effects in the training population, (3) computing GEBV of new breeding lines using genotype data and (4) selection (Heffner et al. 2009), which is also depicted through Fig. 7.3. There are currently only a few

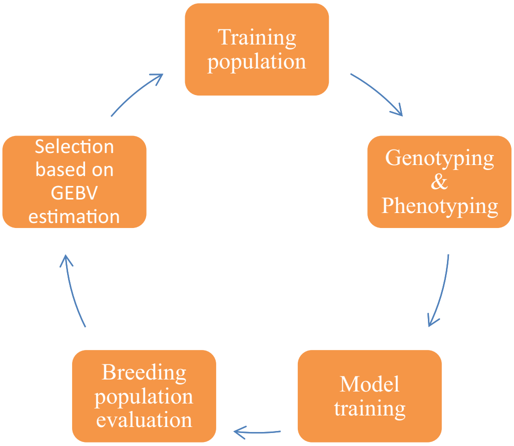

Fig. 7.3 Flow chart of genomic selection

empirical investigations of GS in crops, but they have a lot of potentials. To get a basic understanding of the value of investing in marker density and training population size, studies in a variety of species and populations will be required. The lines used in GS represent the diversity of alleles seen in elite oat breeding populations, making them a useful sample for cross-validation with application in breeding programmes.

New sequencing technologies, collectively known as next-generation sequencing (NGS), have opened new avenues for studying transcriptomes. The genome and transcriptome of oat, on the other hand, are the least studied of any cereal grain crops, while the complexity of its huge and repetitive genome (allohexaploid, $2n = 6x = 42$) is a hindrance, and it is obvious that oat genome research has received less attention (Gutierrez-Gonzalez et al. 2013). NGS has enabled high-throughput transcriptome sequencing (RNA-Seq) resulting in a multitude of transcriptomes and transcript profiling studies in a variety of organisms, including a variety of plant species. Cabral et al. (2014) used RNA-Seq to create and characterise the first hexaploid oat gene expression atlas. Huang et al. (2013) genotyped 746 different oat types and 622 progenies from eight biparental populations using genotyping by sequencing (GBS).

7.11 Recent Concepts and Strategies Developed

The sequencing of the oat's whole genome must be elucidated and described before it can reach its full potential. However, because oat is an allohexaploid, its genome sequencing has been difficult and expensive until recently. ScanOat has a one-of-a-kind opportunity to start and run an oat genome sequencing project. It will substantially be speeding up the molecular characterization of a number of oat lines with better features seen in a mutagenised oat population. With the availability of an oat genome, precise site-directed mutagenesis utilising CRISPR/Cas9 and other gene editing methods would be possible. Furthermore, an oat genome reference sequence would be a valuable asset to both academic and industrial research groups since it would encourage more investment in oat product development, resulting in more advancements in the field.

Agriculture is well-known as a significant source of human food. Current agricultural processes, on the other hand, must be modernised and strengthened in order to meet the expanding food demands of the world's population. Plants with enhanced yields and nutritional value, as well as greater resistance to herbicides, insects and diseases, have been created using genome editing (GE) technology. Several GE tools have recently been developed, including the customisable and successful clustered regularly interspaced short palindromic repeats (CRISPR) with nucleases technique. Transgenes or CRISPR are introduced into plants by particular gene delivery methods in the first step of the GE process. However, GE tools have some drawbacks, such as lengthy and difficult processes, the risk of tissue damage, DNA incorporation into the host genome and low transformation efficiency. Nanotechnology has emerged as a ground-breaking and cutting-edge technique for addressing these difficulties. Because it improves the transformation efficiency for both temporal (transient) and permanent (stable) genetic alterations in numerous plant species, nanoparticle-mediated gene delivery outperforms traditional biomolecular techniques. Such technologies and systems must be purchased under the oat improvement programme for a variety of qualities (Ahmar et al. 2021).

7.12 Brief on Genetic Engineering for Resistance/Tolerance Traits

Biotechnology has the potential to not only solve the challenges that are currently restricting crop output in underdeveloped nations but also to improve long-term agricultural sustainability. As a result, careful selection of genetically promising types or generation of resistant cultivars through genetic engineering technology may aid in improving oat output under stress situations. Tissue culture (TC) and genetic engineering (GE) of useful trait genes have been used to boost cereal crop yield recently. However, there is a scarcity of data on genotype independence in the in vitro regeneration and genetic engineering of oat. Zhang et al. created a genotype-independent efficient regeneration technique for the genetic transformation of commercial oat cultivars from shoot apical meristems in 1996. However, because of the hazards of somaclonal abnormalities appearing in callus cultures owing to prolonged tissue culture, embryo-derived callus is not deemed practical in routine oat transformations.

Maqbool et al. (2009) used biolistic bombardment to genetically co-transform three oat cultivars with pBY520 (carrying hva1 and bar) and pAct1-D (containing gus). Herbicide resistance and GUS as a marker were used to select and regenerate transgenic plants. The co-integration of the hva1 and bar genes was validated by molecular and biochemical studies of putative transgenic plants with a frequency of 100%, and 61.6% of the transgenic plants carried all three genes (hva1, bar and gus). The characteristic of HVA1 expression for osmotic tolerance in transgenic oat progeny was analysed in vitro as well as in vivo. Transgenic plants exhibited significantly ($P < 0.05$) increased tolerance to stress conditions than non-transgenic control plants.

Gene downregulation can reveal the functional significance of biotic/abiotic stress-responsive genes; i.e. chemical, irradiation, transposon, T-DNA insertional mutagenesis, and posttranscriptional gene silencing (PTGS)-based methods are some of the most extensively utilised gene downregulation methods. RNA interference (RNAi), virus-induced gene silencing (VIGS) and artificial micro RNA (amiRNA) are three common PTGS approaches that are now being much used in other crops; i.e. RNAi has been frequently utilised to investigate stress-responsive gene function in agricultural species particularly to investigate abiotic stress tolerance (Fu and Yang 2017).

7.13 Brief Account on Social, Political and Regulatory Issues

Intellectual property rights (IPR) are the rights granted to individuals over their mental creations. For a set amount of time, they usually grant the creator exclusive rights to utilise his or her creations. Inventions and literary and artistic works, as well as symbols, names, images and designs utilised in business, are all examples of intellectual property (IP). For a short time, they offer the creator the right to prevent others from making unlawful use of their property. Industrial property (functional commercial innovations) and artistic and literary property are two types of intellectual property (cultural creations). For two main reasons, intellectual property protection has never been more crucial to the plant breeding industry than it is today. To begin with, commercial plant breeding is now primarily carried out by private companies or public-private partnerships that rely substantially on private finance. Second, the amount of private investment necessary might be significant. Commercial plant breeding increasingly necessitates large capital investments in research and development (R&D), particularly when biotechnology techniques are employed. Rights protected under intellectual property are patents, copyrights, trademarks, industrial designs, protection of integrated circuits layout design, geographical indications of goods, biological diversity, plant varieties and farmers' rights.

A plant patent is a specialised and narrow type of patent protection that differs from utility patent protection. Plant patents were first introduced in the United States in 1930, in response to nursery lobbying. Asexual reproduction of nursery stock (fruit trees, ornamentals and roses) is accomplished by grafting cuttings onto rootstock. It's no surprise, then, that only asexually reproduced variants are protected under plant patent laws (and which meet several additional requirements, including novelty and nonobviousness). Fifteen plant patents, on the other hand, only protect against unauthorised asexual propagation of protected plants.

Almost all IP laws are national. There are numerous conventions and accords under which countries agree to provide the basic level of IP protection as well as to safeguard IP developed by nationals of other countries. There are over 20 treaties and agreements on the registration, classification and protection of intellectual property which are administered by the World Intellectual Property Organization (WIPO). This Practice Note goes over some of the most important conventions and treaties that it oversees. The Patent Cooperation Treaty (PCT), the European Patent Convention (EPC), the Budapest Treaty, the Paris Convention for the Protection of Industrial Property, the UPOV Convention and the Convention on Biological Diversity (CBD) are some of the accords.

7.14 Future Perspectives

Wheat, rice, barley, maize, pearl millet and sorghum, in comparison to oat, are enriched with a huge number of genetic resources. Because of the genomic complexity and lack of a whole genome sequence, oat has made less progress in molecular genetic research than other staples. The development of DNA marker-based genetic linkage maps in distinct oat genetic groups reveals marker-trait associations that can be used to identify genes/QTLs for further use in marker-assisted breeding. However, because oat is an essential food grain, the majority of the found genes/QTLs/markers are associated with agronomic and nutritional value crops owing to its high protein content.

However, sequencing of whole oat genome would open new opportunities for oat breeders to create a large number of SNPs and to aid in the identification of disease resistance genes via linkage disequilibrium mapping and genomic selection. Exploring new genome editing techniques would not only allow for more accurate breeding, but it would also give oat breeders a remarkable new possibility. Integrating conventional breeding approaches with current genomics-assisted breeding to produce consensus linkage maps would open up new avenues for the identification and precise mapping of major and minor genes/QTLs governing disease resistance.

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8 Millets: Role and Responses Under Abiotic Stresses

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Abstract

Agriculture is severely affected by the multi-environmental stresses and changing climatic scenarios. An increase in temperature of 3–4 °C can reduce crop yields by 35%. South Asia and Africa regions are mainly affected due to global warming and climate change. In this context, millets are a good alternative for providing food and nutritional security in the alarming situation. They are the most important crops over other crops and can grow under a variety of agroecological situations and harsh conditions. They can be used both as human food, feed and fodder for livestock. They possess C_4 anatomy with robust nature and tolerance against high temperature and can survive in adverse conditions. Millets have many nutraceutical and health-promoting properties. They contain major and minor nutrients in good amounts along with dietary fiber. Millets are gluten-free and are a substitute for wheat or gluten-containing grains for celiac patients and many more. Here, we review the various roles and responses of millets under abiotic stresses.

Keywords

Millets · Abiotic stresses · Climate resilience · Nutri-cereal

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8.1 Introduction

Millets are the most important crops over other crops as these can grow on shallow, low fertile soils with pH ranging from 4.5 (acidic) to 8.0 (basic). They are mainly cultivated in various agro-ecological situations like plains, coasts, hills and diverse soils with varying rainfall and can be used both as human food, feed and fodder for livestock (Kumar et al. 2020b). Millets like pearl millet and ragi can sustain soil salinity of 11–12 dS/m. Even the water requirement for the millets is very minimal, as compared to other cereals. Millets have a very short maturity period (45–70 days) which is half of the maturity period of most important crops. Being C_4 plants, they possess robust nature and tolerance against high temperature and can survive in adverse conditions ensuring food and nutritional security.

The term millet includes a number of small-grained cereal grasses. Millets can be divided into two subfamilies, viz., Panicoideae and Chloridoideae. Panicoideae is comprised of pearl millet, foxtail millet, Indian barnyard millet and Japanese barnyard millet, while Chloridoideae contains finger millet, tef and eight genera as described in Table 8.1. The ploidy level and chromosome number of different millets vary from diploid pearl millet ($2n = 2x = 14$) to hexaploid fonio ($2n = 6x = 54$) (Mann et al. 2011). They also differ in plant height, seed weight, size and color of seeds and shape of the panicles. Millets possess a small grain size except for pearl millet [*Pennisetum glaucum* (L.) R. Br.] and sorghum which have large seed sizes. Based on the size of the grain, they are classified as major millets which include sorghum and pearl millet, while minor millets include various small grained millets like foxtail millet (*Setaria italica*) (kangni), finger millet (*Eleusine coracana*) (ragi), kodo millet (*Paspalum scrobiculatum*) (kodo), Japanese barnyard millet (*Echinochloa esculenta*) (sawan), proso millet (*Panicum miliaceum)* (cheena), Indian barnyard millet (*Echinochloa frumentacea*), little millet (*Panicum sumatrense*) (kutki) and tef (*Eragrostis tef*) (Fig. 8.1). Tef [*Eragrostis tef* (Zucc.) Trotter] was included in millets 30 years ago during First Small Millets Workshop held in Bangalore, India (Seetharam et al. 1989), while both tef and fonio or acha [*Digitaria exilis* (Kippist) Stapf and *D. iburua* Stapf] were categorized under small millets by international agricultural organizations in mid-1990s (ICRISAT-FAO 1996). Minor millets are generally short, slender and grassy plants and cultivated in arid, semiarid or mountain zones as rainfed crops. They possess the capacity to grow under adverse climatic conditions in marginal and submarginal soils. They are usually of short duration (60–80 days) and produce about 0.5 t/ha which is better than other crops.

Millets are a good source of nutrients and are rich in vitamins, calcium, iron, potassium, magnesium and zinc. The grains of most of the millets have higher levels of proteins in comparison to wheat and rice. The grains lack gluten and are very effective in regulating the acidity in our bodies. They have very high fiber content which helps in dealing with constipation. They also help in reducing cholesterol due to the presence of niacin (Kumar et al. 2020b). The absence of gluten in their grains makes them the most suitable diet for celiac patients. The straw and crop residues of millets are used as livestock feed in developing countries. In spite of the several

Table 8.1 Description of different millets

Common name	Pearl millet	Foxtail millet	Japanese Barnyard millet	Indian Barnyard millet	Kodo millet	Little millet	Proso millet	Finger millet
Other names	Bulrush millet	Italian millet	Japanese millet	Billion dollar grass	Koda millet		Common millet	Ragi, African millet
Botanical names	*Pennisetum glaucum*	*Setaria italica*	*Echinochloa esculenta*	*Echinochloa frumentacea*	*Paspalum scrobiculatum*	*Panicum sumatrense*	*Panicum miliaceum*	*Eleusine coracana*
Subfamily	Panicoideae	Panicoideae	Panicoideae	Panicoideae	Panicoideae	Panicoideae	Panicoideae	Chloridoideae
Tribe	Paniceae	Paniceae	Paniceae	Paniceae	Paniceae	Paniceae	Paniceae	Eragrostideae
Distribution			Japan, Korea, China	India, Pakistan, Nepal				
Ploidy level	Diploid	Diploid	Hexaploid	Hexaploid	Tetraploid	Tetraploid	Tetraploid	Tetraploid
Chromosome number	$2n = 2x = 14$	$2n = 2x = 18$	$2n = 6x = 36$	$2n = 6x = 36$	$2n = 4x = 40$	$2n = 4x = 36$	$2n = 4x = 36$	$2n = 4x = 36$
Purpose	Food, feed	Food, biofuel	Food, feed	Food	Food, feed	Food	Food, feed	Food, feed
Agronomic benefits	Drought and heat tolerance	Drought tolerance	Early maturity	Early maturity, anti-fungal	Drought tolerance	Abiotic stress tolerance	Drought tolerance	Drought and salt tolerance, early maturity
Health benefits	No gluten	No gluten	No gluten	No gluten	Anti-oxidant, low glycemic index	Anti-diabetic	Anti-cancer	Anti-oxidant, low glycemic index

Pearl millet **Sorghum red** **Kodo Millet**

Little millet **Foxtail millet** **Finger millet**

Barnyard millet **Proso millet**

Fig. 8.1 Different types of millets. (Source: Kumar et al. 2020b)

benefits of millets, the increase in their yield is reduced by various environmental stresses and the changing climate (Singh et al. 2017; Ullah et al. 2019). With the increase in temperature of about 3–4 °C, crop yield is reduced by 35% (Bita and Gerats 2013; Zhao et al. 2017). Global warming reports reveal that Africa and South Asian region are severely affected due to increased global warming and climatic change (Warren et al. 2018; Satyavathi et al. 2021a, b).

With the increasing population and changing climatic scenario, there is a dire need to increase the productivity of millets which is greatly affected by various abiotic stresses like drought, salinity, heat and cold stress. Heat and drought stresses have become a major threat to the millets. Drought stress occurring at the seedling stage and terminal drought affecting the reproductive stage has caused 60% and 40%

yield losses in pearl millet and tef, respectively (Bhattarai et al. 2020). Drought along with heat stress causes a substantial effect on the cellular, molecular and physiological mechanisms of plants. Crop yield and productivity depend on photosynthesis and respiration, and these processes are severely affected by these stresses (Bita and Gerats 2013; Bhattarai et al. 2020; Satyavathi et al. 2021a). Studies suggest that temperature above the threshold level has very harmful effects which in turn limits the adaptation mechanism of the crop (Schlenker and Roberts 2008; Bita and Gerats 2013; Bhattarai et al. 2020). Thus, there is a dire need to develop stress-tolerant high-yielding varieties to prevail over the effects of climate change-associated stresses and improve the yield of millets.

8.2 Origin and Taxonomy

The cereals belong to 8000 species and millets account for 1% of total food grains in the world. *Sorghum bicolor* (L.) Monech originated in Africa about 5000–8000 years ago. The Indian subcontinent is the secondary center of origin. Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is an important millet and originated in western Africa and the Indian subcontinent 2000 years ago. Among small millets, little millet (*Panicum sumentranse* Roth), kodo millet (*Paspalum scrobiculatum* L.), and Indian barnyard millet (*Echinochloa frumentacea* Link) are indigenous, while finger millet (*Eleusine coracana* (L.) Gaertn), foxtail millet (*Setaria* (L.) P. Beauv), and common/proso millet (*Panicum miliaceum* L.) have originated in other parts of the world but reached India long ago.

Sorghum is the most important among the millet group at the global level and belongs to the Poaceae family with the genus sorghum. It is a self-pollinated crop with chromosome $2x = 2n = 20$. The pearl millet belongs to the Gramineae family, subfamily Panicoideae. It possesses $2x = 2n = 14$ and is a cross-pollinated annual C_4 crop (Satyavathi et al. 2021b). Finger millet is an annual herbaceous crop of arid and semiarid areas in Africa and Asia. It is a tetraploid and self-pollinated crop with chromosome number $4x = 2n = 40$ belonging to the family Poaceae. Foxtail millet belongs to the family Poaceae; it is one of the small millet and is cultivated in 23 countries. Barnyard millet also called Indian Barnyard millet which belongs to the family Poaceae with chromosome number $4x = 2n = 36$. Kodo millet is also known as cow grass or Indian crown grass. It originated in tropical Africa and belongs to the family Poaceae with chromosome number $2n = 40$. Little millet is a native crop of India and well adapted to varied soil and environmental conditions. Little millet and proso millet belong to the family Poaceae with chromosome number $2n = 36$.

Pearl millet is an important millet with the greatest potential among all millets. It is drought and heat tolerant of all the grain crops being grown under harsh environmental conditions like high temperature, light soil and semi-growing conditions (Satyavathi et al. 2021a, b). Foxtail millet is high-yielding and drought-resistant and is grown in China, India, Japan, and Russia. Proso millet is a comparatively quick-season, short-duration and irrigated crop with low moisture requirements. After hulling, the grain can be used as nutritious flour for preparing unleavened bread. It was grown in Russia, China, Balkan countries, and Northern India in ancient times. Little millet seems to be related to proso millet but is usually shorter with small panicles and seeds are cultivated on a limited scale with minimum care on poor lands. It matures quickly and can survive under both drought and heat stress. The crop is cultivated mostly in India. Finger millet has a relatively wide range of adoption within moderate temperatures and moisture ranges. Finger millet is highly self-pollinated and South-Central India and Africa are the principal producing regions. Kodo millet is widely cultivated on the poorest soils throughout India.

8.3 Domestication of Millets

Finger millet (*Eleusine coracana* (L.) Gaertn.) has evolved from its progenitor *E. coracana* sub sp. Africana. Domestication of finger millet started almost 5000 years ago in Western Uganda and the Ethiopian highlands and later it extended to the Western Ghats of India in 3000 BC (Hilu et al. 1979). Foxtail millet is an ancient crop cultivated around 10,500 years ago in China (Yang et al. 2012). Proso millet is an annual herbaceous crop belonging to genera *Panicum* with chromosome number $2n = 36$ ($x = 9$). According to Vavilov (1926), China is the primary center of diversity, while Harlan and de Wet (1971) suggested that proso millet was probably domesticated in China and Europe.

8.4 Status of Millets in World and India

The total world production of millets was 31,019,370 tons in 2018 (FAO 2020). Millets contribute around 2% of the total world cereal production, and Asia and Africa produce around 95% of the world's millet (Fig. 8.2). India is the world's largest producer of millets and shares around 41% of the total global production followed by Africa. In India, the area under millets cultivation has declined from 51.44 lakh hectares (1950–1955) to 6.23 lakh hectares (2015–2019), while production has decreased from 21.13 lakh tons to 4.01 thousand tons during this period. On the other hand, productivity declined up to 2005, but later it showed an increasing trend. The trend in the area, yield, and production of millets during 1950–1951 to 2018–2019 are shown in Table 8.2. Sorghum is one of the main staple foods for the people across semiarid tropics. Globally, sorghum is cultivated on 40.67 mha to produce 57.60 million tons with a productivity of around 1.4 tons per hectare. United States (16.04%), Nigeria (12.03%), Mexico (8.42%), Ethiopia (8.35%) and India (7.93%) are the five largest producers of sorghum in the world. With 9.35 million tons of pearl millet grains produced from an occupied area of 7.41 million ha and average productivity of 1391 kg/ha, India is the world's largest producer of pearl millet. The major pearl millet growing states are Rajasthan, Maharashtra, Uttar Pradesh, Gujarat and Haryana contributing to 90% of total production in the country. Rajasthan contributes nearly 45% followed by Uttar Pradesh (19%), Haryana (9%), Gujarat (9%), Maharashtra (6%) and Tamil Nadu (2%). Small millets are cultivated

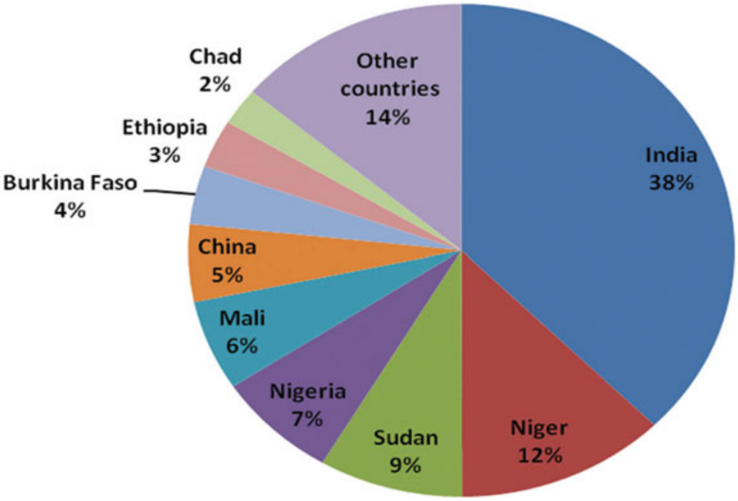

Fig. 8.2 Production of millets (%) in different countries of the world (FAO 2018)

Table 8.2 Trends in area, production and productivity of millets (1950–1951 to 2018–2019)

Year	Area ('000 ha)	Production ('000 ton)	Productivity (kg/ha)
1950–1951 to1954–1955	5144	2113	409
1955–1956 to1959–1960	5098	1987	389
1960–1961 to1964–1965	4755	1960	413
1965–1966 to1969–1970	4697	1697	361
1970–1971 to 1974–1975	4512	1758	389
1975–1976 to1979–1980	4465	1813	405
1980–1981 to 1984–1985	3623	1462	403
1985–1986 to1989–1990	2895	1204	417
1990–1991 to 1994–1995	2040	931	456
1995–1996 to 1999–2000	1540	688	447
2000–2001 to 2004–2005	1246	533	428
2005–2006 to 2009–2010	970	466	480
2010–2011 to 2014–2015	725	429	596
2015–2016 to 2018–2019	623	401	655
CGR	−16.21	−13.58	3.23

on an area of 6.19 lakh hectares with a production of 4.41 lakh tons and productivity of 714 kg/ha in India. Small millets are mostly cultivated in 11 states viz., Madhya Pradesh, Chattisgarh, Maharashtra, Uttarakhand, AP, Odisha, Tamil Nadu, Gujarat, Karnataka, Rajasthan and Nagaland. Among these, Madya Pradesh contributes nearly 30% share in area followed by Chattisgarh (14.41%) and Maharastra (13.52%), while 25.57% of production is done by Madhya Pradesh followed by Uttarkhand (19.23%) and Maharashtra (10.12%). Millets consumption has declined at the rate of nearly 1% at the global level and is anticipated to observe positive movement during 2019–2024 (Anbukkani et al. 2017). During the last two decades, the importance of millets as a staple food in India and the global level has declined due to demand and supply factors, government policies, urbanization and increasing incomes (Michaelraj and Shanmugam 2013; King 2017). More than 50% of the millets production is presently being used as an alternative option in industries instead of their consumption as a staple food (Gowri and Chandrasekaran 2011). Hence, it indicates that there is a need to pay attention to the promotion of these very important nutrient-rich grains to overcome malnutrition and ensure nutritional security. Pearl millet was designated as a nutri-cereal (Gazette of India, No. 133 dtd 13th April, 2018) for production, consumption, and trade and was included in the public distribution system due to its excellent nutritional features. The Government of India has declared the year 2018 as the "Year of Millets," and the FAO Committee on Agriculture (COAG) forum has declared the year 2023 as the "International Year of Millets" to bring millets into the mainstream for exploiting their nutritional rich properties and promoting their cultivation.

8.5 Millets and Various Abiotic Stresses

The climate is changing at a frightening rate, eliciting different abiotic stresses which in turn affect food crops and global food supply. A direct link between the decrease in crop yield and heat/drought stress has been also observed (Bita and Gerats 2013; Alhaithloul 2019; Bhattarai et al. 2020). The millets can play a vital role in mitigating the effects of various stresses like drought, heat, flooding, water logging stress and lodging.

8.5.1 Agronomic Features

Millets have proven to be resilient to the extreme soil and climatic conditions prevailing in the semiarid regions of Africa and Asia. They have C_4 photosynthetic system and can prevent photorespiration by closing their stomata for longer periods and hence can be efficiently used for moisture conservation in scanty water conditions present in the semiarid regions (Warner and Edwards 1988; Brutnell et al. 2010). They can also escape terminal drought which generally takes place at a later stage during the growing season and thus are considered crops of low water requirements (Goron and Raizada 2015). Proso millet is extremely resistant to drought and is believed to be domesticated before rice in China (Lu et al. 2009; Jones and Liu 2009). Similarly, tef was also reported to be tolerant to drought and water logging and considered very useful in poorly drained soils where other crops like maize and wheat are unable to grow. On the other hand, foxtail millet can be also used as a model plant for biofuel studies (Doust et al. 2009).

8.5.2 Millets and Drought Stress

The arid and semi-arid areas face the issue of water scarcity affecting the yield and production of crops to a large extent. Detrimental effects of drought have been reported on the productivity of different crops as well as nutritional quality such as mineral and protein content (Maqsood and Ali 2007; Saleh et al. 2013; Chanyalew et al. 2019). However, millets are quite useful as they can survive even under very low soil moisture content. In studies on wild millet (*Setaria glauca*), foxtail millet (*Setaria italica*), little millet (*Panicum sumatrense*) and proso millet (*Panicum miliaceum*), tef suggest that they can tolerate water scarcity to a great extent. Thus, in sub-Saharan Africa, millets are well adapted to low water potential and are cultivated as a staple food (Maqsood and Ali 2007; Hadebe et al. 2017). Plants employ various abiotic stress tolerance mechanisms (Duque et al. 2013; Mickelbart et al. 2015) to survive in drought-prone areas. The four main mechanisms of adaptation of millets in drought affected areas of the world are (1) drought avoidance, which is the ability of the plant to maintain the balance of water during stress in order to avoid water deficiency; (2) drought tolerance, referred as plant's capacity to produce biomass under reduced water potential; (3) drought escape, a mechanism where plants mature before drought stress; and (4) drought recovery, a state where plants can recover from drought effects after the availability of moisture and give some yield. Millets are supposed to ensure food security in the future and can be used as model crops for stress tolerance in adverse conditions and are a good substitute in drought-prone areas (Plaza-Wüthrich et al. 2016). Various physiological mechanisms like osmotic adjustment, stomatal conductance and cell membrane stability are used by millets for drought tolerance (Kusaka et al. 2005). Osmotic adjustment helps the millets to uphold leaf turgor pressure and hence they can survive under severe drought conditions by absorbing water even from dry soils (Debieu et al. 2018). Similarly, increased root elongation is also very helpful to survive under drought stress (Dichio et al. 2003). Ayele et al. (2001) and Debieu et al. (2018) also observed that a deep, broader and more extensive root system in tef was effective against drought stress.

8.5.3 Millets and Heat Stress

The majority of the millets were found to be resistant to heat stress conditions. Heat stimulates several physiological and molecular mechanisms. Respiration and photosynthesis are mainly affected due to heat stress and exhibit a significant effect on the productivity of crops (Ayele et al. 2001). The annual increase in temperature due to changing climate is a major concern for food security and huge yield losses have been reported in many crops due to heat stress (Barnabás et al. 2008). Crop yield generally increases with an increase in temperature up to a threshold level, but a slight increase in temperature beyond the threshold level can have a detrimental effect on its growth and yield (Deryng et al. 2014). High-temperature stress decreases the electron transport, disturbs the function of photosystem II (PSII) and increases the accumulation of reactive oxygen species (ROS) (Ray et al. 2019). It can also dehydrate the reproductive parts of the plant resulting in seed abortion, reduction in seed number, plant sterility and a short grain filling period (Asthir 2015). Plants have adapted different acclimatization, avoidance and adaptive mechanisms against heat stress through evolution. Millets possess different mechanisms of tolerance like up-regulation of the antioxidant system, heat-shock proteins, transcription factors, ion transporters, signaling molecules and accumulation of osmoprotectants to overcome heat stress (Hatfield and Prueger 2015; Sankar et al. 2021). Millets use different pathways having antioxidants to overcome ROS against different abiotic stresses (Gupta et al. 2013). Various stress-responsive genes such as dehydration responsive element binding (DREB), abscisic acid-stress and ripening-induced (ASR), NAD^+-dependent amino aldehyde dehydrogenase (AMDH), heat shock protein (Hsp), late embryogenesis abundant (LEA) protein, NAC, ERECTA (ER), and cyclase-associated proteins (CAP2) promoter have been found with different adaptive mechanisms against drought/heat stress (Ashraf and Hafeez 2004; Reddy et al. 2012; Divya et al. 2019; Shinde et al. 2020; Meena et al. 2020; Kummari et al. 2020).

8.5.4 Millets and Salinity Stress

Salinization of arable lands has significantly affected soil characteristics and has caused a hazardous effect on the growth of many plants. Improper water drainage systems, irrigation of crops with saline water in arid and semi-arid areas, underlying high salt content rocks and lack of good-quality water due to scanty rainfall are some of the factors causing salinization. Excess levels of Na^+ and Cl^- ions in poor-quality water cause ion-specific toxicity, osmotic changes and nutritional disorders in plants ultimately causing salinity stress (Raipuria 2012; Kumar et al. 2016b, 2020a; Singh et al. 2017; Ullah et al. 2019). It has been reported that 30% of the overall irrigated agricultural land and 20% of the cultivable land have been affected by salinity and it has been projected to elevate to a level of 50% by the year 2050 (Bhattarai et al. 2020). Salinity stress reduces relative water content owing to the osmotic stress in roots because of high salt content and it ultimately leads to dehydration (Makarana et al. 2019; Yadav et al. 2020). Moreover, salinity stress results in reduced germination rates, chlorophyll content, root and shoot growth. Similarly, leaf relative water content and K^+ concentration of leaves result in chlorosis and increase salt and malonaldehyde contents in finger millet (Winkel et al. 1997). Raipuria (2012) conducted salinity studies in pearl millet and reported that out of 21 genotypes studied, genotypes DPR and 18 D23 showed tolerance to salinity with good seedling vigor index and other seedling parameters. Finger millet was also reported to be moderately tolerant to salt stress and combat its detrimental effects by inducing several mechanisms and salt-tolerant genes. On the other hand, proso millet was found to be more tolerant against salinization and alkalization in comparison to finger millet (Abraha et al. 2015). Under saline conditions, the tolerant accessions of proso millet were found to possess higher chlorophyll a content indicating that chlorophyll a content is associated with salt tolerance in proso millet (*Panicum miliaceum*). Hence, the salt tolerance of a plant species decides the degree of reduction in total chlorophyll.

8.5.5 Millets and Water Logging Stress

Water logging stress is the main cause of low productivity in high-precipitation areas. Under water logging stress, the soil pores are filled with water which leads to the accumulation of toxic compounds and inhibition of gas diffusion. This eventually affects roots, stomatal conductance and photosynthesis. Crops like wheat and maize are mostly affected by water logging in black clay soil (vertisols), which has a high water-holding capacity. However, wild millet and proso millet were reported to prove helpful in combating this stress. Plants have various mechanisms to cope with water logging stress (Matsuura et al. 2016), which are induced by hypoxia (reduced oxygen level) or anoxia (complete absence of oxygen). Plants respond to diminished oxygen by carrying out anaerobic respiration, which has also been reported in finger millet (*Eleusine coracana*) (Hossain and Uddin 2011). Anaerobic metabolism is not as efficient as aerobic metabolism, but ATP produced through fermentation supports the cell for a short period. This mechanism requires more sugar than aerobic metabolism; thus, alterations in carbohydrate metabolism are observed in water logging-tolerant species such as finger millet and rice (Kulkarni and Chavan 2013). During water logging stress, spongy tissue containing air gaps, i.e., aerenchyma, which allows gases to move to roots from stems, is formed in tolerant plants (Kulkarni and Chavan 2013). These spaces are developed without (schizogenous) or with (lysigenous) cell death (Parent et al. 2008). Another strategy employed by water logging-tolerant species includes the formation of adventitious roots (Matsuura et al. 2016). The development of adventitious roots has been observed in finger millet (Ni et al. 2018) and sorghum (*Sorghum bicolor*) (Kulkarni and Chavan 2014). Additionally, water logging-tolerant plants possess abundant solubilized sugar (Kumar et al. 2013). Plants such as tef respond to water logging stress by enhancing the activity of nitrogen reductase in the shoots (Sairam et al. 2008).

8.5.6 Millets and Lodging

Lodging can be defined as the permanent bending of a stem from an upright position due to various forces like rain, wind, irrigation water or their combinations (Cannarozzi et al. 2018.) Stems and roots are the main targets of lodging stress. In case of stem lodging, the stem gets tilted towards the soil or breaks, while bending/root disanchoring or a change in the angle between stem and soil because of wind force on the stem or crown causes root lodging (Pinthus 1974; Van Delden et al. 2010; Piñera-Chavez et al. 2016). Millets have been reported to be resistant to various abiotic stresses as well as lodging under low-input conditions in comparison to other cereals. Pearl millet is resistant to various biotic/abiotic stresses and lodging

(Opole 2012). However, there is a need to develop new approaches or improve existing techniques in order to improve lodging tolerance in millet crops. Genetic manipulations for the reduction in plant height or exogenous application of chemicals are some common strategies applied in cereals for lodging. Some other crop management practices that can reduce lodging include tilling practices, changes in seed sowing date, increasing intra-row space and reducing the number of plants in a row (Piñera-Chavez et al. 2016; Cannarozzi et al. 2018). In a study, the application of silicon amendments has been reported to increase the yield in millet tef (Ligaba-Osena et al. 2020). Inhibition of plant growth regulators (PGRs) like gibberellic acid (GA) can be also effective in reducing plant height and improving lodging tolerance. In addition, several other strategies have been used in millets to mitigate or reduce lodging stress and improve the yield. Application of paclobutrazol (PBZ) has been observed to reduce plant height and lodging stress in tef and finger millet (Bizuayehu and Getachew 2021). Jency et al. (2020) informed that mutation in the kodo millet CO3 variety using gamma radiation or ethyl methane sulfonate (EMS) produced non-lodging mutants. M2 mutant was observed to have higher lodging tolerance because of photosynthetic efficiency (PhE) and culm thickness. The lodging-tolerant cultivar "Kegne" was produced by mutation of the alpha-tubulin-1 gene in tef using EMS (Jöst et al. 2015).

8.6 Morphological Responses of Millets to Various Abiotic Stresses

Various traits like short life cycle, thickened cell walls, plant height, dense root systems and small leaf areas are useful for millets in resisting stress. Millets are C_4 plants and hence very beneficial in increasing the water use efficiency (WUE) and nitrogen use efficiency (NUE) (Bandyopadhyay et al. 2017). Drought-related grain filling impairments can be minimized by cultivating high tillering varieties and small panicles and small-sized grains (Aparna et al. 2014). Rainfall patterns can also affect the flowering of pearl millet (Bidinger et al. 2007). It was also observed that pearl millet possesses a fast mechanism of colonization of deeper soil horizons along with a rapidly growing primary root system (Passot et al. 2016). Grain filling and seed set both are affected due to water stress after flowering, which in turn leads to reduced yield in pearl millet. An increase in root length and decrease in shoot length was observed in *Panicum sumatrense* under drought treatments (Ajithkumar and Panneerselvam 2014). It was observed that farmers in dry areas prefer short-duration, high-tillering varieties of pearl millet rendering a good fodder value along with better yield. Short "flowering time" is a good drought escape mechanism in pearl millet (van Oosterom et al. 1996). Depth of pearl millet root can range from 140 cm to 3 m with lateral root spreading depending on the water limitation. Stomatal movements can be adjusted to keep a high transpiration rate leading to maximum fixation of carbon (Vadez et al. 2012). An increased root length to increased water uptake is a good adaptive response of pearl millet to drought stress (Faye et al. 2019).

Stay green, a drought-tolerance trait, is a very useful feature of some genotypes where active photosynthesis gets prolonged due to delayed leaf senescence by a complex signaling network. This allows plants to continue the photosynthesis in spite of soil water content which in turn helps in maintaining a good grain yield even under drought conditions (Serba and Yadav 2016). Several physiological and morphological responses are found among drought-tolerant pearl millet accessions such as upright folding of leaves to reduce the surface area of evaporation, more capacity of young leaves and stems for osmotic adjustment, and higher accumulation of NO_3^-, K^+, amino acids, sucrose, proline, glucose, and ammonium compounds (Kusaka et al. 2005). In dry soils, foxtail millet plants form a large rhizosheath with the help of longer and denser root hairs enabling deeper penetration and production of more root biomass (Liu et al. 2019). Phenotypic adaption of large root systems was observed in plants due to phosphorus (P) limitation. Phosphorus adaptation caused lateral root proliferation in foxtail millet by increasing root number, length, and density which helped in increasing the root absorptive surface area. Under stress conditions, auxins and gibberellins stimulate root development (Nadeem et al. 2020). Finger millet exhibited higher metal tolerance than pearl millet and oats. It showed maximum accumulation of nickel (Ni) in roots which can be useful for the plants to mitigate the effects of metal toxicity (Gupta et al. 2017). The increased leaf tensile strength resulting into increased drought tolerance was observed among three species of *Eragrostis* (Balsamo et al. 2006).

8.7 Biochemical and Physiological Responses to Various Abiotic Stresses in Millets

Osmoprotectants may play an important role in enhancing hyperosmolarity caused by salinity stress and thus can establish cellular ionic homeostatic conditions. Proline is a compatible osmotic molecule and plays a significant role in osmotic potential adjustment leading to improved drought tolerance. It is also involved in antioxidative defense, metal chelation and stress signaling pathways (Shivhare and Lata 2019). Antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) are involved in the mechanism of adaptation of the plants exposed to oxidative damage under stress conditions. An elevated expression of secondary metabolite genes involved in alkaloid, flavanols, wax, terpenoid, mevalonic acid (MVA), lignin and Shikimic acid (SA) metabolic pathways were reported in pearl millet at the flowering stage under drought conditions in comparison to the vegetative stage and assisted in maintaining osmotic potential and membrane integrity (Shivhare and Lata 2019). An increase in proline, total soluble proteins, and epicuticular wax contents were observed in pearl millet under a saline environment indicating that various physiological and biochemical responses are triggered to overcome salinity stress (Makarana et al. 2019). Ascorbate, a water-soluble antioxidant found in plants, is required for the efficient activity of APX and thus can play a significant role in the scavenging process of converting H_2O_2 into H_2O. An increase of 200% ascorbate was observed in drought-tolerant varieties of finger millet indicating that ascorbate is essential for increasing tolerance against drought stress (Bartwal et al. 2016). In finger millet, the biochemical adaptive response to salt stress resulted in a reduction in sugar concentration, elevated proline content and total leaf proteins (Mukami et al. 2020). Phytohormones like auxin, cytokinin, ABA, gibberellin and ethylene play a significant role in stress-adaptive responses and regulation of gene expression under stress conditions (Xu et al. 2019). Heat-tolerant variety of foxtail millet recorded reduced root respiration, low photosynthetic and stomatal conductance rates and accumulation of protective metabolites (serine, valine, threonine, glucose, fructose, maltose, itaconate, isomaltose, malate) in roots with the enhanced deployment of carbon and nitrogen (Aidoo et al. 2016). The effects of drought/heat stress were observed to act as major regulators of abscisic acid (ABA) biosynthesis leading to 7–8 times increase in ABA level in foxtail millet (Saha et al. 2016). Metal stress in millets increased activities of POD and SOD with reduced CAT activity (Gupta et al. 2017). Salt-tolerant varieties of finger millet recorded lower shoot Na^+/K^+ ratios and much higher leaf carbohydrate content indicating that ion regulation along with carbohydrate metabolism can lead to salt tolerance in finger millet (Vijayalakshmi et al. 2014). The different physiological and biochemical adaptations of millets to various abiotic stresses are summarized in Table 8.3.

8.8 Molecular Responses of Millets to Various Abiotic Stresses

Plants perceive and differentially express the responses to different environmental factors at the molecular level. Drought-responsive genes like NAC2, CDPK and U2-snRNP (small nuclear Ribonucleo Protein particles) help in regulating gene expression, while plant synaptotagmin is responsible for maintaining the integrity of plasma membrane, aquaporin forms membrane channel, MPK17–1 (Mitogen-Activated Protein Kinase) involved in signaling while Scy protein was reported to regulate the pathways of apoptosis during drought tolerance in minor millets (Patil et al. 2017). The upregulated expression of SiPHT1;1 and SiPHT1;4 in roots and that of SiPHT1;2 in roots and shoots for enhanced uptake and translocation of phosphorus was observed in stress conditions in foxtail millet (Faye et al. 2019). SiLEA14, a late embryogenesis abundant (LEA) gene, was induced by osmotic, NaCl stress and ABA in foxtail millet. In transgenic *Arabidopsis,* it increased salt tolerance, but when overexpressed in transgenic foxtail millet, it led to increased tolerance to drought and salt stresses (Wang et al. 2014). Lipid transfer gene (SiLTP) enhanced salt and drought tolerance by escalating the total soluble sugar and proline contents upon expression in foxtail millet tissues. Pan et al. (2016) reported that this gene in turn may prove helpful for enhancing salt and drought stress tolerance in crop plants. In foxtail millet, CBL-interacting protein kinase (CIPK) genes were reported to play a major role in stress responses and signaling pathways during plant development. The majority of SiCIPK genes are mainly induced by cold and salt stresses and other genes by giving PEG and ABA treatments (Zhao et al. 2019). SiMYB42 (myeloblastosis) transcription factor was upregulated under salt, drought and low

Table 8.3 Physiological and biochemical adaptations of millets under different abiotic stresses

Millet	Variety	Trait (drought/ heat/salt adaptive)	Adaptive mechanism	References
Pearl millet	AVKB-19	Salt adaptive	Accumulated higher osmolyte (soluble protein, proline) concentration	Makarana et al. (2019)
Foxtail millet	Damaomao (DM)	Drought tolerant	Increase in soluble sugar and proline concentrations, moderate rate of decline of RWC and chlorophyll, significant increase in ABA and JA phytohormones	Xu et al. (2019)
Foxtail millet	523-P1219619	High soil temperature tolerance	Efficient utilization and assimilation of membrane carbon and nitrogen, accumulation of stress-related protective metabolites (fructose, serine, valine, threonine, malate, glucose, itaconate, isomaltose maltose) in roots	Aidoo et al. (2016)
Finger millet	Trichy 1	Salinity tolerant	Accumulation of high concentration of carbohydrates, maintain low Na+/K+ ratios under stress conditions	Vijayalakshmi et al. (2014)
Finger millet	PRM6107 and PR202	Drought tolerant	200% increase in ascorbate content, limiting accumulation of ROS	Bartwal et al. (2016)
Finger millet	FM/ST/01	Drought tolerant	Elevated accumulation of proline, glycine betaine, and total soluble sugars. Increased activity of antioxidant enzymes (SOD, CAT, APX, GPX)	Mundada et al. (2020)

nitrogen stresses and regulated the expression of nitrate transporter genes by enhancing the plant tolerance to low nitrogen conditions in foxtail millet (Ding et al. 2018). Similarly, calcium-dependent protein kinases (CDPK) genes of foxtail millet have a crucial role in signaling pathways and improving drought resistance. There are 29 CDPK genes in foxtail millet that play an important role in drought stress resistance and SiCDPK24 had the highest transcript levels under drought conditions (Yu et al. 2018). NAC (NAM, ATAF, and CUC) like transcription factor, SiNAC110, localized in the nucleus was found to be induced by salt, drought and other abiotic stresses in foxtail millet. Overexpression of this gene resulted in increased salt and drought tolerance in *Arabidopsis* due to increased gene expression for Na^+/K^+ transport, aqueous transport proteins and proline biosynthesis (Xie et al. 2017). In foxtail millet, SiNF-YA1, NF-Y (Nuclear Factor Y) genes and SiNF-YB8 were greatly induced by H_2O_2 and ABA under drought and salt stresses. These genes activated stress-related genes, chlorophyll contents, SOD, RWC, CAT and POD and enhanced the antioxidant system (Feng et al. 2015). SiATG8a, an autophagy-related gene, confined in the membrane and cytoplasm, was reported to be involved in plant responses to nitrogen starvation and drought stress in foxtail millet. Overexpression of SiATG8a was responsible for plant tolerance to nitrogen starvation and drought in transgenic *Arabidopsis* (Li et al. 2015).

Terpene synthase (TPS) gene, SiTPS19, exhibited significantly higher expression under both abiotic and biotic stresses in foxtail millet revealing that it can be useful for crop resilience and can play a major role in defense and environmental adaptation (Karunanithi et al. 2020). Upregulation of the AKR1 gene (Aldo-Keto Reductases) was observed in leaves and roots of foxtail millet with increased drought and salt stress indicating that AKR1 gene is involved in physiological defense against oxidative stress (Kirankumar et al. 2016). Ten LIM genes with cis-acting elements were also reported in foxtail millet for abiotic stresses. SiWLIM2b was reported to be highly upregulated in foxtail millet under abiotic stress. It enhanced survival rate with elevated relative water content and less cell damage when overexpressed in transgenic rice under drought conditions indicating that SiWLIM2b is associated with phenylpropane pathway and gene regulation and improves drought stress tolerance (Yang et al. 2019). Stress-induced gene, SiARDP (ABA-responsive DREB-binding protein gene), showed increased transcription level in foxtail millet seedlings against salinity, drought and low temperature stresses and ABA treatment. SiAREB1 and SiAREB2 (ABA-responsive element binding) transcription factors regulate gene expression of SiARDP which is associated with signaling pathways and plays an important role in stress response and increased stress tolerance in plants (Li et al. 2014). SiSET14 gene showed upregulation in foxtail millet under cold stress. SET [(Su (var) 3–9, E (Z), and Trithorax)] domain proteins are putative candidates for histone lysine methyl transferases. It showed abiotic stress tolerance to transgenic yeast cells on expression in a yeast system suggesting the role of SiSET genes in abiotic stress tolerance in foxtail millet (Yadav et al. 2016). The acetyl-coenzyme A carboxylase (ACCase) gene in foxtail millet showed herbicide (sethoxydim) resistance and can be used in the development of transgenic maize with herbicide resistance and higher oil content (Dong et al. 2011).

In pearl millet, three antioxidant genes, namely, APX, SOD and glutathione reductase (GluR), showed higher expression level genotypes resulting in higher osmotic stress tolerance in the seedlings under drought stress induced by polyethylene glycol (PEG) (Shivhare and Lata 2019). A drought-tolerant QTL was identified in pearl millet which played role in reducing salt uptake and enhancing growth under salt stress conditions (Sharma et al. 2014). Three abiotic stress-inducible promoters-(i)—Cytoplasmic Apx1 (Ascorbate Peroxidase) which is involved in the removal of H_2O_2, (ii) Dhn (Dehydrin)—plays role in the stabilization and protection of cell membrane and enzymes from low temperature and ROS and (iii) Hsc70 (Heat Shock Cognate) which is known for chaperone function by proper folding and translocation of newly synthesized proteins were also reported in pearl millet. They are stimulated under high temperature, drought and salt stresses to confer abiotic stress tolerance and can be helpful to develop stress-tolerant crops (Divya et al. 2019). PgPAP18 gene of the purple acid phosphatase (PAP) family exhibited 2 to 3-fold upregulation under drought, salt, heat and metal stresses in pearl millet. In addition, they can play a crucial role in abiotic stress tolerance by scavenging ROS and crosstalk between stress signaling pathways (Reddy et al. 2017). Pearl millet WRKY transcription factors can also provide resistance against different biotic/abiotic stresses. Ninety-seven pgWRKY genes with 127 cis-regulatory elements were identified in pearl millet for various abiotic and biotic stresses (Chanwala et al. 2020).

In finger millet, stress-induced transcription factors, EcNAC1 (NAM, ATAF1/2, and CUC2), stimulated by drought and salinity were characterized and expressed in transgenic tobacco plants resulting in increased tolerance to different abiotic stresses like salinity and osmotic stress (Ramegowda et al. 2012). Proteolipid genes of the plasma membrane (PgPmp3-1 and PgPmp3-2) along with other proteins played role in enhancing the expression of genes during cold, drought, and salt stresses and imparted abiotic stress tolerance by encoding hydrophobic proteins and maintaining cellular ion homeostasis in pearl millet (Yeshvekar et al. 2017). Transcriptome analysis of finger millet confirmed up-regulation of several drought stress signaling cascade genes like Calcineurin B-like protein (CBL) Interacting Protein Kinase 31 (CIPK31) which is, highly stress responsive; Protein Phosphatase 2A (PP2A) caused 2 fold increase in drought stressed finger millet; Farnesyl Pyrophosphate Synthase (FPS) for regulating farnesylation of proteins involved in ABA signaling; Signal Recognition Particle Receptor (SRPR α); and basal regulatory gene TBP (TATA-binding protein) Associated Factor 6 (TAF6). Thus, it was revealed that drought can activate different genes associated with housekeeping or basal regulatory processes in finger millet (Parvathi et al. 2019). EcHSP17.8, a heat-shock protein gene, showed upregulation of up to 40-folds under heat, NaCl, mannitol and oxidative stresses in finger millet and showed maximum expression in root tissues (Chopperla et al. 2018). Transcription factor, EcbZIP60, of basic leucine zippers (bZIPs) family was found to be highly upregulated under drought, osmotic and salinity stresses in finger millet indicating the association of EcbZIP60 in adaptation to different stresses by upregulation of genes involved in unfolded protein-protein-responsive pathways (Babitha et al. 2015). Upon recognition of stress signal by different cell membrane receptors and transporters like enzyme-linked receptor (ELR), GPCR (G-protein-coupled receptor), calcium channels, and ion transporters, abiotic stress signaling cascade was activated. The cytosolic Ca^{2+} resulted in an increased response to hyperosmotic stress, while oxidative stress elevated ROS levels. The signal is transmitted downstream with the help of relay molecules and converted into the intracellular signal by secondary messengers [i.e., Ca^{2+}, ROS, cAMP, cGMP, nitric oxide (NO)] which in turn further activate the kinase cascade (protein kinases i.e. CDPK; MAPK) and enhances phytohormone signaling (abscisic acid, ABA; ethylene-ET; salicylic acid, SA; jasmonic acid, JA). Kinases regulate the sequential phosphorylation/dephosphorylation of proteins and activation of cascade components. The phosphorylation/dephosphorylation of transcription factors (TF's) result in their upregulation/downregulation. Various up-regulated TFs from different millets such as [*Eleusine coracana* (EcNAC1, EcbZIP60), *Setaria italica* (SiMYB42, SiNAC110, SiNF-YA1, SiNF-YB8, SiAREB1, SiAREB2) and *Pennisetum glaucum* (pgWRKY)] are involved in regulating the expression of stress-responsive/defensive genes in different millets [*Setaria italica* (SiLEA14, SiARDP, SiCDPK24, SiCIPK,SiATG8a, SiLTP, SiWLIM2b), *Pennisetum glaucum* (PgApx pro, PgDhn pro, PgHsc70, PgPAP18, PgPmp3–1, PgPmp3–2), *Eleusine coracan*a (EcHSP17.8), APX, SOD, GlutR, U2-snRNP, MPK17–1, AKR1]. These genes play a significant role in various abiotic stress responses like protective metabolites accumulation, osmoregulation, increased root length and denser roots, decreased transpiration, reduced stomatal conductance, elevated nitrogen content, reduced rate of photosynthesis, increased epicuticular wax content, improved activity of antioxidant enzymes and phytohormones, maintenance of membrane integrity and increased NUE and WUE. Various genes identified in different millets for tolerance to abiotic stresses are summarized in Table 8.4.

8.9 Crop Improvement

Though millets are considered good for health and have food and health-related benefits in addition to adaptation to adverse environmental conditions, still their productivity is very low and there is a high need to enhance their deployment as food crops. Conventional breeding approaches like selection from landraces, pedigree selection, mutation breeding, hybridization to create new variations and exploitation of hybrid vigor resulted in significant improvement in the production and release of new cultivars of different millets (Serba and Yadav 2016; Vetriventhan et al. 2020; Serba et al. 2020; Srivastava et al. 2022). However, even under optimum growth conditions, the yield of millets is still much lower than the major cereals. There are various potential approaches like markers, next-generation sequencing and genomics-assisted breeding to enhance the stress tolerance and productivity of millets. Different sources of resistance available against abiotic stresses in millets are summarized in Table 8.5.

8.9.1 Genomic Tools Used for the Improvement of Millets

With the advances in genome sequencing technologies, the whole genome sequences of sorghum, pearl millet, foxtail millet, finger millet, tef and proso millet (Paterson et al. 2009; Zhang et al. 2012; Bennetzen et al. 2012; Cannarozzi et al. 2014; Varshney et al. 2017; Hittalmani et al. 2017; Zou et al. 2019; VanBuren et al. 2020) are available and can be used for genetic improvement of these crops. Expressed sequence tags (ESTs) of sorghum, pearl millet, finger millet and foxtail millet are also available in the public database and can be used as an important source for the development of SSRs, insertion-deletions (indels), single nucleotide polymorphisms (SNPs), intron length polymorphism (ILP) markers, etc. through computational approaches using bioinformatics tools. Genome-wide SNPs have been identified in pearl millet (Tift 23D2B1-P1-P5) recently through whole-genome shotgun (WGS) and bacterial artificial chromosome (BAC) sequencing approaches (Varshney et al. 2017). In addition, 1994 pearl millet genotypes, comprising of

Table 8.4 Role of different millets and genes identified for conferring tolerance to abiotic stresses

Type of stress	Genes involved	Role	References
Pearl millet			
Cold/salt stress	PgPmp3-1 and PgPmp3-2	Upregulation of PgPm3 genes under salt/cold stress governed salt/cold stress tolerance in plants	Yeshvekar et al. (2017)
Drought/ salinity/ oxidative stresses	Glutathione reductase	Identification and characterization of genes and their families suggested their significant role in stress responsive pathways	Achary et al. (2015)
	Dehydroascorbate reductase		Pandey et al. (2014)
	Late embrogenesis abundant (LEA) protein		Reddy et al. (2012)
	B-carbonic anhydrase		Kaul (2011)
	Ascorbate peroxidase		Reddy et al. (2009)
	Voltage-dependent anion channel (VADC)	Structural and functional characterization of VDAC and heterologous overexpression in yeast lead to tolerance against different abiotic stresses	Desai et al. (2006)
Foxtail millet			
Drought stress	SiCDPK24	Overexpression in transgenic *Arabidopsis* improved its drought resistance	Yu et al. (2018)
	SiWLIM2b	Increased drought resistance in transgenic rice with higher RWC and less cell damage	Yang et al. (2019)
Drought/salt stress	SiNF-YA1 and SiNF-YB8	Increased stress tolerance in tobacco by activating stress-related genes and improving physiological traits	Feng et al. (2015)
Salt/drought stress	SiLEA14	Enhanced salt tolerance of transgenic *Arabidopsis*; it's overexpression in transgenic foxtail millet led to improved salt and drought tolerance	Wang et al. (2014)
Drought/salt stress/low temperature	SiARDP	Enhanced drought and salt tolerance in transgenic *Arabidopsis*. The DREB transcription factors can regulate the expression of SiARDP	Li et al. (2014)
Herbicide stress	ACCase	Overexpression in transgenic maize lead to increased herbicide (sethoxydim) resistance	Dong et al. (2011)
Osmotic/salt stress	AKR1	Role in antioxidant defense-related pathways	Kirankumar et al. (2016)

(continued)

Table 8.4 (continued)

Type of stress	Genes involved	Role	References
Nitrogen starvation/ drought stress	SiATG8a	Overexpression in *Arabidopsis* conferred tolerance to nitrogen starvation and drought stress	Li et al. (2015)
Salt/drought stress	SiLTP	SiLTP expression increased salt and drought tolerance in transgenic tobacco	Pan et al. (2016)
Drought/ oxidative stress	Abscisic acid stress ripening gene	Overexpression of ASR1 in tobacco confers to drought and oxidative stress	Feng et al. (2016)
Drought stress	Autophagy-related gene (ATG)	Overexpression of ATG 8a in *Arabidopsis* resulted in drought tolerance	Li et al. (2015)
	Late embryogenesis abundant protein (LEA)	Overexpression of LEA 14 in *Arabidopsis* and foxtail millet resulted in drought tolerance	Li et al. (2014)
	WD-40	Identification of the association of WD-40 in dehydration stress-responsive pathway	Mishra et al. (2012)
	12-Oxophytodienoic acid reductase (OPR1)	Cloning and characterization of OPR1 showed hormone-independent role of OPR1 in conferring drought tolerance	Zhang et al. (2007)
Finger millet			
Drought/ salinity/ oxidative stress	EcbZIP60	Expression in transgenic tobacco caused tolerance to drought, salinity, and oxidative stresses by maintaining cellular homeostasis via upregulation of unfolded protein responsive pathway genes	Babitha et al. (2015)
Heat stress/ NaCl stress	EcHSP17.8	40-Fold upregulation under heat stress and early responsive gene under heat stress tolerance	Chopperla et al. (2018)
Drought stress	NAC67	Overexpression of NAC67 gene in rice for drought stress tolerance	Rahman et al. (2016)
Drought/ salinity/ oxidative stresses	NAC1	Overexpression of NAC1 gene in tobacco confers tolerance to different abiotic stresses	(Ramegowda et al. 2012)
	bHLH57	Overexpression of bHLH57 gene in tobacco resulted in tolerance to drought stress, salinity and oxidative stresses	Babitha et al. (2015)
Drought stress	Dehydrin7	Overexpression of Dehydrin 7 gene in tobacco plays role in drought tolerance	Singh et al. (2015)

Table 8.5 Sources of resistance for abiotic stresses to meet the climate change

Crop	Traits	Sources
Sorghum	Drought	SPV772 X S35-38, SPV 772 X S35-29, SPV 772 XS 35-21, IC 343573, IC 343584, IC 392147, IC 392124, IS 3267, IS 3265, IS 3306, IS 3302, IS 331
Pearl millet	Heat	H77/833-2, H77/29-2, 77/371, 77/371XBSECTCP1, 96AC-93, 1305, CVJ 2-5-3-1-3, Togo II, 99HS-18, G73107, 77/371
	Drought	863B, PRLT 2/89-33, CZP 980, ICMP 83720, ICMV 9413, ICMV 94472
	Salinity	ICMB 02111, ICMB 00888, ICMB 95333, ICMB 94555, ICMB 01222, ICMP 451; IP 3732, IP 3757, IP8210; PRLT 2/89-33, 10876, 10878 (Sudan) 18406 18570 (Namibia); ICMV93753, ICMV 94474 (India); and DPR-18, 863-B, CZI 9621, CZI 98-11, HTP 94/54
Finger millet	Drought	TNAU 1226, VL 348
	Root traits	GE 4999, GE 1013, GE 5192, GE 3069, GE 4222
	Heat tolerance	HR 374, GE 4, Chilika, GE 1013, GE 99, GE 1274, L 5, GE 128, GE 3885, GE 145, GE 909, GE 1815, GPU 26, GE 2370, KR 301, GE 3090, Poorna, GE 3265, GE 3266
	High photosynthesis	GE 1013, GPU 67, GE 996
Foxtail millet	Early maturity	TNSI 327, RAU 12, TNSI 329, SiA 326, TNSI 323, early and grain yield, prasad, early maturing, SiA 3221, ISe 1547, TNAU 26, RFM 68, SiA 3159, SiA 3088, SiA 3222, SiA 3093, TNAU 264, SiA 3095, SiA 3232
Kodo millet	Early maturity	SVT 8, RK 390–25, early maturing, TNAU 85, TNAU 192, RK 77, RPS 1011
Little millet	Early maturity	GKM 368, early maturing, RLM 42, BR 1, RLM 4-2, KRI 10-03, RLM 368
Proso millet	Early maturing	IPM 6826, IPM 1621, IPM 2880, IPM 2495, IPM 2816, early maturing, TNAU 201, TNAU 207, TNAU 202, TNAU 194, IPM 2559, GPUP 23

963 inbred lines and 31 wild accessions were re-sequenced for understanding the population structure, genetic diversity and domestication (Varshney et al. 2017). Next-generation sequencing (NGS)-based and array-based platforms are popularly used for high-throughput SNP genotyping in many crop species, while platforms such as targeted GBS/low-density arrays and single markers were also employed for medium-to-low-throughput genotyping (Varshney et al. 2017; Srivastava et al. 2020; Jarquin et al. 2020). Pearl millet inbred germplasm association panel (PMiGAP) developed at ICRISAT comprises 346 lines consisting of germplasm lines, landraces and breeding lines representing global pearl millet diversity. Genome editing is another approach for trait improvement which has gained a lot of attention in recent times because of its good potential for specific allele manipulation. The CRISPR/Cas9 system has become a very effective technique for editing plant genome/genes for stress tolerance and gaining high productivity. Precise and high-throughput genotyping and phenotyping of individuals of the mapping/

breeding population either for trait mapping or cultivar development is vital for the identification of effective genomic regions or quantitative trait loci (QTL) for the target traits and also for the development of superior lines with climate resilience. The different genomic tools available in millets are summarized in Table 8.6.

8.10 Nutritional and Health-Related Benefits of Millets

Millets have several nutritional advantages and health-related benefits and are hence considered nutritious and healthy foods (Saleh et al. 2013; Goron and Raizada 2015; Satyavathi et al. 2021a, b). Their grains are rich in protein, micronutrients and phytochemicals. They contain 7–12% protein, 2–5% fat, 65–75% carbohydrates and 15–20% dietary fiber. Even the quality of the proteins in millets is better than in major cereals like rice and maize. Due to the presence of fewer cross-linked prolamins, they have a higher protein digestibility index as compared to other grains. Though millet proteins are a poor source of lysine, they have a better profile of essential amino acids in comparison to other cereals. Millets also contribute to the high antioxidant system of the body due to the presence of phytates, polyphenols, phytosterols, pinacosanols, tannins etc. They protect the body from aging, different types of metabolic diseases, cancer, cardiovascular diseases etc. but the dietary constituents responsible for such associations are not fully understood. Antioxidants like carotenoids (β- carotene), tocopherol (vitamin E) and ascorbic acid (vitamin C) have been reported to contribute to the observed protection. Recent epidemiological evidence further indicates that the beneficial effects of a high intake of millets on the risk of diseases of aging may not be exclusively due to the antioxidants only but other antioxidant phytochemicals like flavonoids. Millet grains are also rich in phytic acid, which is known to lower cholesterol and phytate and is associated with reduced cancer risk. Millets are gluten-free, therefore an excellent option for people suffering from celiac diseases often irritated by the gluten content of wheat and other more common cereal grains.

Hence, the potential of millets like foxtail millet and tef is known worldwide among people due to gluten-free grain (Jeffrey 2015). They are also useful for people who are suffering from atherosclerosis and diabetic heart disease. Seeds of finger millet possess important amino acids like methionine, threonine, valine and lysine which are deficient in the diets of millions of the poor people who usually consume starchy staples like cassava (Sripriya et al. 1997). Proso millet contains essential amino acids like leucine, isoleucine and methionine making its protein quality higher than wheat (Kalinova and Moudry 2006). The seeds of fonio contain leucine, methionine and valine making it a very nutritious millet (Vodouhè 2004). The grains of widely cultivated pearl millet possess high amounts of starch, minerals, vitamins and fibers (Satyavathi et al. 2021a, b).

The millet species (foxtail, kodo, proso, pearl millet, finger and little) were reported to have an anti-proliferative property and are found to be very useful in the prevention of cancer (Bhatt et al. 2011). The presence of phenol extracts is responsible for the anti-proliferative properties in millets. Kodo millet was reported

Table 8.6 Genomic tools available for improvement of millets against various abiotic stresses

Types of DNA markers	No. of markers	References
Sorghum		
Genomic SSRs	2306	Bhattramakki et al. (2000), Kong et al. (2000), Taraminio et al. (1997), Li et al. (2009), Jaikishan et al. (2013), Mutegi et al. (2011) and Billot et al. (2012)
Genic SSRs	2929	Schloss et al. (2002), Ramu et al. (2009), Arun (2006), Srinivas et al. (2009) and Reddy et al. (2012)
Genomic-wide SSRs	5599	Yonemaru et al. (2009)
ILPs	37,861	Jaikishan et al. (2015)
EST-SNPs	53,010	Girma (2009) and Singhal et al. (2011)
Genome-wide SNPs	6,551,543	Zheng et al. (2011), Nelson et al. (2011), Morris et al. (2013) and Mace et al. (2013)
Pearl millet		
Genomic SSRs	112	Qi et al. (2001, 2004), Allouis et al. (2001), Budak et al. (2003) and Yadav et al. (2007)
Genic SSRs	326	Senthilvel et al. (2008) and Rajaram et al. (2013)
Genomic SNPs	228	Sehgal et al. (2012)
Genome-wide SNPs	100,525	Hu et al. (2015) and Punnuri et al. (2016)
DArT markers	514	Supriya et al. (2011) and Ambawat et al. (2016)
Finger millet		
Genomic SSRs	10,501	Dida et al. (2007), Gimode et al. (2016) and Musia (2013)
Genic SSRs	862	Arya et al. (2009), Naga et al. (2012), Obidiegwu et al. (2014), Nirgude et al. (2014), Nnaemeka (2009) and Kalyana et al. (2014a, b)
Genome-wide SNPs	46,285	Gimode et al. (2016) and Kumar et al. (2016a)
Foxtail millet		
Genomic SSRs	395	Jia et al. (2007, 2013), Heng et al. (2011) and Gupta et al. (2012, 2013)
Genic SSRs	17,105	Jia et al. (2007, 2013), Kumari et al. (2013) and Xu et al. (2013)
Genome-wide SSRs	29,075	Pandey et al. (2013) and Zhang et al. (2014)
Indels	55,348	Bai et al. (2013)
ILPs	5221	Gupta et al. (2011) and Muthamilarasan et al. (2013)
Genome-wide SNPs	4,261,599	Bai et al. (2013) and Jia et al. (2013)
Genome-wide miRNA-based markers	176	Yadav et al. (2014a)
Genome-wide TE-based markers	20,275	Yadav et al. (2014b)
Proso millet		
Genomic SSRs	525	Cho et al. (2010) and Liu et al. (2016)

(continued)

Table 8.6 (continued)

Types of DNA markers	No. of markers	References
SSRs transferable from switchgrass	339	Hu et al. (2009) and Rajput et al. (2014)
SSRs from transcriptome sequence	35,000	Yue et al. (2016)
EST-SSRs	8139	Jiang et al. (2018)
SNPs from transcriptome sequence	406,000	Yue et al. (2016)
Genome-wide SNPs	69,981 raw	Rajput et al. (2016)
Kodo millet		
Genome-wide SNPs	3641	Johnson et al. (2018)
Little millet		
Genome-wide SNPs	2245	Johnson et al. (2018)
Barnyard millet		
Genome-wide SNPs (*E. colona*) genome-wide SNPs (*E. crus-galli)*	10,816	Wallace et al. (2015)

to have maximum phenolic content, while it was minimum in foxtail millet (Rao et al. 2011). Little millet is considered to be an antidiabetic grain and has a lower glycemic index than rice, wheat and sorghum (Itagi et al. 2013). Proso millet significantly elevates plasma adiponectin and HDL cholesterol levels and caused a significant decrease in insulin levels relative to a casein diet in type 2 diabetic mice (Park et al. 2008). Processing of the grain can also enhance the value of useful antioxidants and related products. Various processing techniques like germination, roasting and steaming enhanced levels of phenolics, tannins and flavonoids significantly in little millet (Pradeep and Guha 2011). A novel peptide extracted from barnyard millet and foxtail millet was found to have strong antifungal properties and useful against four fungal species like *Alternaria*, *Botrytis*, *Fusarium*, and *Trichoderma* (Xu et al. 2011; Nolde et al. 2011).

8.11 Future Prospects of Millets

Millets have an untapped potential under adverse soil and climatic conditions and survive the harsh climatic conditions. This makes them an ideal solution to the challenge of climate change. Millets with their versatility in stress adaption and nutritive value are becoming more important crops in the present era of extreme climate variability and high dietary-induced malnutrition. There is an immediate need for giving high priority to millets to face the present-day challenging scenario including global warming, water scarcity mounting to frightening proportions and malnutrition in the developing countries. In order to improve the demand for millets, it is important to popularize the health benefits of these millets and crop improvement should focus on trait-specific breeding. Thus, there is a great necessity for interdisciplinary research to address these issues and to evolve efficient technology and its transfer to the farmers' fields for millet utilization and improvement.

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Triticale (X *Triticosecale* Wittmack): Role and Responses Under Abiotic Stress

9

Seyyed Hamid Reza Ramazani and Mohammad Zabet

Abstract

Triticale (X *Triticosecale* Wittmack) is an allotetraploid and man-made cereal generated by the initial crossing between wheat (*Triticum*) and rye (*Secale*) with an AABBRR genome, hoping to combine different indices of high yield potential and quality grain protein of wheat and high resistance to abiotic stresses of rye. In the meantime, although suitable traits such as high-yielding storage and grains have been transferred to the mentioned plant, it is still sensitive to most abiotic stresses. However, there are several approaches, including planting-resistant cultivars, alternative cultivation, intercropping, bio-fertilizers, etc., to overcome abiotic stresses, e.g., drought, salinity, temperature, elements, and others. In general, since triticale is a promising crop hybrid that can be a good alternative to cultivating cereals in adverse environmental conditions, appropriate strategies to overcome the adverse effects of abiotic factors should be considered, and further studies are needed to understand this area.

Keywords

Grain yield · Selection · Stress resistance · Triticale · Selection

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9.1 Introduction

Cereals have been a major component of the human diet for thousands of years and played an essential role in human health and the formation of human civilization (Yang 2018; Ramazani 2020). In the meantime, triticale (X *Triticosecale* Wittmack), the first successful human-made small grain cereal with A and B genomes of wheat (*Triticum turgidum* L., *Triticum aestivum* L.) and the R genome of rye (*Secale cereale* L.), is an allotetraploid (or amphipolyploid) and self-pollinated cereal developed by crossing between wheat as the female parent and rye as the male parent by the botanist Wilson in 1875 (Lelley 2006; Hills et al. 2007; Mergoum et al. 2009, 2019; Dumbravă et al. 2014; Ramazani et al. 2016; Biel et al. 2020). This plant can be grown in a wide range of agroecologies, up to 3000 m above sea level, and under soil conditions (Bezabih et al. 2019). Also, it seems to be an interesting alternative to other cereals under unfavorable conditions so that its cultivation is easily done in rainfall conditions of less than 350 mm (Gobeze et al. 2007; Estrada-Campuzano et al. 2008). In general, triticale is involved in the diet of humans and animals (as a commercial cereal with high potential and has a better dry matter in comparison with different wheat genotypes), spirits, and beer (Krusteva and Karadjova 2011; Ramazani et al. 2016). Triticale grains have a high degree of nutritional value like wheat (Glamočlija et al. 2018) with slightly lower contents of fats (2.09%), proteins (13.05%), and moisture (10.51%) (Hammad 2012). However, the ash content and percentages of some amino acids (e.g., lysine, arginine, aspartic acid, and alanine), mineral balance, and total carbohydrate in its grains are higher than in wheat grains (Hammad 2012; Biel et al. 2020). Accordingly, the majority of the triticale produced around the world is consumed for the animal feed in the form of silage or hay due to its advantage for the swine and poultry industries (Peña 1996; Glamočlija et al. 2018). It was also stated that triticale contains slightly higher levels of some nutrients, e.g., potassium, phosphorus, sodium, manganese, iron, and zinc, compared to other cereals (National Research Council 2002). In addition, Biel et al. (2020) reported that it can play a key role in the rising healthy food market and the formulation of new cereal products. Some scholars also argued that triticale selection should be performed based on the best characteristics of both parental lines to adapt to different soil conditions, abiotic stresses, and low nutrient requirements, e.g., high grain yield and grain quality of wheat and stress tolerance and nutrient use efficiency of rye (Ramazani et al. 2016; Ayalew et al. 2018). In the meantime, although programs have been developed to induce resistance to various types of stress in triticale (biotic and abiotic stresses), there are various reports in this field. The triticale plant has also been used for biorefining to produce more forage protein or sugar for fuel (Jorgensen et al. 2020). In this study, the change in triticale harvest time was reported to produce more biomass for bioremediation to produce animal forage protein or produce sugar for fuel.

Shanazari et al. (2018) investigated the effects of drought stress on some agronomic and biophysiological traits of 27 genotypes of *Triticum aestivum*, *Triticale*, and *Tritipyrum* genotypes and showed that all genotypes were affected by stressful conditions; however, triticale cultivars received fewer impacts of drought stress.

Finally, these findings attributed to accumulating compatible osmolytes in drought-tolerant cultivars. Ayalew et al. (2018) attributed the higher resistance of triticale in comparison to the other small grain cereals under unfavorable conditions to large canopy cover, strong and profuse roots, high nitrogen acquisition capabilities, and nitrogen use efficiency. In addition to drought stress, there are several studies about the adverse effects of other abiotic stresses, including salinity, temperature, pH, etc., on triticale growth and development. Concerning the effects of salinity stress on triticale, an experiment was done to evaluate four promising triticale accession (PI-429166, PI-429152, PI429101, and Syria-1) and investigate those potentialities with respect to three levels of salinity (15.6, 30.1, and 33.5 dS m^{-1} soil salinity) by Abu et al. (2017). They indicated that no significant differences were observed for grain yield, straw yield, and harvest index between the accessions of triticale, while salinity levels had significant effects on grain yield and the number of tiller per plant. Also, Akgün et al. (2011) investigated the effects of salinity concentrations (e.g., 3.9, 6.1, 8.3, 10.5, 14.9, 19.3, and 25 dS m^{-1}) on emergence rate, dry weights of green parts/roots, salt tolerance index, nutrient uptake (N, P, K, Ca, Na, Fe, Mn, Mg, Zn, and Cu), and proline content of triticale genotypes. They indicated that values of emergence rate, shoot and root length, dry weights of green parts and roots, and mineral contents of both roots and leaves were dependent on salinity concentrations and significantly decreased with increasing salinity levels. However, the proline concentration increased under higher salt levels. On the other hand, there were different reactions for different genotypes, which were attributed to early periods of plant growth, blockage of water intake into the seeds, and reduction in the ability to intake water and nutrients by the root tissue.

In addition to the above, evidence reported that triticale is a disease-resistant crop (Mergoum et al. 1992; Gerema et al. 2020), and some researchers also stated that triticale generally exhibits high levels of resistance to some pathogens (Gaudet et al. 2001; Emebiri et al. 2019). However, this opinion is no longer true, and there are conflicting reports about it (Arseniuk 1996). In this regard, Wójtowicz et al. (2020) reported that disease development in plants is strongly dependent on weather conditions and climate changes. Hence, although triticale might be a healthier crop compared to wheat and rye, its healthiness has been steadily declining because of its worldwide expansion, which has been exposed to a variety of stressful environmental conditions and harmful organisms and pathogens (Arseniuk and Góral 2015). In a study, Arseniuk and Góral (2015) introduced main diseases affecting triticale worldwide, including stem rust, leaf/stem/stripe rusts, powdery mildew caused by *Blumeria graminis*, and diseases caused by necrotrophic pathogens like fungal species from the *Septoria complex*, *Cochliobolus sativus*, *Fusarium culmorum*, *Fusarium graminearum*, *Microdochium nivale*, *Bipolaris sorokiniana*, *Pseudocercosporella herpotrichoides*, and *Gaeumannomyces tritici*. In addition, it was stated that triticale is a crop that meets pathogens of wheat and rye and is affected by common and dwarf bunts, Karnal bunt, flag smut fungi, Spot blotch, basal glume rot, and bacterial leaf blight diseases (Arseniuk 1996). On the other hand, since pests can damage plants in some seasons and greatly reduce yield and grain quality (Krusteva and Karadjova 2011), numerous insects and pests, including

Rhopalosiphum maidis, *Schizaphis graminum*, *Sitobion avenae*, *Philaenus spumarius*, *Leptopterna dolabrata*, *Lygus rugulipennis* Poppius, *Notostira erratica*, *Balclutha punctata*, *Balclutha rhenana* Wagner, *Empoasca pteridis*, *Hardya anatolica* Zachvatkin, *Macrosteles laevis*, *Psammotettix alienus*, *Psammotettix provincialis*, *Psammotettix striatus*, *Psammotettix* spp., *Zyginidia pullula*, *Laodelphax striatellus*, *Mayetiola destructor* Say, *Oscinella frit*, *Oscinella pusilla*, *Phorbia fumigata* Meigen, and *Delia platura* Meigen, were known as the most important pests affecting yield, yield components, and grain quality of the triticale plant (Krusteva and Karadjova 2011).

Commonly, although both biotic and abiotic stresses have negative impacts on plants, meanwhile abiotic stresses are known as the main causes of decline in plant yields so their effects have been estimated to be more than 50% (Koyro et al. 2012; Shahmoradi and Naderi 2018). In acid, alkaline, and sandy soils, some researchers reported that triticale showed to be very competitive compared to other cereal crops and has more resistance to adverse climatic conditions, grazing, and edaphic conditions (Mergoum and Macpherson 2004; Ramazani 2020). Since the main topic of this chapter is abiotic stresses and how triticale reacts to them, they are discussed after a brief history.

9.2 History of Triticale

In general, different types of triticale with different ploidy levels and chromosome structures have been produced so far (Mergoum et al. 2019). Also, it was reported that triticale can be classified as primary (the direct amphidiploids of wheat and rye), secondary (the most common cultivated type that originated from crossing between synthetic hexaploid wheat and rye), and substituted (some of the rye genomes preferentially substituted by the D genome of wheat) types (Ayalew et al. 2018). In this regard, the evolutionary history of several types of triticale is summarized by Smartt (1976) in Fig. 9.1.

9.3 Production and the Area Under Cultivation

Evidence demonstrated that triticale, as a commercial crop, was evaluated slowly until the mid-1980s. Then, its production increased by about 18% per year, i.e., about 150,000 tons per year, and reached nearly 11 million tons in 2002 (Mergoum and Macpherson 2004) and 14 million tons in 2019 (FAO 2021). The increase in triticale production has been mostly due to increases in the area cultivated from 1975 to 2019 (Fig. 9.2), and, at present, the total area planted to triticale worldwide is assessed to equal to four million ha in 2019 (FAO 2021).

On the other hand, evidence indicated that the highest and lowest global shares of triticale productions (90.1 and 1.5%) were in Europe and the Americas (Fig. 9.3). In the meantime, Poland, Germany, France, Belarus, Russian Federation, Australia,

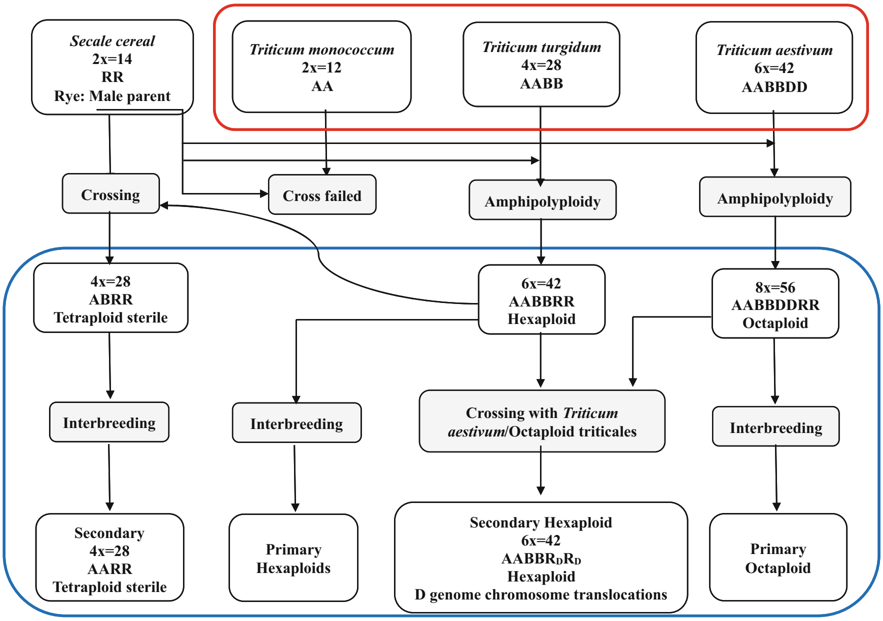


Fig. 9.1 A schematic of the origins of different types of triticale. (Adapted from Smartt 1976)

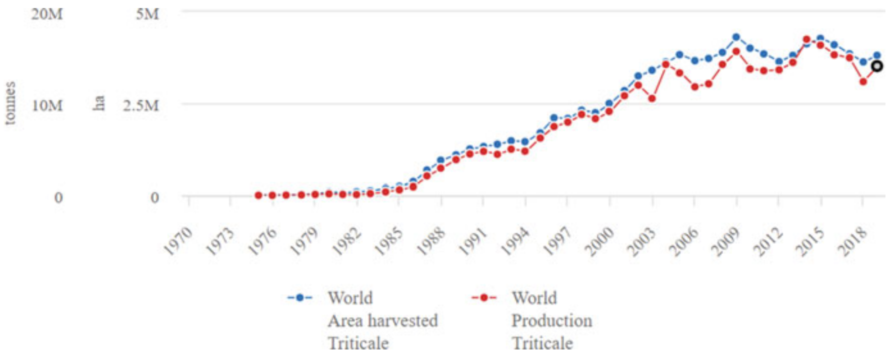


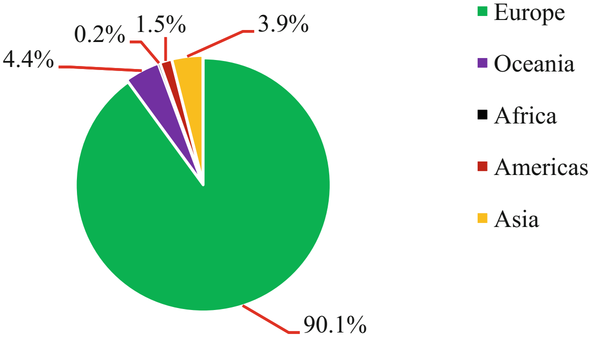
Fig. 9.2 Production/yield quantities of triticale in the world (average 1970–2019)

China (mainland), Hungary, Lithuania, and Sweden countries were also reported as the top 10 producers of triticale, respectively (FAO 2021; Fig. 9.4).

9.4 Factors Affecting Growth, Yield, and Yield Components

In general, plant growth and development are dependent on the environment, genetics, and their interactions (Rao et al. 2006). Dhindsa et al. (2002) examined yield and yield components of 20 triticale varieties under diverse conditions and

Fig. 9.3 Production share of triticale by region (average 1970–2019)



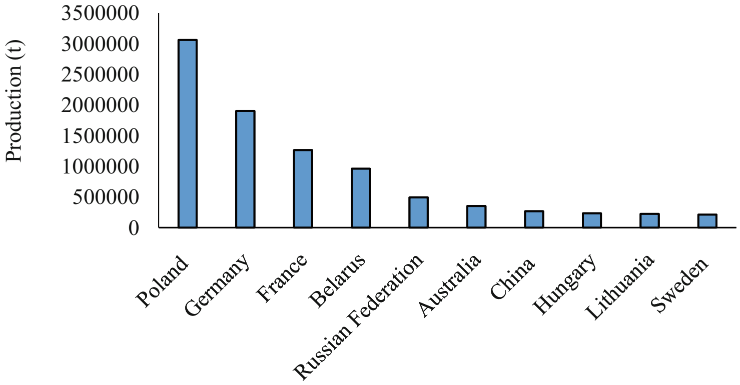


Fig. 9.4 Production of triticale: top 10 producers (average 1970–2019)

revealed that genotype, environment, and genotype by environment (G × E) interaction had significant effects on the investigated traits. They also stated that G × E was essential to obtain unbiased estimates of genetic components. In general, G × E interactions frequently interfere with the selection process of widely adapted genotypes (Ramazani et al. 2016) and are considered the major factors limiting responses to selection and the efficiency of breeding programs (Lule et al. 2014). Plus, since plants are generally exposed to numerous biotic and abiotic stresses, plant growth, development, and productivity indices have inverse associations with unfavorable biotic and abiotic factors/stresses (Mahajan and Tuteja 2005; Xu et al. 2011; Meena et al. 2017). In this context, Koyro et al. (2012) reported that environmental stresses are responsible for the production of very toxic radicals, called reactive oxygen species (ROS), and disturb normal conditions of plants by enhancing them. Also, they noted that chloroplasts, mitochondria, and peroxisomes are known as the main sources of their production in plants (Fig. 9.5).

Hence, the most important abiotic factors affecting growth, yield, and yield components of the triticale plant are as follows:

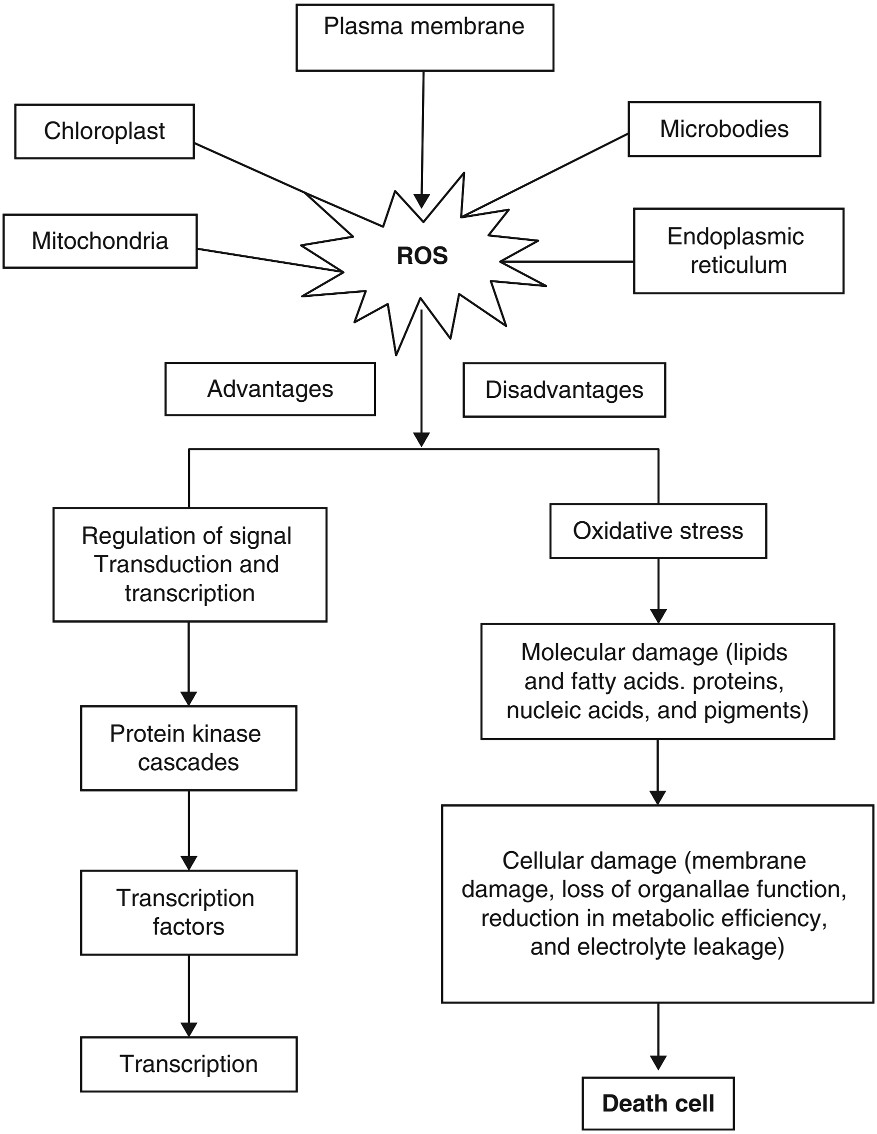


Fig. 9.5 Sites of reactive oxygen species (ROS) and the biological consequences leading to a variety of physiological dysfunctions that can lead to plant cell death. (Adapted from Koyro et al. 2012)

9.4.1 Drought Stress

Abiotic stresses are the main causes of the decline in the growth and productivity of plants and crops (Shahmoradi and Naderi 2018; Chandra et al. 2021; Godoy et al.

2021). On the other hand, since plants are exposed to various factors, such as high/low temperature, drought, salinity, and others, they are known as stress induction factors plants (Jiang et al. 2016; Fazeli and Naderi 2019). Drought is one of the main limiting factors for crop production in the world, especially in C_3 plants (Ghorbani et al. 2019; Ramazani and Taherpour Kalantari 2019), which in plants occurs when plants have limited access to water in the soil for several reasons, including low rainfall, salinity, high and low temperatures, high intensity of light, and so on (Salehi-Lisar and Bakhshayeshan-Agdam 2016). The drought factor affects plants through changing physiological, morphological, biochemical, and molecular traits in plants (Kapoor et al. 2020); exacerbates the effects of the other stresses, e.g., salt and cold stresses (Cruz de Carvalho 2008); and induces ROS and oxidative stress leading to cellular damage and ultimately cell death (Ahanger et al. 2017). However, in developing programs to enhance the drought resistance in crop plants, it is necessary to increase understanding concerning the genetics and physiological mechanisms involved in adapting plants to drought stress and maintaining growth, development, and productivity during stress periods (Inoue et al. 2004; Lonbani and Arzani 2011; Roohi et al. 2013).

Silva et al. (2020) studied the effect of four water regimes (including (187 mm, 304 mm, 410 mm, and 535 mm) on the physical and chemical qualities of triticale in Planaltina, Brazil. The 1000-grain weight and grain color indices (represented by the hue angle, chroma, and luminosity) were evaluated for physical quality protein, carbohydrate, ash, lipid, and micro- and macrominerals contents was determined for the chemical quality. The grain yield under the application of water stress conditions is reduced by reducing the 1000-grain weight trait. There was also a reduction of chroma and hue angle. Also, it was stated that water deficit also affected lipid, protein, ash contents, and carbohydrates.

In another study, Al-Ghamdi et al. (2021) studied the effect of drought stress on *Triticosecale rimpaui* growth and crop yield production. They declared that water deficit had less affected grain yield when crosschecked with vegetative growth. Also, soluble proteins in the shoots and grain were decreased with increasing drought levels. Plant pigments content reduced gradually with the increase of drought stress. Giunta et al. (1993) compared responses of durum wheat and triticale under different moisture levels and explained that drought stress significantly reduced yield and yield components of wheat, but triticale showed just slight and nonsignificant decreases in the studied traits compared to the control treatment. The previous researchers stated that the greater drought resistance of triticale might be attributed to the earliness of its heading date and the greater capacity of its roots to absorb water from the soil. In agreement with the mentioned comments, Estrada-Campuzano et al. (2008) stated that triticale reaction and its higher resistance to stressful conditions could be partly associated with its morphological structure and phenological responses. On the other hand, Hossain et al. (2021) reported that proline accumulation is the first response to reducing cell injury in plants exposed to water deficit/drought stress and said that higher plant resistance to drought stress was associated with biochemical traits. Furthermore, Lonbani and Arzani (2011) investigated morphophysiological traits associated with terminal drought stress tolerance in triticale and wheat and showed that triticale was superior to wheat under normal and stressful conditions. In this regard, they showed that the drought tolerance superiority of triticale was associated with lower flag leaf angle, lower leaf area index, and lower number of stomata. Concerning triticale responses to drought stress, Akbarian et al. (2011) stated that the drought-tolerant index and grain yield of different lines of triticale have significantly directly correlated with chlorophyll contents, carotenoids, and relative water content. Shanazari et al. (2018) found that higher resistance of triticale genotypes was associated with higher levels of relative water content (RWC) and lower levels of malondialdehyde and H_2O_2. Upadhyay et al. (2020) declared that drought tolerance in wheat genotypes is associated with enhanced antioxidative protection and declined lipid peroxidation. Overall, there are no comprehensive studies to fully understand the higher resistance of triticale against drought conditions compared to other crops; however, efforts should be continued to find the right response in drought-prone areas.

9.4.2 Salinity Stress

Among abiotic stresses, salinity stress (which refers to high concentrations of solute salts including Na^+, Cl^-, Ca^{2+}, and Mg^{2+} in soil) can be considered one of the most influential abiotic factors limiting germination, growth, development, and productivity of different plants (Hasanuzzaman et al. 2014; Tavakoli Neko et al. 2018), so that affected about 20% of total cultivated lands worldwide (Hossain 2019). In addition, salt stress can induce several changes in both physiological and metabolic processes of different plants (James et al. 2011) and lead to ROS-induced oxidative, osmotic, and ionic stresses in plant cells (Shahmoradi and Naderi 2018). Like other stressful conditions, different enzymatic and nonenzymatic reactions are responsible for decreasing ROS effects in plants, e.g., superoxide dismutase, ascorbate peroxidase, glutathione reductase, catalase, carotenoids, proline, and soluble sugars (Tuna et al. 2013; Hasanuzzaman et al. 2014). In agreement with the adverse effects of salinity stress, Mohsen et al. (2013) also reported a general reduction in growth and yield as the most important plant response to salt stress. In this regard, Salehi and Arzani (2013) investigated the effects of salinity stress on the grain quality-related traits in 18 triticale lines and two bread wheat. Their findings showed that salinity conditions significantly affected the studied traits, which attributed to the distribution effects of salinity on the uptake, translocation, and accumulation processes of mineral elements. They also stated that salinity stress at the post-anthesis period could shorten the duration of storage proteins accumulation and change the rate of accumulation of gliadins and glutenins. In another study, Atak et al. (2006) investigated the effects of different levels of salinity (2.4, 4.2, 5.9, 7.7, 10.6, and 13.2 dS m^{-1}) on the germination, seedling growth, and water uptake indices in different triticale cultivars and showed that increased NaCl significantly affected mean germination time without significantly affecting germination percentage and water uptake. They also found that salinity increased the accumulation of Na^+ and decreased the K^+ content in roots, shoots, and seeds. Finally, they concluded that the delay in germination was mainly related to a higher accumulation rate of Na + in the seeds rather than osmotic stress in triticale.

Mohammadi Alagoz et al. (2021) studied water deficiency at different phenological stages on oxidative defense, ionic content, and yield of triticale irrigated with saline water. Treatments contained three salinity levels (no-salt, 50, and 100 mM NaCl) and water-deficit stress (control, irrigation disruption at heading, flowering, and kernel extension stages). Results indicated that salinity, water deficit stress, and their combination decreased grain yield, grain number/spike, biomass, potassium content of leaf and root, and the ratios of leaf and root K^+/Na^+. They increased malondialdehyde, hydrogen peroxide, sodium content, and the activity of catalase, peroxidase, and ascorbate peroxidase enzymes in triticale. The salinity with water-deficit stress at the heading, flowering, and kernel extension stages reduced grain yield by 77.85, 86.06, and 73.62, respectively. They introduced the flowering stage as the more sensitive stage to the coincidence of salinity stress and water shortage.

9.4.3 Temperature

Temperature is the primary factor affecting and controlling plant growth and development (Ehtaiwesh 2016). In this regards, it was reported that in different stages of plant growth and development, there are many physiological and biochemical reactions, such as stability of many proteins, membranes, the efficiency of enzymatic reactions, metabolic balance, evapotranspiration, water availability, vernalization, leaf formation, leaf senescence, photosynthesis, respiration, etc., that are regulated by temperature factor (Simões-Araújo et al. 2003; Hasanuzzaman et al. 2013; Nievola et al. 2017). On the other hand, since most plants and their functions have relatively narrow ranges of temperature window, higher temperatures (temperatures above the optimum) expected with climate change will impact the pollination stage (as one of the most sensitive phenological stages to temperature extremes) and plant productivity (Hatfield and Prueger 2015; Ehtaiwesh 2016; Raza et al. 2019). Hlaváčová et al. (2017) also confirmed the above statements and advised that heat stress around anthesis is known as an affecting factor on cereal yield. However, despite the effects of temperature stress on cereals (especially in the anthesis stage of the small grain cereals) and numerous studies in this field on wheat and barley, no report of temperature stress on triticale has been unfortunately reported. Hence, since temperature effects are increased by water deficits, excess soil water, salinity conditions, and so on, understanding these phenomena will be needed to develop more effective adaptation strategies to offset the impacts of greater temperature extreme events associated with a changing climate (Hatfield and Prueger 2015; Ehtaiwesh 2016; Raza et al. 2019).

9.4.4 Nutrients (Deficiency or Toxicity)

Since triticale has several basic characteristics, such as hardiness and nutrient-use efficiency of rye and high grain yield and nutritional qualities of wheat, improved cultivars produce higher biomass and grain yield than other small grain cereals. Accordingly, this makes triticale a suitable alternative, especially in nutrient-deficient environments (Randhawa et al. 2015; Liu et al. 2017; Ayalew et al. 2018). However, toxic effects of ions in plants (excessive amounts of Na and Cl ions) are among the important causes of yield decline in plants grown under saline conditions that can cause the deterioration of ion balance in plants, nutrient intake, transport problems in the different parts of plants, and deterioration of such physiological functions, e.g., photosynthesis and respiration (Akgün et al. 2011).

Triticale biomass has been used for biorefining to produce more forage protein or sugar for fuel (Jorgensen et al. 2020). Michas et al. (2020) studied the growth of triticale (X *Triticosecale* Wittmack) in multi-metal contaminated soils by use of zeolite. This study declared that the addition of 1% zeolite to pollution soils with Pb, Cd, and Zn could minimize pollution and positively contribute to the increased biomass for animal use. Another research confirmed this subject that triticale has the ability to Co, Pb, and Sr accumulation from soil to crop and food chain to a different degree (László 2009).

Influence of heavy metal ions and toxic compounds on triticale growth was studied (Brezoczki and Filip 2016). The triticale plant has distinct characteristics compared to the other grasses, respectively: very good resistance to a wide variety of diseases, increased growth, and very good tolerance for aluminum ions present in acid soils. They concluded that the roots have a very great sensibility to $CuSO_4$ solutions compared to their stalks. A positive effect for triticale stalks was seen for low $CuSO_4$ solution concentrations; thus, for 5 mg Cu/l, the growth is 19.44%. A positive effect for triticale roots can see for low $ZnSO_4$ solution concentrations so for 5–15 mg Zn/l, the growth is 24.4%. In the presence of the $CdSO_4$ solution, germination and growth are inhibited even for low concentrations of this toxic (Brezoczki and Filip 2016).

9.5 Approaches to Improving Yield and Yield Components Under Stressful Conditions

Since triticale is a promising crop hybrid, in which combines the yield potential and grain quality of wheat with the disease and environmental tolerance of rye (Wójcik-Gront and Studnicki 2021), appropriate strategies to overcome the adverse effects of abiotic factors should be considered as follow:

9.5.1 The International Maize and Wheat Improvement Center (CIMMYT) Program

Overall, a comprehensive strategy that emphasizes the maintenance and generation of genetic diversity needs for long-term success in crop production (Mergoum et al. 2009). Hence, the yield of triticale has also improved since the mid-1980s, particularly when the shorter, spring-type varieties became commercially available allowing an escalation in the use of fertilizers (Mergoum and Macpherson 2004). In this field, it was reported that the (CIMMYT) program had a key role in enhancing harvest index and grain yield in triticale (Mergoum et al. 2009). In this regard, the CIMMYT triticale breeding program began in 1965 and has achieved significant progress in terms of growth, development, yield, and yield components to this crop, e.g., introduction lines with insensitive to photoperiod (Ramazani et al. 2016).

9.5.2 Plant Breeding and Resistant Cultivars

The principle aim of crop/plant selection is to improve productivity in the face of adverse environmental conditions (e.g., water deficit, salinity stress, etc.) and has great importance among breeding researchers (Gonzalez et al. 2010). Evidence confirmed crop breeding, crop improvement methods, and the use of resistant cultivars/genotypes as the most important strategies against abiotic stresses to modify their adverse effects (Parmar et al. 2017; Ramazani et al. 2018; Raza et al. 2019). In some studies, researchers had shown that new triticale varieties are characterized by top agronomic characteristics under unfavorable climate and soil conditions (Dumbravă et al. 2014). Ramazani and Izanloo (2019) evaluated drought tolerance of triticale genotypes compared to different genotypes of bread wheat and barley and revealed that drought stress had adverse effects on yield and yield component characteristics of all investigated genotypes. Eventually, the latter researchers observed that although drought stress had adverse effects on biological and grain yield of various triticale genotypes, there were different degrees of drought stress resistance among triticale cultivars, and the Pazh genotype was introduced as the superior genotype in Iran conditions. Also, Shanazari et al. (2018) reported that the high frequency of post-anthesis water deficits in cultivated regions makes it essential to develop new drought-tolerant crop cultivars. In confirmation of the above statements, Fang and Xiong (2015) also explained that due to the reduction of annual precipitations in arid regions, the necessity of drought-resistant genotypes or substitute crops is essential as a priority. In relation to the application of resistant variety, Manchanda and Garg (2008) also revealed that this approach is one of the most important strategies to solve salinity problems in arable farms. Regarding the effects of abiotic stresses (alone or combined stresses) on different plant genotypes, Ehtaiwesh (2016) reported that there are several genetic variations between different plant genotypes, which could be used in breeding programs to improve their yield under unfavorable/stressful conditions. Raza et al. (2019) also declared that genetic engineering techniques could aid in overcoming food production and food security problems against environmental conditions, by producing transgenic plants and stress-tolerant cultivars. Water deficit was studied within genotype of triticale (BRS Ulisses) in Brazil (Silva et al. 2020). They declared that, in drought conditions, grain yield is reduced through the reduction of weight of thousand grains.

9.5.3 Intercropping

In the process of agricultural production, new environmentally friendly and sustainable methods have been proposed (Martin-Guay et al. 2018; Ramazani 2020; Khanal et al. 2021). Intercropping is one of the most important agricultural systems in many countries (Ibrahim et al. 2014) that has been considered due to the optimal and effective use of environmental resources, plant nutrition balance, soil fertility, and increasing production per unit area (Ramazani 2020). It was also suggested that intercropping could increase field diversity and plant resistance to pests, diseases, and weeds (Mundt 2002) and increase growth rate, development, photosynthetic efficiency, yield, and yield components in plants and crops (Li et al. 2020; Wang et al. 2020; Luo et al. 2021). Accordingly, for the above reasons, especially the establishment of nutritional balance and soil fertility, intercropping can mitigate adverse effects of environmental and stressful conditions.

9.5.4 Bio-Fertilizers and Polyamines Under Abiotic Stress

Bio-fertilizers, such as plant growth-promoting rhizobacteria (PGPRs) and mycorrhiza, can increase the availability of nutrients and also help to enhance soil health and subsequently lead to an increase in soil fertility (Gendy et al. 2013) through colonizing the rhizosphere and roots (Gusain et al. 2015). Also, it was reported that mechanisms involved in promoting plant growth and development by bio-fertilizers are not fully understood. However, they can be effective on plants in stressful conditions by producing phytohormones, siderophores, symbiotic N2 fixation, antibiotics, enzymes, and solubilizing nutrients (Ahmad et al. 2008). In this regard, Kheirizadeh Arough et al. (2016) examined the effects of bio-fertilizers on some physiological parameters of triticale under water limitation conditions and found that inoculation of plants with bio-fertilizers improved plant growth and development through increasing both enzymatic and non-enzymatic activities, namely, catalase, polyphenol oxidase, peroxidase, and photosynthetic pigments. In addition, bio-fertilizers have been shown to enhance tolerance against abiotic stresses and adverse environmental conditions by improving plant water absorption via altering root morphology and stimulating gas exchange by increasing sink capacity and maintaining ionic balance in the cytoplasm (Borde et al. 2011; Dodd and Pérez-Alfocea 2012). Hence, changing rhizosphere flora is the main reason for the positive effect of bio-fertilizers through the microorganisms that make up them (El-Haddad et al. 1993). However, suitable rhizobial species that can survive under drought conditions are of utmost importance (Zahran 1999; Giller 2001). Therefore, further studies are needed to understand this area (Igiehon and Babalola 2018). Also, changing the rhizosphere flora is recognized as one of the main reasons for the positive effects of bio-fertilizers (El-Haddad et al. 1993). Microorganisms involved in bio-fertilizers make a symbiotic association with plant roots and facilitate plant growth and development through enhancing uptake of several macronutrients and micronutrients, e.g., phosphorus, zinc, copper, and others, and plant growth and development and physiological functions (photosynthesis, water status, stomatal conductance, photosynthetic efficiency, osmolytes, mineral nutrition) subsequently promote plant tolerant to abiotic stresses (Pawar et al. 2018; Schütz et al. 2018; Anli et al. 2020).

Polyamines (PAs) are ubiquitous and small positively charged organic molecules that are found in higher plants and all living cells (eukaryotic and prokaryotic cells) in three main forms of spermine, spermidine, and putrescine and actively respond to different abiotic stresses such as drought, salinity, extreme temperatures, heavy metals, and UV radiation (Groppa and Benavides 2008; Gill and Tuteja 2010; Chen et al. 2019) to improve plant tolerance, photosynthetic capability, and osmotic adjustment (Alcázar et al. 2011; Hossain et al. 2021). These substances are considered hormone-like plant growth regulators that play critical functions in the regulation of germination, growth and development, cell division, gene expression, dormancy, flower development, embryogenesis, organogenesis, senescence, fruit maturation, fruit development, and other processes (Matilla 1996; Xu 2015; Sergiev et al. 2018; Chen et al. 2019; Killiny and Nehela 2020). Therefore, plants can accumulate a wide range of these metabolites in response to adverse environmental conditions (Anjum et al. 2014). In this regard, Sergiev et al. (2018) investigated different impacts of UV-B irradiation and Biomin on the content of endogenous polyamines (e.g., spermine, spermidine, and putrescine) and free amino acids in shoots and roots of young triticale seedlings, and they demonstrated that Biomin alleviates the negative consequences of UV-B stress. Hence, the researchers suggested that the protective effects of Biomin on triticale against UV-B irradiation might be related to adjustments in PAs and amino acids pools. Hura et al. (2015) worked on polyamines under long-term water stress at different growth stages of *X. Triticosecale* Wittmack. They explained that water deficit seemed to decrease in the content of free polyamines and an accumulation of cell wall-bound polyamines.

9.6 Summary

Agriculture and abiotic factors are internally correlated with each other in many aspects, and abiotic stresses (including salinity, drought, temperature, climate change, minerals, etc.), which have negative impacts on agricultural sectors in the world, create the biggest concerns for food production and food security. On the other hand, since triticale is a suitable and viable alternative for small grain cereals, here, we summarized the effects of the most important abiotic stresses (e.g., drought, salinity, mineral, and temperature) and suggested some efficient approaches to overcome these stressful conditions and improve yield.

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Quinoa: Role and Responses Under Abiotic Stress

10

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Abstract

Quinoa (*Chenopodium quinoa* Willd.) is a hereditarily distinct Andean crop that has received remarkable interest globally owing to its nutritional and health advantages. It is extremely tolerant to harsh environmental conditions, for instance, salt- and water-deficit agroecosystems. Salinity along with drought constitute the major abiotic environmental cues examined in quinoa, whereas additional stressors like heat, frost, heavy metals, waterlogging, and UV-B light are relatively less examined. Moreover, stresses usually act in combinations of two or more. Presently, large gaps exist in our knowledge regarding quinoa's response to several abiotic stresses, particularly at the molecular level. Even as large genetic variability exists in quinoa species, substantial exploration is necessitated to exploit this genetic diversity. With the recent publication of quinoa reference genome, categorization of genes responsible for abiotic stress tolerance would be intensely facilitated, and a genetic approach should assist in improving our knowledge of varied abiotic stress tolerance mechanisms operative in quinoa, ultimately leading to better propagation approaches. By way of these advances, quinoa has great potential for providing sustainable solutions needed for food safety issues in dry and semi-dry areas worldwide. More or less, not much research has been carried out on quinoa, and relatively lesser has been carried out to explicate the genetics supporting quinoa's endurance to abiotic factors. With this background, the chapter aims to present (1) a brief overview of quinoa's history, botanical features, distribution, and economic importance and (2) a recent understanding of the responses and tolerance of quinoa to different

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abiotic stress factors, focusing on physiological and biochemical responses, possible molecular machinery, and genetic regulation.

Keywords

Abiotic stress · Chenopodium · Drought · Heat · Quinoa · Salinity

10.1 Introduction

Plants have been surviving in intrinsically hostile environmental conditions ever since their appearance on earth. A diverse range of physical or chemical factors exerts adverse effects on them, such as temperature and water extremes, salinity, metals, and ultraviolet (UV) radiations, to name a few (Wania et al. 2016). Additionally, plants are usually confronted with an erratic amalgamation of various stresses and not just a single one (Wania et al. 2016). These stressors, together referred to as abiotic stresses, are causing a grave peril to agriculture and the ecosystem as a whole, ultimately resulting in enormous crop yield losses. Photosynthesis diminution, membrane destabilization, nutrient imbalance, alterations in water relations, and over-generation of reactive oxygen species (ROS) comprise the major physiological alterations in plants exposed to several abiotic stresses (Munns and Gilliham 2015). Global climate transformation epitomizes a chief limitation on the world food requirement by influencing the environment under which crops can be cultivated as a result of rising abiotic stressful conditions which are speculated to affect more than 50% of all farming areas by the year 2050 (Banerjee et al. 2017). These days, acclimatization of agriculture to diverse stresses is a field of key scientific attention as these abiotic stress factors intensely affect universal plant productivity (Flowers and Colmer 2015). An exploration of prospective alternate crop species needs to be carried out which could be employed as tolerant crops, offering the possibility of lessening the harmful effects of changed climatic conditions on agricultural produce and dietary needs along with an expansion of the limited arable areas in global parched and semi-dry zones (Eisa et al. 2012).

One of the propitious plant species with great potential is *Chenopodium quinoa*, which has been the focus of attention of the scientific community in the last few years on account of its high ability to tolerate different abiotic stresses (Benlhabib et al. 2015). Excellent nutritional value and health benefits of quinoa are vital features for fostering its worldwide farming and consumption (Nowak et al. 2016). Seeds of quinoa do not contain gluten, possess a small glycemic value, and have an exceptional poise of indispensable lipids, amino acids, carbohydrates, fibers, minerals, and vitamins (Gordillo-Bastidas et al. 2016). Quinoa can be easily raised on a broad range of marginal soils which are not fit for growing other major crops, such as saline ones and those which are likely to face drought conditions (Angeli et al. 2020). This potential was acknowledged when United Nations Food and Agriculture Organization (FAO) announced 2013 as "International Year of Quinoa" (Bazile and Baudon 2015) to publicize it as one of the crop species that can ease world starvation and poverty. In spite of its agronomic potentiality, quinoa is still an underexploited crop (Massawe et al. 2016). The inborn variability in diverse attributes, for instance, type of inflorescence, seed color and size, time period of life history, salt tolerance, saponin amount, nutritional worth, etc., permits quinoa to adjust to varied environments (Bhargava and Ohri 2016) and for that reason very pertinent for regions susceptible to food insecurity. Several researchers have examined salinity and drought tolerance in quinoa (Zurita-Silva et al. 2015; Choukr-Allah et al. 2016). Further, given that the quinoa's genome has been documented (Jarvis et al. 2017), new transcriptomic investigations related to its salt and drought tolerance have also been accomplished. Noteworthy, there is inadequate information regarding quinoa's resistance to other abiotic stressors, for example, UV-B and temperature extremes (Hinojosa et al. 2018). The present chapter is an attempt to briefly summarize the literature available on quinoa's historical background, morphological and genomic characteristic features, worldwide distribution, its importance in terms of nutrition, therapeutic and economic value. Specifically, we discuss in detail the morphological, physiological, and biochemical responses of quinoa to different abiotic stresses along with their molecular mechanisms and genetic control. Current information available in literature related to quinoa's tolerance to various abiotic factors is also highlighted.

10.2 Quinoa: A Promising Multipurpose Agricultural Crop

10.2.1 Historical Background

Quinoa (*Chenopodium quinoa* Willd.) was reported initially by a botanist and pharmacist from Germany, named Carl Ludwig Willdenow, in 1797 as a species indigenous to South America and whose place of origin, as stated by Buskasov, is in the Andean mountains of Bolivia and Peru (Cardenas 1944). Further, its occurrence in Calama, Tarapacá, and Arica tombs in Chile, and a few areas of Peru, points out its origin in the mountainous regions of Bolivia, Chile, and Peru. Quinoa is referred to as "kinwa" or "kiuna" in Quechua dialect and "jiura" and "jupha" in Aymara speech (Tapia 2015). In line with historical facts, Quinoa has an impressive ancient past of 5000 years in one of the most dominant civilizations on the American mainland. The Incas, who believed the crop to be holy (González et al. 2015), termed it chisaya mama or "mother of all grains," and "Gold of the Incas." Incas armies used to nourish themselves with a concoction of quinoa and fat called "war balls" (Tanwar et al. 2019). Quinoa was probably foremost domesticated over 7000 years previously by pre-Columbian civilizations, but the utilization almost disappeared following the Spanish invasion; afterwards, it continued to be the cuisine of Aymara and Quechua people of the countryside mountainous regions (James 2009). However, quinoa's role transformed the Spanish colonial era. Taking into account its traditional and sacred connections, Spaniards perceived it as "non-Christian," thus substituting it with other cereal crops (Bazile and Baudon 2015). Consequently, quinoa production and utilization started declining in urban lands, but it was preserved in the communal regions ("aynokas"). This resulted in the formation of diverse quinoa varieties, based on the locations of "aynokas." Such distinct varieties present varied dietetic profiles and diverse visual features (Bazile and Baudon 2015). The National Academy of Sciences (NAS) of the United States (1975) chose quinoa as one of the 36 underutilized plants with potential economic worth. Later in 1993, the US National Aeronautics and Space Administration (NASA) gained interest in quinoa due to its enviable nutritional excellence for astronauts on lengthy-period space operations (Schlick and Bubenheim 1993). In the last few decades, quinoa cultivation and consumption have enhanced enormously. These days, though quinoa is grown largely in Peru and Bolivia, its cultivation is being tried in more than 95 countries (Mizuno et al. 2020).

10.2.2 Plant Characteristic Attributes

Quinoa is a pseudocereal, belonging to class Dicotyledoneae, family Amaranthaceae (previously Chenopodiaceae), genus *Chenopodium*, and species Quinoa (Golicz et al. 2020). *Chenopodium* comprises around 250 species, utilized in the form of whole plant or parts. Quinoa is a herbaceous and gynomonoecious species exhibiting an annual cycle. Main stem bears lateral branches having alternate leaves displaying different colors depending on the amount of anthocyanins and carotenes. Quinoa plant exhibits good growth in Colombia, with different cultivars attaining height up to 2.3 m (Montes-Rojas et al. 2018). Secondary roots in the root system are spread in bulk based on soil conditions, sometimes entering into the soil up to 1.5 m depth where adequate water conditions are available (Alvarez-Flores et al. 2014). It has a panicle inflorescence, 15–100 cm in length, that develops at the apex, either of the main stem or sideway branches. Numerous secondary branches extend from the middle axis, corresponding to lax, compact, or mixed inflorescences, supporting unisexual or hermaphrodite flowers (Abdelbar 2018). Thus, hermaphrodite flowers are localized at the farthest point of the main, secondary, and tertiary branches of the inflorescence. Two main types of the inflorescence are found in quinoa: (1) Type I, glomerulate inflorescence, and (2) Type II, amaranth from inflorescence (Bertero et al. 1996). Branched behavior is more widespread in races grown in the Andean regions of Southern Bolivia and Peru, while unbranched habit is found in a few races cultivated in Altiplano and several races of northern and central Ecuador and Peru. Seeds are spherical and with an average diameter of 1.4–1.6 mm (James 2009). The seed is identified as an achene with ellipsoidal, lenticular, spherical, or conical architecture which differs depending on genetic characteristics (Veloza et al. 2016). Seeds contain a huge perisperm situated centrally and the embryo at the peripheral position. Endosperm is located exclusively at the micropylar area of the seed in the form of a cap enveloping the tip of the radicle. The accumulation of reserve food is well compartmentalized: starch is present in the perisperm, whereas lipids and proteins are located in the endosperm as well as the embryo (Prego et al. 1998). Legumin-type globulins (chenopodin) and high-cysteine globulins are the storage proteins of quinoa, possessing sedimentation coefficient of 11S and 2S, respectively (Brinegar et al. 1996). Indigenous chenopodin is hexameric, containing six subunits, each one consisting of acidic as well as basic polypeptides (Müntz 1996). According to the environmental conditions and saponin content, seed color changes may be gray, black, red, pink, green, yellow, purple, or orange. Quinoa saponins are made up of a triterpenoid or steroidal aglycone having one or additional sugar moieties. Quinoa varieties usually ripe in 90–125 days after planting.

10.2.3 An Overview of Genome

With continuing sequencing attempts, three separate reference genomes of quinoa have been published (Yasui et al. 2016; Jarvis et al. 2017). Quinoa characteristically has a base chromosome number of 8–9. The quinoa genome ranges approximately between 1.38 and 1.50 Gb (Yasui et al. 2016; Jarvis et al. 2017). It has highly diverse germplasm. Regarded as a facultative autogamous plant, quinoa shows heterogeneity and an outcrossing degree varying from 0.5% to 17% (Fuentes et al. 2012). It is an allotetraploid ($2n = 4x = 36$) species developed from hybridization involving two diploid species, viz., ancestral A (female American *Chenopodium*) and B genome (male Old World), and its tetraploidization took place 3.3–6.3 million years ago (Jarvis et al. 2017; Maughan et al. 2019). Possible diploid ancestors having B genomes possess around 30% bigger genomes compared to A genome species (Kolano et al. 2016). rRNA genes, such as 5S- along with 18S-5.8S-25S have been categorized and confined to the chromosomes of prospective A and B genome ancestors of quinoa (Kolano et al. 2019). Since quinoa contains two different subgenomes, A and B, its genome is highly complex compared to a usual diploid species (Walsh et al. 2015). Its genome contains a high percentage of repetitive sequences (64.5% of the genome), over 50% of which are retrotransposons. The transposon enlargement probably occurred after the divergence between *Amaranthus* and *Chenopodium* but earlier than the genome union, since quinoa's genome size matches the additive count of A and B parent genomes (Kolano et al. 2016). Single-gene sequencing endeavors earlier recognized Eurasian and North American diploids as parents of the A and B sub-genomes, respectively, in addition to hybridization happening in North America (Štorchová et al. 2015). Jarvis et al. (2017) sequenced, assembled, and annotated both A-genome diploid *C. pallidicaule* (generally referred to as kañiwa or cañahua) and B-genome diploid *C. suecicum* (Štorchová et al. 2015). Several interbreeding tetraploid species have developed from tetraploid progenitors after hybridization, including *C. hircinum* and *C. berlandieri*. Jarvis et al. (2017) sequenced 15 samples of quinoa corresponding to highland and coastal groups of quinoa and proposed the possibility of its independent domestication in uplands and coastal areas. Orthologue investigation in quinoa discovered CqB05 along with CqA12 as homoeologous. CqA02 and CqA04 are considered to be orthologous to chromosomes of *Beta vulgaris* (Bvchr8 and Bvchr2), while CqB01 seems to be the product of the fusion of chromosomes. Likewise, CqA07 was the result of the fusion between antecedent chromosomes orthologous to Bvchr3 as well as Bvchr7 (Jarvis et al. 2017). Similar to *C. rubrum*

(Cháb et al. 2008) and *B. vulgaris* (Pin et al. 2010), quinoa also possesses two genes orthologous to *Arabidopsis thaliana* gene FT, which controls the time of flowering. Because of tandem duplication, quinoa has two homoeologous replicas of FT2 along with three of FT1. FT induces flower formation in *A. thaliana*, and its orthologues have been reported in other plant species (Pin and Nilsson 2012). Nevertheless, *B. vulgaris* contains another FT gene that operates oppositely by inhibiting flowering earlier than vernalization. Recently, Golicz et al. (2020) employed a computational technique for the detection and scrutiny of 611 orthologues of flowering genes of *A. thaliana* in quinoa genome and identified genes corresponding to gibberellins, photoperiod, and autonomous pathways along with the non-existence of orthologous genes implied in vernalization pathway (FRI, FLC-FLOWERING LOCUS C). Furthermore, their analysis suggested two orthologous copies of each *Arabidopsis* flowering gene in quinoa. Many genes, such as orthologues of FT (FLOWERING LOCUS T), MIF1 (MINI ZINC FINGER), and TSF (TWIN SISTER OF FT) have been recognized as homologue-rich genes in quinoa. A total of 459 genes are exclusively expressed in flower and/or meristem of quinoa, with no orthologues identified in other species (Golicz et al. 2020). Occurrence of saponins in seeds is regulated by TSARL1 gene, and its dominant expression corresponds to the presence of saponins. Presence or lack of saponins is associated with variations in the thickness of seed coat, with sour lines containing thicker seed cover than sweet lines. Heitkam et al. (2020) discovered and classified seven satDNA families, along with 5S rDNA model replicates in quinoa. The chloroplast genome of *C. quinoa* contains 152,099 bp (Hong et al. 2017). Some reports have provided details regarding chloroplast genes of quinoa, for instance, rbcL (Kadereit et al. 2003), noncoding rpl32-trnL (Krak et al. 2016), and matK/trnK genes (Fuentes-Bazan et al. 2012). By means of next-generation sequencing tools, Hong et al. (2017) achieved entire genome sequences of chloroplast of two *Chenopodium* species, namely, *C. album* and *C. quinoa*. Similarly, Wang et al. (2017) also revealed the total genome of chloroplast of quinoa via PCR sequencing and reported 151,169 bp in its chloroplast genome, with a characteristic quadripartite arrangement of large (83,576 bp) and small (18,107 bp) single-copy areas, segregated through a duo of inverted repeat locations (IRs, 24,743 bp each). It possesses 120 gene species, comprising 87 genes coding for proteins, 29 tRNA, and 4 rRNA gene species.

10.2.4 Genetic Diversity and Geographical Distribution

Molecular markers, viz., amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD), single nucleotide polymorphism (SNP), inter-simple sequence repeat (iSSR), and simple sequence repeat (SSR), have been used to evaluate genetic variability in diverse quinoa genotypes/accessions (Jarvis et al. 2017; Morillo et al. 2020). Additionally, 85 dimorphic insertion/deletion (indel) markers have been exploited together with 62 SSR markers to examine quinoa's genetic variability (Zhang et al. 2017). Collectively, these techniques have explained two main diverse clusters of quinoa: Andean mountains (in Peru and Bolivia) and coastal (in central and southern Chile). Though molecular genetic investigations have validated the variability in lowland Chilean coastal material (Fuentes et al. 2009), it denotes a branch separated from more diverse quinoa germplasm belonging to High Andes (Christensen et al. 2007). The coastal Chilean genetic material comprises genotypes that are extremely tolerant to high temperatures and are insensitive to day length. Benlhabib et al. (2016) developed 72 F2:6 recombinant-inherited lines and parents by hybridization between coastal (NL-6) and highland (0654) germplasm groups to assess the degree of genetic diversity via selfing. Hossein-Pour et al. (2019), for the first time, put forward iPBS (inter-primer binding site) marker as an appropriate technique for identifying the genetic diversity of quinoa genotypes which was also employed by Barut et al. (2020). Notably, quinoa has abundant diversity, and an upcoming difficulty for plant breeders is to sustain this inherent variability as a vital source for acclimatizing its diverse genotypes to severe environmental alterations (Curti et al. 2012).

Initially, five groups of quinoa were reported depending on morphology, distribution, and agronomic relevance: (1) Valle, (2) Altiplano, (3) Yungas, and (4) Salares groups in uplands of South America and (5) Nivel del Mar group adjacent to south-central coast of Chile. Subsequently, quinoa groups were categorized into 2 major types based on 21 isozyme loci along with two external features: (1) coastal form from South West Chile and (2) Andean upland form from Northwest Argentina to South Colombia; with upland type further sub-categorized into northern and southern sub-clusters (Wilson 1988). These clustering attempts were based on groups of 143 accessions from the United States Department of Agriculture (USDA) supported by 36 extremely reproducible SSRs. Quinoa is raised at about 4000 m above sea level (m.a.s.l.). Its native geographic allocation extends from South Colombia (2°N) to the South-Central Chilean coast (43°S), comprising a part in Northwest Argentina along with a few subtropical plain areas of Bolivia. Recently, Quinoa has been categorized into five ecotypes, depending on geographical adaptation: (1) Valle = cultivated at 2000–3500 m.a.s.l. in Ecuador, Colombia, Bolivia, and Peru; (2) Altiplano = raised at elevations of over 3500 m.a.s.l. surrounding Lake Titicaca across the boundary of Peru and Bolivia; (3) Salares = produced in the saline plains of Chile and Bolivia and possessing great endurance to salinity; (4) sea level = cultivated in less elevated regions of South and Central Chile; and (5) Yungas or subtropical = raised in low-lying, damp basins of Bolivia comprising late-flowering varieties (Tapia 2015). Quinoa is believed to be an oligocentric species having a wide origin and manifold variations; the coast of Titicaca Lake is regarded as the region having the highest genetic diversity (Mujica 1992). Rojas (1998) believed that the distribution of quinoa varies from South Colombia (5° north latitude) to Xth zone of Chile (43° south latitude), with its elevation distribution extending from sea point in Chile to 4000 m in Altiplano of Bolivia and Peru. The highest topographic distribution of global quinoa production is in countries like Peru, Bolivia, and Ecuador. Nevertheless, because of over 20 years of research in countries of Asia, Europe, Australia, Africa, North America, and Andean area, the production of quinoa is expanding to diverse geographic regions owing to its highlands of South America (Bazile and Baudon 2015).

10.2.5 Nutritional Profile

High nutritional profile of quinoa makes it apt for production and utilization. Its seeds are small in size, largely digestible, and have high lysine content which is considered to be more nutritious than vegetables. Carbohydrates are present in the perisperm of quinoa seeds, whereas embryo and endosperm contain minerals, proteins, and fats (Reguera et al. 2018; Tanwar et al. 2019). Quinoa possesses a highly precise poise between fats (4–9%) and proteins (approx. 16%) along with carbohydrates (64%) (Zurita-Silva et al. 2014; Capraro et al. 2020). It has plentiful natural antioxidants, for example, phenols as well as α- and γ-tocopherols (Vidueiros et al. 2015). Nowak et al. (2016) reported variations in nutrient contents among various quinoa varieties from diverse locations. Contents described in g per 100 g edible part (based on fresh weight) in quinoa varies in the manner: protein (9.1–15.7 g), dietary fiber (8.8–14.1 g), total fat (4.0–7.6 g), and water content (about 15%) (Viktória Angeli et al. 2020). Quinoa oil contains essential fatty acids including linoleic (49.0–56.4%), oleic (19.7–29.5%), and linolenic (8.7–11.7%). Out of total fatty acids found in quinoa seeds, polyunsaturated fatty acid amounts to 87–88% (Filho et al. 2017). Seeds are a rich source of vitamins, for instance, niacin; riboflavin; thiamine; pantothenic acid; folic acid; vitamin B6; vitamin C, E, and A; β-carotene; and minerals like calcium, copper, iron, magnesium, zinc, etc. (Scanlin and Lewis 2016; Saeed et al. 2020). Nevertheless, the nutritional composition of quinoa seeds varies according to the variety and environmental conditions. For example, the Ecuadorian variety of quinoa has a higher protein and fat content as compared to Andean varieties.

10.2.6 Medicinal Importance

Seeds and leaves of quinoa are used to yield drugs (analgesic, anti-inflammatory, and disinfectants), alcohol, and insect repulsive chemicals (Vega-Gálvez et al. 2010; Okumuş and Temiz 2021; Villacrés et al. 2022). Though quinoa has lesser amounts of aromatic and sulfur amino acids compared to cereals like wheat, corn, and rice, they are sufficient to meet the nutritional requisites of both young children and adults. Increasing global incidences of adverse reactions, for example, lactose intolerance and allergies, have increased the attention among the masses for using milk alternative products. Quinoa milk is one of the milk substitutes that contain high protein content and a low glycemic index of 52 which is comparatively lesser than rice milk (79), thus suitable for diabetic people (Pineli et al. 2015). Antinutrients and/or phytonutrients, such as flavonoids, phenolic compounds, saponins, phytic acid, and betalains, found in quinoa are responsible for its anti-thrombotic, anti-cancer, anti-allergic, anti-viral, diuretic, and hypocholesterolemic properties (Vega-Gálvez et al. 2010; Villacrés et al. 2022). Saponins combine with cholesterol and decrease its intestinal absorption, resulting in reduced cholesterol levels in the blood. Therefore, quinoa could be used for minimizing the occurrence of diseases, such as cardiovascular diseases comprising cerebrovascular disease and coronary, rheumatic, peripheral, and congenital heart diseases. Extract of quinoa contains significant quantities of sinapinic, ferulic, and gallic acids, isorhamnetin, kaempferol, and rutin. All these compounds inhibit cell division and motility in prostate cancer patients (Saeed et al. 2020). Because quinoa lacks gladians and gladians are relevant proteins, it is excellent for consumption by people suffering from celiac disease (James 2009). Presence of high levels of α- and γ-tocopherol antioxidants present in quinoa oil imparts it long shelf life, protecting fatty acids of cellular membrane from damaging effects of free radicals (Filho et al. 2017).

10.2.7 Economic Importance

Quinoa has diverse traditional and non-traditional applications along with value-added industrial improvements which are available in the market nowadays (Rane et al. 2019). Further, several breeding programs are being undertaken to develop high-yielding quinoa varieties having desired nutritional qualities and better adapted to diverse agro-ecological regions. Particular focus is directed toward wealthy westernized nations since quinoa has recently emerged as a "superfood" (Reguera et al. 2018). In Altiplano, about 35 food items made of quinoa have been reported, including desserts, soups, pastries, dry snacks, and drinks. The nutritional regime of rural families comprises a plethora of p'esques, kispiñas, mucuna, soups, and pito (toasted flour), and on particular occasions, they make non-traditional food items, such as cakes, biscuits, doughnuts, and juices (Flores et al. 2008). Similarly, biscuits, bread (fermented/steamed), snacks, pasta, and beverages are a few of the recent food products being developed using quinoa (Alvarez-Jubete et al. 2010; Singh et al. 2021). Quinoa-based tempeh is another food product made from quinoa and fungus which is a white-colored paste having a pleasant odor (Soria et al. 1990). It is also utilized as a powerful natural insecticide that does not cause harmful effects on human beings or animals, highlighting its prospective role in pest control programs. Quinoa plays an important role in poultry nutrition due to its high protein and energy levels. The assimilatory potential of amino acids is in the range of the majority of feed ingredients, though it is less for valine or threonine (Olukosi et al. 2019). All parts of quinoa like grains, leaves, residues, and processing by-products can be used as livestock feed (Blanco Callisaya 2015; Singh et al. 2021). Broken grains can be given as food to domestic animals, such as fish and guinea pigs. Bran of quinoa grain is used to feed guinea pigs, camelids, and sheep in the Altiplano. Thirty percent quinoa bran can be exchanged for natural feed consumption owing to its anti-parasitic effects (Angeli et al. 2020).

10.3 Responses of Quinoa Under Diverse Abiotic Stresses

10.3.1 Salinity

Salinity is the occurrence of chief inorganic cations and anions, largely Na^+, Ca^{2+}, Mg^{2+}, Cl^-, K^+, $SO_4{}^{2-}$, $CO_3{}^{2-}$, and $HCO_3{}^-$. Salt stress in soils comprises soluble as well as easily dissolved solutes in the soil or liquid medium and is determined by the electrical conductivity (EC) of saturated soil extract. The land is said to be salt affected when EC is above 4 dS m^{-1} at 25 °C (Rhoades 1996).

10.3.1.1 Seed Germination and Growth

Commonly, quinoa can endure medium to elevated concentrations of salinity stress, varying from 150 to 750 mM NaCl (Orsini et al. 2011), which is greater compared to the salt level of marine water (Adolf et al. 2013). Though NaCl levels ranging from 100 to 250 mM usually do not influence seed germination in the majority of genotypes of quinoa (Fischer et al. 2017), few studies have reported delayed germination (Orsini et al. 2011). Ruiz-Carrasco et al. (2011) reported considerable impediment of 300 mM salt on root and shoot lengths in southern genotype BO78 only and 15–30% reduction in germination in central genotypes PRJ, PRP, and UDEC9. Alterations in sugar metabolism and invertase activity have also been observed during germination in salt-stressed quinoa (Rosa et al. 2004). Wilson et al. (2002) witnessed a considerable decrease in quinoa height raised in salt-stressed soil containing a mixture of $CaCl_2$, Na_2SO_4, NaCl, and $MgSO_4$ (3–19 dS m^{-1}). Salt stress causes specific ion toxicity and osmotic effect which impacts several processes of quinoa during seedling establishment, such as osmotic and ionic homeostasis, protein and lipid synthesis, carbon partitioning, photosynthesis, and ultimately entire plant metabolism (Dinneny 2015; Becker et al. 2017). Recently, Rodríguez-Hernández et al. (2021) performed an experiment using 'Titicaca' cultivar of quinoa and demonstrated a reduction in its shoot length when grown under 200 mM NaCl and root length with >50 mM NaCl.

10.3.1.2 Photosynthesis

High salt concentrations induce osmotic stress which in turn increases the synthesis of abscisic acid in roots of quinoa followed by its subsequent translocation to leaves where it functions as a signal for regulating stomatal conductance. This causes stomatal closure and decreases not only the rate of transpiration but also the uptake of CO_2, eventually hampering photosynthesis (Dinneny 2015). To determine photosynthesis, various experiments were conducted in semi-controlled conditions under 400 mM NaCl treatment in two varieties of quinoa, 'Titicaca' and 'Utusaya,' and CO_2 fixation was reported to be reduced to 67% and 25%, respectively (Adolf et al. 2012). In the Altiplano variety of quinoa 'Achachino,' intensification of salt stress from non-saline water to 250 mM NaCl decreased the net photosynthetic rate from 30 to 10 CO_2 mol m^{-2} s^{-1} under the photosynthetic level of 1500 mol m^{-2} s^{-1} (Becker et al. 2017). A different experimental setup with a valley variety named 'Hualhuas' revealed 70% decline in net assimilation rate under 500 mM NaCl stress

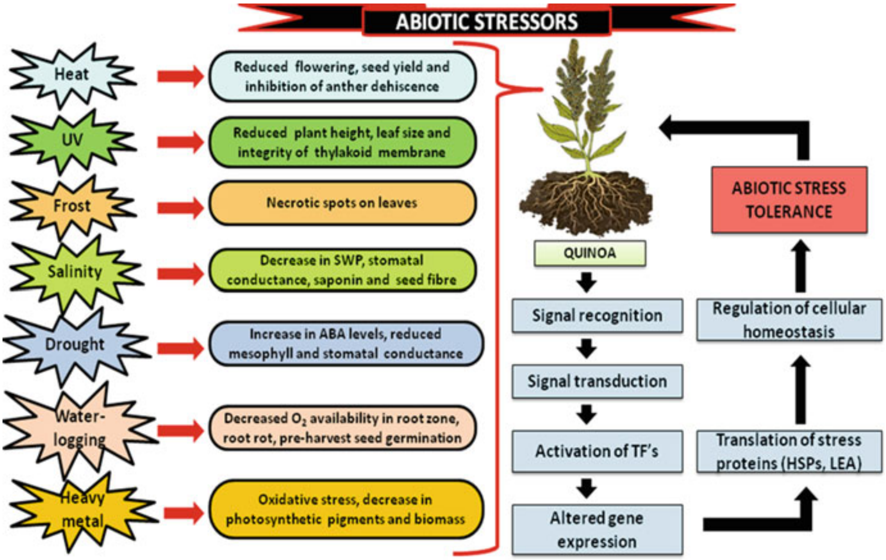

Fig. 10.1 Effects of various abiotic stressors on quinoa and simple overview of signaling mechanism involved in its abiotic stress tolerance. *ABA* abscisic acid, *HSP* heat shock proteins, *LEA* late embryogenesis abundant proteins, *TF* transcription factor, *SWP* shoot water potential

(Eisa et al. 2012). In an experiment with 'Titicaca' quinoa variety, results revealed that with an increase in salt level from 100 to 400 mM NaCl, the net CO_2 fixation rate and seed yield reduced by 48% and 72%, respectively (Talebnejad and Sepaskhah 2016). The area of stomata and its density has been examined in quinoa exposed to different salinity levels. Four hundred millimolar NaCl reduced the stomatal number per leaf area in immature, intermediate, and mature foliage of 'Titicaca' (Shabala et al. 2012). Similarly, quinoa variety 'BO78' exhibited the greatest decline in stomatal density (54%) when exposed to 750 mM NaCl level (Orsini et al. 2011). A different experiment involving 14 varieties of quinoa revealed a decrease in stomatal densities in all varieties grown under 400 mM NaCl (Shabala et al. 2013). Razzaghi et al. (2011a) observed a lowering of soil water potential in quinoa plants with an increase in salinity levels which subsequently diminished leaf water potential and finally stomatal conductance (Fig. 10.1).

On the contrary, several studies have reported no impact of varying salinity levels on photosynthetic performance (Hariadi et al. 2011; Adolf et al. 2012). However, there is little evidence vis-a-vis the influence of salt stress on the photosynthetic apparatus of quinoa. In this context, Manaa et al. (2019) noticed ultrastructural alterations in the chloroplast (thylakoids swelling, breakdown of envelope, and accretion of plastoglobuli) and loss of photosynthetic activity of quinoa plants exposed to 300 mM NaCl salinity level for long-duration stress (21 days). Researchers further observed negligible changes in PSII under a moderate salinity level of 100 mM NaCl, as revealed by chlorophyll a fluorescence transients exhibiting modest modifications in photochemistry and PQ pool and no clear effects on minimal (F_0) and maximal fluorescence (F_m) (Manaa et al. 2019). Moreover, under 100 mM NaCl, stable Chl a/b ratio along with LHCII protein content at all NaCl concentrations indicated steady antenna size. Hence, high PSII efficiency under moderate salinity could be associated with the maintenance of maximal photochemical efficiency (F_v/F_m) and great firmness of OEC complex (PsbQ and PsbO proteins) (Duarte et al. 2014; Manaa et al. 2019). In a recent study, Rodríguez-Hernández et al. (2021) demonstrated decreased levels of photosynthetic pigments as the salinity concentration increased in cv. 'Titicaca' of quinoa. According to the findings of these researchers, quinoa cultivar 'Titicaca' is not much effective in enduring salinity as 100 mM salt used in their experiments for a week was sufficiently harsh for reducing the photosynthetic rate and shoot biomass of plants.

10.3.1.3 Nutritional Value of Seeds

Quinoa has gained worldwide attention due to its endurance in stressful environments and its excellent nutritional profile of seeds. Similar to other salt-tolerant plants, quinoa can generate reasonably good seed yield under salinity levels in which most agricultural crop plants cannot reproduce. Hereditary improvements of cultivars of quinoa from its indigenous Andes habitation have been carried out by many researchers to acclimatize this crop to various geographical regions found in diverse dryland countries. Accordingly, several quinoa cultivars display varying levels of salt resistance (Peterson and Murphy 2015; Hinojosa et al. 2018). One hundred twenty-one genetic lines obtained from US Department of Agriculture (USDA) were assessed at the trial station of the International Center for Biosaline Agriculture (ICBA), UAE, where the improved germplasm of quinoa 'Q5' exhibited enhanced plant growth, early ripening, and consistent high seed yield (Choukr-Allah et al. 2016). Seeds of Andean cultivars generally exhibit elevated tolerance to NaCl stress because of greater synthesis of proline (Shabala et al. 2013). Among the salts, Na_2CO_3 is considered to exert the most harmful effects on quinoa seed germination, reducing the germination rate by ~50% (Shabala et al. 2013). An increment in antioxidant activity and total polyphenols in methanol extracts of salt-stressed quinoa seeds have been observed, indicating that stressed conditions may promote the content of these compounds in seeds (Ruiz et al. 2016a). Choukr-Allah et al. (2016) demonstrated negative effects of 2.3, 16.3, and 18.9 dS m^{-1} saline water on quinoa seeds, especially mineral content. The results of Toderich et al. (2020) experiment revealed a large extent of inconsistency in the nutritional values of quinoa seeds exposed to different salinity concentrations. These researchers found high Na levels in quinoa seeds produced from plants grown under salt stress, similar to the findings of Choukr-Allah et al. (2016). Toderich et al. (2020) further reported that salt stress decreased the amino acid levels of quinoa seeds to a smaller degree compared to fatty acids and no change in most of the essential amino acids. Additionally, contents of Fe, Mn, and Ca along with stearic acids, saturated fatty acids, and amino acids (alanine, glycine, isoleucine, proline, leucine) increased under the combination of salts (NaCl + Na_2SO_4) in quinoa variety, 'Q5', confirming the exceptional nutritional profile of seeds with regard to salt tolerance (Toderich et al. 2020). González et al. (2021) observed high tolerance of quinoa variety, 'CICA-17', to two different edaphic conditions in Egypt containing salt levels up to 26 dS m^{-1} in soils. Researchers detected Na in the pericarp of seed only and suggested a protective role of pericarp in preventing the entry of Na but not Cl^{-}. They also observed increased Mg levels in pericarp, endosperm, embryo, and perisperm. Saponins are found in different parts of quinoa, although high amounts are present in seed coats. These saponins should be eliminated by various physical or chemical methods to prevent imparting a bitter taste to quinoa products (González et al. 2021). Therefore, desaponification is an essential process before utilizing quinoa either in the form of flour or grain as the prescribed content of saponin in quinoa products for human intake ranges between 0.06 and 0.12%. Desaponification also removes Na from quinoa seeds, thereby avoiding its harmful effects, if consumed, as it exists in pericarp. González et al. (2021) detected several ultratrace mineral elements (Sn, Rb, Nd, Th, Nb, Pr, Sm, Y, Ni, Ce, La, Ti, As, Ge, Zr, V, Zn, Ga, Pb, and Ba) in quinoa in nonsaline as well as saline conditions. Similarly, Cs was observed in shoot system of quinoa plants (Isobe et al. 2019). It is noteworthy that under salinity stress, the nutritional profile of quinoa seeds, particularly proteins, essential amino acids, minerals (Mg, Fe, and Ca), and vigor-improving substances, for instance, flavonoids, generally remain unaffected (Vega-Gálvez et al. 2010). Two quinoa varieties 'Q52' and 'Titicaca' were studied in Italy under an open field environment employing diverse irrigation regimes containing saline water. Results revealed that saponin content and seed fiber declined in response to the highest treatment of salinity (Fig. 10.1), whereas protein levels were not affected (Gómez-Caravaca et al. 2012; Pulvento et al. 2012).

10.3.1.4 Salt Tolerance in Quinoa

Quinoa is a facultative halophytic plant whose varieties can endure high salinity similar to those found in marine water having EC of 40 dS m^{-1} or 400 mM NaCl. Quinoa easily grows on saline lands, ranging from Salares and Altiplano of Bolivia, to coastal regions of Chile. The salt-resistant character of quinoa has also been proved in trials, for instance, Hariadi et al. (2011) examined cv. 'Titicaca' grown under 6 different salt concentrations for 70 days and observed a considerable negative effect on germination of seeds only in levels more than 400 mM NaCl, whereas optimum growth was achieved at 100–200 mM NaCl treatments. It has been reported that the highest EC causing zero yield is 51.5 dS m^{-1}, and 50% decrease in yield occurs at EC 25 dS m^{-1}, suggesting the high salt resistance capability of quinoa (Razzaghi et al. 2015). Razzaghi et al. (2011b) measured the EC50 for quinoa and found it to be 24 dS m^{-1}, thereby authenticating its categorization as a halophytic crop species.

10.3.1.5 Mechanisms Implicated in Quinoa's Salt Tolerance

Quinoa possesses many exceptional mechanisms which enable it to develop and breed in extremely salt-affected soils, hence making it an ideal crop species for determining the mechanisms engaged in certain transportation of ions under salt stress (Wilson et al. 2002). Some of these mechanisms include (1) sequestration of

Na^+ in leaf vacuoles, (2) loading of Na^+ in xylem, (3) high ROS tolerance, (4) efficient K^+ retention, (5) maintenance of low Na^+ levels in cytosol, (6) decreased slow and rapid action of channels present in tonoplast membrane, and (7) large space of H^+ pumping in mesophyll cells of leaves (Adolf et al. 2013; Bonales-Alatorre et al. 2013a, b; Ruiz et al. 2016b). Cellular transport occurs through membranes, and it is believed that differences in the activity of membrane transporters are accountable for quinoa's varied salt tolerance (Bonales-Alatorre et al. 2013a). Quinoa is a halophytic species that is similar to glycophytes concerning its physiology and anatomy; however, halophytes have more efficient salt tolerance mechanisms. A unique characteristic trait of halophytes (including quinoa) is the occurrence of salt bladders or glands which sequester and expel surplus salt from plant tissues. Mechanisms implicated in quinoa's salt tolerance are discussed in the following subsections:

10.3.1.5.1 Osmotic Regulation

For sustaining growth in salt-stressed conditions, plants regulate the external osmolality by accumulating various molecules in the cytosol which are categorized into two main groups: (1) compatible solutes (osmolytes) and (2) inorganic ions (Shabala and Shabala 2011). Synthesis of osmolytes occurs at the expense of energy, ensuing yield compromises. Consequently, the majority of the halophytic plants uphold turgor via Na^+ along with Cl^- sequestration in vacuoles of leaves and employ osmolytes for adjusting the osmotic potential in the cytoplasm (Shabala and Mackay 2011). It has been revealed that osmotic regulation in mature leaves (95%) and in immature foliage (80–85%) was accomplished by way of accumulating K^+, Na^+, and Cl^- in quinoa plants exposed to varying NaCl levels [0–500 mM] (Hariadi et al. 2011). Similarly, Cai and Gao (2020) reported higher correlations of inorganic ions with salt tolerance than organic osmolytes (i.e., proline, proteins, and sugars) in quinoa leaves, suggesting that probably the former contributed to a larger extent in osmoregulation. Previous investigations have demonstrated the accretion of both organic solutes and inorganic ions in salt-stressed quinoa plants (Orsini et al. 2011); nevertheless, inorganic osmoregulation plays the strongest role in osmotic adjustment (Hariadi et al. 2011). Accumulation of high levels of Na^+ in the cytoplasm is harmful to halophytes as well as glycophytes and thus should be averted through effective Na^+ compartmentalization in vacuoles of foliage. Immature leaves possessing a lower extent of vacuolation have higher K^+ and lower Na^+ contents than old leaves under salinity (Hariadi et al. 2011). Enhancement in Na^+ content inside vacuoles (necessary for upholding cell turgidity) must be complemented with simultaneous increment in cytosolic osmotic potential which is accomplished either by augmenting cytoplasmic K^+ levels or synthesis of osmoprotectants in the cytosol. Increment in soluble sugars, proline, and glycine betaine has been well demonstrated in salt-stressed quinoa (Muscolo et al. 2016; Saleem et al. 2017). Osmotic regulation also takes part in the germination of seeds and seedling emergence. When osmotic potential in the soil declines, sufficient water content should be retained in the seed which protects it from desiccation. Proteins, for instance, dehydrins, act as osmoprotectants and are produced as a result of water deficit during salinity (Saleem et al. 2017). Four dehydrins have been detected in quinoa seeds produced under salt-stressed conditions. Among them, a 30 kDa dehydrin has been found to build up in seeds of quinoa plants exposed to high salinity. Because of its occurrence in the nucleus and connection with embryo chromatin, it is believed to have a protective function for cellular DNA in the water-deficit environment (Burrieza et al. 2012). In quinoa cv. 'BO78,' shoot proline levels enhanced by tenfold at the highest NaCl dosages (600 and 750 mM) than controls (Orsini et al. 2011). On the contrary, an antagonistic relationship observed between proline accumulation and salt tolerance in highland quinoa varieties could be due to the high requirement of nitrogen and energy by proline synthesis which is met at the cost of plant growth (Ruiz-Carrasco et al. 2011).

10.3.1.5.2 Na^+ Exclusion and Loading into Xylem

Na^+ exclusion is a strongly desirable feature of glycophytes. Ruiz-Carrasco et al. (2011) established differential outcomes of Na^+ antiporters toward salinity in roots as well as shoots of genotypes of quinoa. The great homology of sequences of SOS1 of quinoa with other plants coupled with differential NHX1 and SOS1 expression in response to salinity indicates that Na^+ concentration in cytosol and ion homeostasis are maintained by the synchronized action of SOS1 along with NHX Na^+/H^+ exchangers in quinoa. Since SOS1 in quinoa roots is not upregulated under salinity, it is not clear whether Na^+ exclusion is responsible for high salt tolerance in quinoa. Additionally, it indicates that rapid loading of Na^+ into the tracheary elements in the early period of salinity helps adjust osmotic potential in shoots (Shabala et al. 2010). Shabala and Mackay (2011) suggested that loading of Na^+ into the xylem in halophytes is an energy-requiring process that involves the active functioning of SOS1 Na^+/H^+ antiporters present at the border of xylem parenchyma tissue.

10.3.1.5.3 Potassium (K^+) Retention

The extraordinary property of salinity endurance of quinoa could be due to its high efficiency for K^+ retention. Enhanced K^+ contents in seed cotyledons in the course of the seedling phase (Ruffino et al. 2010), and within xylem and leaf sap at the later developmental stage, were observed under salt stress in quinoa (Adolf et al. 2012). Na^+ is an economical osmoticum; therefore, for sustaining an adequate K^+/Na^+ proportion in foliage, enhanced uptake of Na^+ is coupled with enhanced K^+ transport to aboveground plant system (Katschnig et al. 2015). It has been proposed that K^+ is retained in root system of quinoa by averting K^+ efflux via voltage-gated outward-rectifying K^+ channels (KOR) (Shabala and Mackay 2011) whose permeability is controlled by H^+-ATPase activity of membrane. Thus, maintenance of membrane negativity and increment in H^+ expulsion from root system of salt-stressed quinoa has been observed (Hariadi et al. 2011). Because of the similarity of few transporters in quinoa to other plant species along with the difference in their degree of expression in response to salt stress, it is presumed that uptake of ions in quinoa is not carried out by quinoa-exclusive transporters but with the assistance of transporters generally found in plants. Na^+ uptake in roots of quinoa has been reported to be carried out by nonselective cation channels (NSCC) (Shabala and Mackay 2011; Adolf et al. 2012). Participation of NORC (nonselective outward rectifying cation channel) is vital when concentration gradients of Na^+ at two sides of the parenchyma membrane support passive uptake of Na^+. For fast osmotic adjustment in shoot system of quinoa, Na^+, as well as K^+ ions, are quickly transported into the xylem elements upon inception of salt stress, with considerable increment in shoot Na^+ content determined immediately after 6 h of salt treatment (Adolf et al. 2012).

10.3.1.5.4 K^+/Na^+ Ratio

NaCl increases K^+ as well as Na^+ levels in roots and aboveground parts of quinoa and stimulates the build-up of inorganic ions, thereby allowing quinoa to regulate turgor along with water loss under salinity via altering water potential (Acosta-Motos et al. 2017). K^+ is transported from belowground parts to stem xylem and then to foliage; enhanced leaf K^+ level is ascribed to switching over of Na^+ and K^+ in proximal root region (Wu et al. 2018). Higher K^+ levels in quinoa with an increase in salinity dosages have been reported in the literature (Cai and Gao 2020). This appears to be contradictory, as Na^+ and K^+ ions undergo a competition for binding to the sites involved in chief plant physiological and biochemical processes, and a dearth of K^+ constantly occurs under saline conditions. In quinoa, K^+ accumulation contributes to osmotic adjustment to a larger extent in leaf cells under high salinity (Hariadi et al. 2011; Adolf et al. 2013). This was explained based on higher free K^+ ions requirement for osmotic adjustment and sustaining leaf development. Since K is essential for various plant metabolic processes under salinity, loss of K^+ from leaves may trigger proteases leading to programmed cell death, hence increased senescence of leaves (Shabala 2009). In this context, the ability of quinoa to enhance uptake of K^+ along with its accumulation in leaves explains its remarkable salt tolerance character (Adolf et al. 2013). Similarly, Cai and Gao (2020) reported enhanced Na^+ and K^+ ions whereas diminished K^+ /Na^+ relative content in roots as well as leaves with an increase in salinity dosage. In other words, K^+/Na^+ proportion in foliage or roots was directly associated with salt resistance while K^+ and Na^+ contents were inversely correlated, indicating that regulation of ionic homeostasis is essential for salt resistance in upland cultivars of quinoa. K^+ normally binds to the catalytic regions which in turn retains an elevated K^+/Na^+ ratio in the cytosol to increase salinity endurance (Wu et al. 2018). As an indicator of salt resistance, K^+/Na^+ ratio in above- or belowground parts can be employed as a decisive factor in the breeding of upland quinoa cultivars (Cai and Gao 2020). Moreover, quinoa retains much of the Na^+ ions in root tissues because of their greater endurance to ionic toxicity compared to foliage, thereby restricting Na^+ transport to shoots as an adaptation to salt. Notably, in 11 quinoa genotypes, a positive relationship was reported relating Na^+ content and salt endurance (Shabala et al. 2013). Exclusion of Na^+ ions from cells coupled with its compartmentalization into leaf vacuoles is the protective mechanism of quinoa in response to salt toxicity (Bonales-Alatorre et al. 2013b). Iqbal et al. (2020) argued that quinoa efficiently manages extreme Na^+ accumulation by locking it up inside leaf vacuoles as well as transporting it to mature leaves. Defending young leaves from surplus Na^+ via compartmentalization is considered an important feature of many plant species, and quinoa is no exception to this.

10.3.1.5.5 Salt Bladders

Another mechanism through which quinoa can tolerate salinity stress is the unloading of surplus salt ions into specific epidermal bladder cells (EBCs) present on leaves, which store and expel them from cells having active metabolism (Adolf et al. 2013; Bonales-Alatorre et al. 2013b). In this context, inward-rectifier high-affinity K^+ transporters (HKT1.2) found in quinoa are engaged in dumping Na^+ into bladder cells (Böhm et al. 2018). Excess salt, chiefly Na^+ ions, are sequestered from the lamina part of leaves into the bladder hairs present on the surface of leaves, from where they are removed away by rainwater. Zou et al. conducted a transcriptomic study on EBCs in quinoa under 100 mM NaCl treatment, and their results revealed higher gene expression associated with anion transporters, for instance, cell anion channels (SLAH), chloride channel protein (ClC), nitrate transporter (NRT), and cation transporters, comprising K^+ transporter (HKT1) and NHX1 in bladder cells than leaf lamina under salinity stress. Further, 180 differentially expressed genes in foliage blade and 525 in bladder cells were recognized, suggesting that both the cells respond differently to salinity. Imamura et al. (2020) performed experiments on mutagen-treated quinoa seeds which produced two mutants: REDUCED EPIDERMAL BLADDER CELLS (rebc1 and rebc2) displaying chloroplast abnormalities and fewer EBCs than wild type (WT). Researchers observed a decrease in salt-induced damage by EBCs, thereby protecting young leaves and shoot apices. EBCs increase by endoreduplication (Barkla et al. 2018), which protects the shoot apex even if EBCs are present in small numbers. Additionally, bladder cells are enriched with genes participating in cutin and suberin biosynthesis under salinity. The expression levels of two NCED (9-cis-epoxycarotenoid dioxygenases) genes (CCG005786.3 and CCG042102.1) in EBCs were sixfold higher, whereas a few short-chain dehydrogenases/reductases (SDR) genes were 1000-fold greater relative to leaf cells. Furthermore, increased expression of ABA receptor as well as ABA transporter genes has been reported in EBCs, suggesting an enhanced level of ABA homeostasis.

10.3.1.6 Genes Responsible for Salt Tolerance

Recently, using new molecular techniques, many novel transcription genes accountable for exceptional salt endurance in quinoa have been reported (Ruiz et al. 2016b). Nevertheless, due to the latest documentation of one vigorous and two draft quinoa genomes (Jarvis et al. 2017; Yasui et al. 2016), various novel prospective genes have been recognized which might have an important function in quinoa under salinity. For example, relative genomics and topology calculation techniques were used to recognize novel candidate genes in quinoa exposed to 300 mM NaCl treatment, and differential expression of 1413 genes in response to salt was found (Schmöckel et al. 2017). Later, 219 genes were examined in 14 varieties of quinoa (6 sea-level, 4 Altiplano, 2 valley, and 2 Salares), 5 *C. berlandieri*, and 2 *C. hircinum* accessions (Jarvis et al. 2017), using sequence and physiological information under salt stress. Through single nucleotide polymorphism (SNPs) and copy number variation (CNV) between the 5 most salt-resistant and salt-sensitive lines, 6 SNPs and 14 potential genes were characterized and found to be localized in the first exon of AUR62043583 gene. Hence, this study reported 15 new genes which could be responsible for variations in salinity endurance among quinoa cultivars (Schmöckel et al. 2017). Betalains are yellow and red-violet pigments, derivatives of tyrosine present solely in Caryophyllaceae plants, with no exception in quinoa. Betalains are considered to be implicated in salinity tolerance owing to their antioxidant property (Jain et al. 2015). Investigations employing ethyl methanesulfonate on the quinoa variety 'CQ127' showed involvement of CqCYP76AD1-1 gene in green hypocotyl mutants (Imamura et al. 2018). Later on, this gene was separated and required light for functioning in hypocotyls of quinoa, suggesting its involvement in the biosynthesis of betalains during the development of pigments in quinoa hypocotyl (Imamura et al. 2018). This gene could be a potential candidate to be examined in salinity stress conditions since betalains could function in shielding quinoa hypocotyl. Transcription factors, for example, basic leucine zipper (bZIP), NAC (NAM, ATAF and CUC), APETALA2/ethylene response factor (AP2/ERF), basic helix-loop-helix (bHLH), WRKY, and myeloblastosis (MYB), regulate the transcript levels of salt-responsive genes, ultimately determining the plant salt tolerance level (Kumari et al. 2017; Liang et al. 2017; Waseem et al. 2019). Twelve transcription factors differentially expressed in two different quinoa genotypes—QQ056 (salt-tolerant) and 37TES (salt-sensitive)—under 300 mM NaCl treatment were categorized in a transcriptome study, comprising three MYBs (AUR62042086, AUR62030018, and AUR62034188), four NACs (AUR62029344, AUR62000536, AUR62015630, and AUR62006885), three WRKYs (AUR62026996, AUR62030836, and AUR62006427), and two ZFPs (AUR62009622 and AUR62042998) (Shi and Gu 2020). Two ZFP members, namely, Zat10 and Zat12, could be stimulated under salinity stress in *Arabidopsis* (Yang et al. 2019; Deng et al. 2019), whereas two homologous genes were highly activated in the study of Shi and Gu (2020), which suggested their potential roles in quinoa exposed to salt stress. Besides four MYBs and four WRKYs, one bZIP (AUR62010368) and one ERF (AUR62028234) were also observed in differentially expressed genes (DEGs) solely in salt-resistant quinoa genotype, indicating their possible roles in improving salinity tolerance. Some ERFs bestowed resistance to high salinity levels by regulating ethylene (ET) and ABA contents (Ebel et al. 2018), whereas some through amplification of mitogen-activated protein kinases (MAPK) induced by ROS in the early stage of salt stress (Deinlein et al. 2014). These findings reveal that salinity tolerance is a complex process engaged in several metabolic pathways and transcriptional networks.

10.3.2 Heat Stress

10.3.2.1 Seed Germination

Several experiments have been performed in diverse temperature treatments to explain the impact of heat stress on seed germination in quinoa (González-Teuber et al. 2017; Mamedi et al. 2017). Temperatures more than 42 °C are regarded as critical, with germination diminishing to 0% (Lesjak and Calderini 2017). Positive as well as the negative correlation between quinoa seed germination and elevated temperature levels have been demonstrated (González-Teuber et al. 2017; Alvar-Beltrán et al. 2020). The favorable germination temperature for quinoa ranges between 30 and 35 °C, maximum being 50 °C along with base temperature (Tb) of 3 °C (González-Teuber et al. 2017). On the contrary, Bois et al. (2006) demonstrated Tb for germination for 10 diverse quinoa varieties ranging between −1.9 and 0.2 °C. Mamedi et al. (2017) employed 3 distinct models and reported the optimal seed germination temperature to be 18–36 °C for the variety 'Sajama' and 22–35 °C for 'Santa Maria' and 'Titicaca.' Quinoa seeds can be stocked to a maximum of 430 days in a controlled environment at 25 °C prior to germination failure (Strenske et al. 2017). Therefore, it can be concluded that quinoa is tolerant to heat during germination and can germinate under a broad array of temperature regimes, ranging from extremely cold (−1.9 °C) to exceptionally hot (more than 48.0 °C).

10.3.2.2 Growth Parameters

The Tb upper limit for quinoa growth and development is changeable; for instance, during flower formation and leaf emergence, Tb is 1 °C, while at the time of leaf expansion, Tb increases to 6 °C (Bois et al. 2006). Tb can also vary because of diverse growth rates and latitude derivation of genotypes (Bertero 2003); for example, for sea-level variety 'Baer I,' Tb has been reported to be 6.4 °C, while for valley variety 'Amarilla de Marangani,' Tb is 3.7 °C (Bertero et al. 1996). The increase in temperature from 18/8 to 25/20 °C promoted the plant's tallness by 100% in 'Titicaca' (Yang et al. 2016). In Bunda, Malawi, having a mean temperature of 20 °C, the length of plants of diverse genotypes of quinoa was greater than those cultivated in Bembeke, Malawi, having a temperature of more or less 15 °C (Maliro et al. 2017). Heat stress (40/24 °C) considerably decreases the aboveground dry mass of quinoa. On the contrary, aboveground biomass from 'Cherry Vanilla,' 'Salcedo,' and 'Red Head' cultivars of quinoa is enhanced under high-temperature exposure (35/29 °C) (Bunce 2017). Alternatively, high night temperature decreased the shoot dry weights in two Chilean genotypes of quinoa (Lesjak and Calderini 2017). Hinojosa et al. (2019) witnessed an increase in the length of branches grown under 40/24 °C in quinoa. Similar findings have been described in 'Achachino' cultivar of quinoa raised at 28 °C (day) and 20 °C (night) (Becker et al. 2017).

10.3.2.3 Chlorophyll Fluorescence and Photosynthesis

Photosynthetic process is believed to be sensitive and influenced by heat stress. Hinojosa et al. (2019) observed that high temperature (40/24 °C) increased maximum photosynthetic rate ($A_{\max}$) and stomatal conductance (g_s) in '17GR' and 'QQ74' genotypes of quinoa. Similar findings were demonstrated in quinoa cv. 'Titicaca,' in which temperature of 25/20 °C enhanced $A_{\max}$ by approximately 44% (Yang et al. 2016). Conversely, 35/29 °C did not influence $A_{\max}$ in 'Red Head,' 'Salcedo,' and 'Cherry Vanilla' and cultivars of quinoa (Bunce 2017). Similarly, heat stress (28/20 °C) did not diminish $A_{\max}$ in 'Achachino' cultivar of quinoa

(Becker et al. 2017). Heat-tolerant plants can maintain high g_s under heat stress, thereby increasing transpiration and eventually heat dissipation. Hence, quinoa under high temperature regimes can regulate transpirational cooling, provided water deficiency is not there (Becker et al. 2017). In ‘QQ74’ genotype, leaf greenness index (LGI) was enhanced due to heat stress, while no change was observed in ‘17GR’ (Hinojosa et al. 2019). Alternatively, LGI was decreased at high night temperature stress in another two quinoa genotypes, viz., ‘Regalona’ and ‘BO5’ (Lesjak and Calderini 2017). Similarly, no changes in F_v/F_m were found in ‘17GR’ and ‘QQ74’ exposed to high temperature. Nevertheless, temperatures of 25/20 °C enhanced F_v/F_m in ‘Titicaca’ (Yang et al. 2016).

10.3.2.4 Photoperiod, Flowering, and Seed Yield

Temperatures more than 35 °C during flowering and seed filling stages cause significant decreases in yield (Fig. 10.1). Peterson and Murphy (2015) and Walters et al. (2016) found such high temperatures near Pullman, WA, and reported that quinoa flowers were without seeds or had unfilled seeds at temperature more than 35 °C. Variations in heat resistance have also been reported in varieties of quinoa. For instance, sea-level varieties ‘QQ74,’ ‘Kaslaea,’ and ‘Colorado 407D’ exhibited higher endurance to heat stress in field areas of Pullman than other varieties (Peterson and Murphy 2015). Similarly, the impact of high night temperatures was examined in landrace ‘BO5’ and sea-level variety ‘Regalona’ raised in fields of Chile (Lesjak and Calderini 2017). Results revealed that elevated night-time temperatures of 20–22 °C during flowering decreased the seed yield by 23–31% and reduced the growth and seed number. However, harvest index and seed protein were not affected (Lesjak and Calderini 2017). As a result, medium increment in night temperature appears to have a greater negative effect on yield than the elevated day temperature. The equilibrium between photosynthesis and respiration gets affected by warmer nights, consequently decreasing carbohydrate content and growth. The quinoa cv. ‘Titicaca’ is extremely affected by high-temperature stress (HTS) during the flowering stage (Alvar-Beltrán et al. 2020). A negative correlation has been observed between HTS during flower and seed formation, with the majority of the losses taking place between 34 and 38 °C (Alvar-Beltrán et al. 2020). Among the diverse HTS, the highest losses in seed yield have been reported between 34–38 and 42–46 °C. Additionally, the highest shoot biomass has been reported between 30 and 34 °C HTS, which could be attributed to the fact that maximum biomass is generated during the vegetative stage, before heat stress at flowering. Therefore, heat stress during flowering and seed filling can considerably decrease yield (Fig. 10.1) and is one of the main obstacles to the expansion of quinoa at the global level (Lesjak and Calderini 2017). In latitudes more than 30°, having temperatures above 30 °C and photoperiods exceeding 14 h, a low yield has been reported in quinoa varieties from Andean valleys (Peterson and Murphy 2015; Walters et al. 2016). In Altiplano variety named ‘Kanckolla,’ seed diameter declined to the extent of 73% on increasing the temperature to 28 °C on long days (16 h) than the seeds exposed to 21 °C under short-day conditions (10.25 h) (Bertero et al. 1999b). In order to measure the effect of temperature and light/night duration in nine short-day quinoa cultivars from appearance to observable formation of a floral bud, two distinct models were employed. Both the attributes were insignificant based on the latitude of origin; nevertheless, an inverse relationship was witnessed when the parameters assessed were kept as constants (Bertero et al. 1999a). Bertero et al. (1999b) evaluated nine varieties, viz., 'Blanca de Junõn,' 'NarinÄo,' 'Ecu-621,' 'Blanca de Julõ,' 'Amarilla de Maranganõ,' 'Kanckolla,' 'Faro,' 'Sajama,' and 'Baer,' and observed that temperature, as well as photoperiod, regulated the degree of leaf emergence. Quinoa varieties from cold or dry climates were most susceptible to temperature than those originating from moist and warm environments (Bertero et al. 2000). In quinoa, sunrays influence phyllochron; therefore, cultivars from Bolivia, Southern Chile, and Peru are more susceptible to radiations compared to those from Ecuador. Nonetheless, Ecuadorian varieties are greatly susceptible to photoperiod and display the highest phyllochron (Bertero 2001). Saponin levels in sea-level cultivars 'Regalona' and 'Roja' along with valley variety 'Tunkahuan' were assessed under long (16 h) and short (8 h) day conditions and exposed to 20 and 30 °C (Delatorre-Herrera et al. 2015). Findings revealed that the maximum saponin level was found in plants exposed to short-day conditions and 30 °C. Heat stress did not affect seed yield in both '17GR' and 'QQ74' genotypes, but seed weight increased in '17GR' only (Hinojosa et al. 2019). Based on the variety, seed yield can enhance or decline, for instance, in the variety 'Cherry Vanilla' seed yield reduced by 30%, whereas in the variety 'Salcedo,' it improved by 70% on increasing the temperature (20/14 to 35/29 °C) (Bunce 2017). It is worth mentioning here that the seed yield of quinoa cv. 'Achachino' was enhanced at 28/20 °C when irrigated with freshwater, while no effects were observed when saltwater was given (Becker et al. 2017). Conversely, heat stress reduced seed yield in the natural environment during floral bud opening, limiting the pollen viability in the hot arid region of Atacama, Chile (Fuentes and Bhargava 2011); in the summer season of Pullman, USA (Peterson and Murphy 2015); and plains of Central Greece (Noulas et al. 2017). Few studies indicated that Chilean germplasm is more resistant to elevated temperatures compared to Andean germplasm (Peterson and Murphy 2015; Choukr-Allah et al. 2016). Nevertheless, the functional performance of cultivars, for example, 'Achachino' from Peru and 'Salcedo' from Bolivia were better under heat stress, indicating that heat resistance is not correlated with geographical origin. In Dubai, temperatures more than 43 °C restricted the grain yield in 5 quinoa genotypes, namely, 'ICBA-Q1', 'ICBA-Q2', 'ICBA-Q3', 'ICBA-Q4', and 'ICBA-Q5'. However, genotypes "NSL 106399" and "Q5" yielded seeds in a meshed house where the temperature was lowered to 35 °C (Hirich 2016).

10.3.2.5 Pollen Viability

Pollen viability considerably declined in two heat-stressed quinoa genotypes ['17GR' (Ames 13,735) and 'QQ74' (PI 614886)] though the latter was more susceptible to elevated temperature compared to the former (Alvar-Beltrán et al. 2020). Pollen grains of quinoa possess a spheroid outline and an indeterminate number of pores. The exterior of pollen has many tiny spinules, and a spherical aperture is protected with a spinulate operculum. It has been reported that the width of both exine and intine along with pore increase under HTS. On the contrary, Hinojosa et al. (2019) observed that pollen viability declined in response to HTS in quinoa (Fig. 10.1) without any impact on seed setting and external alterations in pollen surface. These results may be due to a large number of pollen grains yielded by quinoa and elevated relative humidity ranging between 40–65% in the growth chambers.

10.3.2.6 Phenolics and Carotenoids in Seeds

Carciochi et al. (2016) studied the impact of different roasting temperatures (100–190 °C) on seed phenolic content and found that elevated roasting conditions enhanced the synthesis of phenols. By using sophisticated techniques, Multari et al. (2018) investigated various drying temperature regimes to boost the levels of phenolics and carotenoids in seeds of quinoa growing in Finland. For the first time, these researchers revealed that the roasting process conducted at 70 °C was the most useful for extracting phenolics followed by 60 °C. Further, desiccating quinoa at 60 °C was the most efficient for xanthophylls extraction, which ensued at 50 °C. The heat used may have caused the inactivation of enzymes accountable for the breakdown of phytochemicals, thereby increasing the amounts of phenolics and carotenoids from seeds. Taking into account that the maximum levels of phytochemicals were attained when seeds were roasted at 60–70 °C, the employment of warm air for drying seeds of quinoa has nutritional value since it can increase the contents of phytochemicals.

10.3.2.7 Heat Shock Proteins

Heat shock transcription factor (Hsf) gene family has been examined in quinoa, and 23 *Chenopodium quinoa* heat shock transcription factors (CqHsfs) (CqHsf1-CqHsfs23) genes have been identified (Tashi et al. 2018). Transcript profiles pertaining to CqHSFs genes were investigated by means of RNA-seq data. Four CqHsfs, which were highly expressed, were confirmed in salar ecotype 'Real-Blanca' exposed to an elevated temperature of 37 °C, and findings revealed that CqHsfs9 and CqHsfs3 were upregulated subsequent to 6 h of treatment, whereas CqHsfs10 and CqHsfs4 had greater expression levels at 12 h. Quinoa leaves were exposed to heat treatment of 48 °C for 30 min with recuperation at 26 °C for 2 h to investigate heat shock protein (HSP70) in cucumber necrosis virus (CNV). Results revealed that HSP70 was considerably stimulated 2 h after heat shock and continued to be overexpressed for 3 days, leading to increased CNV genomic RNA, with HSP70 homologs assisting in uncoating of CNV (Alam and Rochon 2017).

10.3.3 Drought

In recent times, drought is turning out to be a common environmental issue, and climate change has, in turn, intensified the threat of drought, especially in dry regions, which may endanger food security. A cost-effective and faster way is to use underutilized crops, for example, quinoa which could be an excellent alternative to meet the ever-increasing demand for food in unfavorable environmental conditions. Quinoa is resistant to drought and can adapt and produce seeds in partly dry environments of Chile, Altiplano area of Bolivia, Peru, and dry mountainous areas of northwest Argentina (Hinojosa et al. 2018). These areas are highly arid, with an annual rainfall of less than 200 mm. Besides this, quinoa can grow and yield seeds in parched and semidry areas out of Andean territory, for instance, North Africa, Asia, the Near East, and the Mediterranean (Choukr-Allah et al. 2016). Though quinoa is drought tolerant, various climatic models forecast increment in drought incidences, particularly in the Altiplano area of the Andes mountains, where quinoa is cultivated conventionally by marginal farmers. Therefore, knowledge of the drought responses in quinoa is crucial for developing cultivars having enhanced endurance to drought.

10.3.3.1 Abscisic Acid (ABA)

Flowering and seed grain stages of quinoa are considered to be the most drought susceptible. Jacobsen et al. (2009) demonstrated enhanced levels of abscisic acid (ABA) in belowground organs of Altiplano variety named ‘INIA-Illpa,’ whereas analogous findings were witnessed in the foliage of sea-level variety ‘Titicaca’ by Yang et al. (2016). Furthermore, under drought stress, ABA amounts increased more rapidly in the xylem of ‘Titicaca’ shoots than roots (Razzaghi et al. 2011a). ABA in xylem sap of ‘Titicaca’ and ‘Achachino’ enhanced 2 days after drought treatment followed by a decline after rewatering, although the former had higher ABA levels than the latter (Sun et al. 2014). ABA has been recorded when quinoa is exposed to very mild water stress (Fig. 10.1), clearly indicating that chemical signaling functions in regulating stomatal conductance under water scarcity environments (Hariadi et al. 2011; Razzaghi et al. 2011a). Additional mechanisms which regulate turgor in response to drought could be osmotic regulation and antitranspirants excluding ABA in xylem elements (Jacobsen et al. 2009; Hariadi et al. 2011). It has been reported that quinoa can maintain photosynthesis under extreme water-deficit conditions for 3 days even after stomatal closure (Jacobsen et al. 2009). In a subsequent study, Jacobsen (2015) argued that in drought conditions, quinoa’s stomata get closed, through which leaves regulate water potential and in turn photosynthetic process, causing increment in the capability of utilizing water. The moderate role of ABA during drought suggests that quinoa depends on hydraulic regulation by altering the turgor or other chemical substances which have not been discovered so far (Zurita-Silva et al. 2015; Jacobsen 2015).

10.3.3.2 Photosynthetic Responses Using JIP Test

The JIP method is used to examine rapid chlorophyll fluorescence transients providing insights into photochemistry. In accordance with Jacobsen et al. (2009) findings, the results of Fghire et al. (2015) indicated a decline in stomatal conductance (g_s) in quinoa under water deficit treatments (Fig. 10.1) depending upon the growth stage. By using the light intensity analysis test (JIP-test), these researchers showed PSII to be more resistant to water deficit during the vegetative period compared to other growth phases. Further, the JIP test pointed to various target sites of PSII in response to water deficit stress, for instance, mean absorption and trapping per active reaction centers (RC) increased because of the deactivation of few RCs and the proportion of total energy dissipation to a number of active RCs enhanced due to elevated dissipation of inactive RCs (Fghire et al. 2015). Similarly, the examination of JIP parameters revealed the sites altered by drought stress in the electron transport chain (Strasser et al. 2010). Performance index (PI) is an extremely sensitive marker of the physiological state of quinoa under field conditions with diverse water regimes. Hence, large alterations in PI of quinoa in response to drought indicate significant modulation of PSII, mainly through deactivation of PSII RCs. PI is considered to be more susceptible relative to F_v/F_m ratio, since the former responds to alterations in rapid fluorescence increase kinetics between two fluorescence levels (F_0 and F_m), whereas the latter simply takes into account the variations in F_0 and F_m values (Fghire et al. 2015). Thus, in quinoa leaves, JIP-technique can be applied for evaluating water-deficit conditions and is a fine method for examining variations in physiological processes along with its target regions, for example, PSI and PSII. The notion that PSII is resistant to water limitations during the vegetative phase compared to other phases might be a strategy used by quinoa for its survival under drought stress (Fghire et al. 2015).

10.3.3.3 Gas Exchange, Root System, and Evapotranspiration

González et al. (2011) assessed leaf gas exchange parameter and $\Delta^{13}C$ in 10 diverse genotypes of quinoa raised in dry mountainous areas of northwest Argentina receiving 160 mm of rainfall and observed that genotypes exhibiting greater stomatal conductance were able to maintain a higher rate of photosynthesis. Further, the authors witnessed differences in seed production among the genotypes and reported a linear relationship between $\Delta^{13}C$ and seed production. Analogous findings were demonstrated by Killi and Haworth (2017), where water-deficit quinoa exhibited mesophyll and stomatal restrictions to carbon-dioxide transport. Nevertheless, in greenhouse trials, indices of photosynthesis, for example, quenching (qP and qN) and F_v/F_m, were tolerant to drought stress. Conversely, F_v/F_m declined under drought conditions in the variety ‘Titicaca’ raised in the greenhouse (Yang et al. 2016). Roots of quinoa elongate faster and have more extensive branching than increasing its foraging efficiency compared to other relatives, such as *C. pallidicaule* and *C. hiricinum* (Alvarez-Flores et al. 2014). A structural and dynamical experiment pertaining to roots was performed in water-scarce environments, evaluating *C. pallidicaule* (growing in arid habitat) and *C. hiricinum* (growing in wet habitat) and two ecotypes (rainy and dry habitat) of quinoa which demonstrated that quinoa genotypes displayed increased root biomass under water-deficit soil conditions than other two species. Moreover, genotypes from arid region exhibited more elongated, rough, and abundant roots relative to the rainy-habitat genotype (Alvarez-Flores et al. 2018). Overall these results support quinoa as a potential model plant to study ecophysiological and biophysical features of rooting into deeper soil layers. In a different study, the completely watered quinoa cultivar ‘Q5’ was cultivated in 3 different planting densities (PD) (150,000, 185,000, and 270,000) in lysimeters and exposed to the hot and arid environment of South Iran, and a maximum seed yield of 3.65 Mg ha^{-1} was detected in medium PD (Ahmadi et al. 2019). Thus, 'Q5' is regarded as a 'super crop' that can endure several abiotic stress factors and can produce seeds in arid and semi-dry regions. In addition to this, quinoa plants have been reported to exhibit extremely high transpiration and evapotranspiration rates resulting in elevated single crop coefficients ranging between 0.96 and 1.21 and dual crop coefficients varying between 1.63 and 1.75 which were higher compared to other field crops (Razzaghi et al. 2012). The key causes for large single as well as dual crop coefficients were increased loss of water from soil because of recurrent irrigations, local advection which enhanced transpiration and evapotranspiration, and a strong root system that assisted in improved water uptake. These findings conclude that quinoa has specific physiological mechanisms that facilitate continuous transpiration for cooling the leaves, eventually resulting in better water use efficiency.

10.3.3.4 Seed Quality

Environmental factors considerably impact the nutritional profiles of quinoa seeds. In seeds of two quinoa sea-level varieties, viz., 'Oro de Valle' and 'Cherry Vanilla,' protein levels augmented to a greater extent when plants were fully irrigated and grown with a clover-medic intercropping relative to the identical intercropping practice devoid of irrigation (Walters et al. 2016). Furthermore, the watered plants displayed an increment in seed contents of Mg, P, and Fe but diminished Ca and Zn than non-watered treatment. Even fiber and saponin content in quinoa seeds have been reported to increase under well-irrigated conditions than lacking irrigation (Pulvento et al. 2012). In southern-central Chile, seed attributes were assessed in sea-level varieties 'AG2010,' 'B080,' and 'Regalona' raised in four diverse water treatments under field as well as greenhouse trials, and results demonstrated increment in the antioxidative aptitude of all the varieties with a negligible decline in seed production of 'AG2010' (Fischer et al. 2013). Furthermore, 20% availability of water in soil enhanced globulin content in 'AG2010,' and rinsing seeds with water altered the levels along with the electrophoretic outline of globulins and albumins (Fischer et al. 2017).

10.3.3.5 Expression of Genes Under Water-Deficit Conditions

Raney et al. (2014) conducted the foremost RNA-seq transcriptome study on two drought-stressed quinoa varieties, Salares variety 'Ollague' and valley variety 'Ingapirca.' Depending on various physiological parameters, such as photosynthetic rate, stomatal conductance, and shoot water potential, 'Ollague' displayed higher drought endurance than 'Ingapirca.' RNA-seq of roots of both the varieties discovered 462 differentially expressed contigs along with 27 genes possibly having regulatory role under various water stress treatments. Besides being upregulated during heat stress, HSP70s also play a crucial role under other stresses, including drought (Grenfell-Shaw and Tester 2021). Liu et al. (2018) discovered and categorized 16 HSP70s (Cqhsp70s) in the recently sequenced genome of quinoa (Jarvis et al. 2017), based on *Arabidopsis* HSP70s. These researchers examined the expressions of 13 Cqhsp70s genes under polyethylene glycol 6000 (PEG6000)-

induced water-deficit conditions and found differences in gene expression in response to drought. For example, out of 13 Cqhsp70s genes, there was downregulation in the expression of 6 genes at the start of water deficit and in the course of recovery. Similarly, the expression of AUR62024018 remained elevated all over the drought regime. Furthermore, 50% of the genes displayed “up and down” expression outline, analogous to the genes of *Arabidopsis*. Morales et al. (2017) performed transcriptional studies on drought-stressed quinoa and reported the Salares variety ‘R49’ to be maximum drought tolerant than ‘BO78’ and ‘PRJ’ sea-level varieties. RNA-seq conducted on ‘R49’ revealed 54 and 51 million reads under control and drought, respectively. All the reads were compiled into 150,952 contigs; 19% of genes, i.e., 306 contigs, did not characterize in available records of homologous genes. These authors chose 15 genes for exploring their expression in response to water scarcity in quinoa and observed upregulation of only 2 plastid genes linked with the synthesis of ABA (CqNCED3a and CqNCDE3b). Likewise, all genes that displayed alterations from representation read, viz., CqCAP160 (cold acclimation protein 160), CqHSP20 (putative chaperones hsp20-protein superfamily), CqAP2/ERF (integrase-type DNA-binding protein superfamily), CqLEA (late embryogenesis abundant protein), CqHSP83 (chaperone protein, protein family HTPG), CqPP2C (protein phosphatase protein family 2c), and CqP5CS (delta 1-pyrroline-5-carboxylate synthase 2) showed upregulation. Particularly, CqHSP20 and CqLEA exhibited expression over 140-fold. Therefore, the abovementioned studies conclude that HSPs are imperative for the acclimatization of quinoa to water-deficit conditions.

10.3.3.6 Field Studies Under Drought Conditions

Five diverse genotypes of quinoa were studied in Egypt under three distinct cultivating seasons, water regimes—820, 500, and 236 mm (rainfall + irrigation)—and findings revealed genotypic differences in external features and productivity. Sea-level variety ‘QL-3’ displayed a maximum decrease in yield under severe drought, while valley variety ‘CICA-17’ exhibited minimum decline (Al-Naggar et al. 2017). Reductions in productivity were also witnessed under arid conditions in sea-level quinoa varieties ‘Oro de Valle’ and ‘Cherry Vanilla’ cultivated in the field in Pullman, WA, with 3 intercropping treatments (fescue grass/clover mix, clover/medic mix, and control) and 3 water regimes (dryland, 64 and 128 mm) (Walters et al. 2016). Moreover, both the intercropping systems influenced the productivity of quinoa under watered or nonirrigated states.

10.3.3.7 Drought-Mediated Tolerance Mechanisms

Responses and mechanisms of plants to tackle water scarcity are of two main types: (1) stress evasion and (2) stress endurance. Stress avoidance strategies aim to balance the uptake and loss of water. Stress resistance mechanisms tend to protect cell under severe stress conditions when stress evasion mechanisms are not adequate. Stress endurance mechanisms comprise detoxification of ROS and accretion of proteins, for example, late embryogenesis abundant (LEA) proteins as well as organic solutes (such as proline, etc.) (Claeys and Inze 2013). Although all water deficit-mediated mechanisms, such as prevention, avoidance, and resistance to drought, are reported in quinoa, they are not found in one genotype. Quinoa can evade the damaging impacts of drought through a compact deep-rooted organization coupled with decreased leaf area or leaf fall (Ali et al. 2019). An additional mechanism could be the presence of specialized epidermal cell vesicles which could function as water storage structures along with small-sized thick-walled cells (Shabala et al. 2012). It has been established that for maintaining leaf water potential (LWP), water-deficit quinoa induces stomatal closure, thereby increasing water use efficiency (Jacobsen et al. 2009). This mechanism is considered to be one of the unique drought endurance traits of quinoa. Ali et al. (2019) investigated two quinoa cultivars, a South American variety 'L119' and a Danish variety 'Titicaca,' and examined soil water content at permanent wilting. Their findings revealed cultivar-dependent differential morphological and physiological responses to water scarcity and recovery. Both 'L119' and 'Titicaca' were sensitive to drought in terms of water potential and relative water content in leaves, stomatal conductance, and stomata closed at the same water-deficit condition; nevertheless, drought tolerance strategies of the two cultivars were different (Ali et al. 2019). Fghire (2014) reported a reduction in LWP in a number of drought-stressed quinoa varieties. Several studies revealed that stomata closed in greenhouse and field cultivated quinoa only after LWP dropped to -1.2 to -1.6 MPa, and therefore quinoa has been categorized as a plant species enduring dehydration (Jacobsen et al. 2009; Sun et al. 2014). Quinoa has developed an extraordinary potential to recommence leaf development rapidly following severe drought, and its wilting peak is also lesser than other Andean crop plants. Anatomical adaptations in quinoa that confer drought tolerance include extremely sunken stomata in leaf epidermis. Negative effects of drought on photosynthesis and stomatal conductance along with plant-water relations at diverse growth stages have been investigated (Razzaghi et al. 2011b), inferring that a few quinoa cultivars display gas exchange traits in the usual C3 plant range and that low osmotic potential could be a key feature related with drought tolerance.

10.3.4 Ultraviolet B (UV-B) Radiation, Frost, Waterlogging, and Heavy Metals

Other abiotic factors, for example, ultraviolet B (UV-B), frost (chilling), and waterlogging, along with heavy metals have also been investigated in quinoa which are briefly discussed in the following subsections:

10.3.4.1 Ultraviolet B (UV-B)

Ultraviolet B (UV-B) corresponds to a minute portion of the electromagnetic band having a wavelength ranging from 280 to 315 nm; but its elevated energy can be injurious to organisms. Palenque et al. (1997) witnessed differential responses about physical features and photosynthetic pigment biosynthesis in Altiplano cultivars of quinoa, viz., 'Robura,' 'Chucapaca,' and 'Sayaña.' The researchers observed an increment in flavonoid levels together with a decrease in leaf size and plant stature

(Fig. 10.1) under UV-B treatment in all three varieties; nevertheless, 'Chucapaca' displayed maximum acclimatization to UV-B. Sircelj et al. (2002) studied the impacts of UV-B at ultrastructure as well as metabolism in UV-B exposed quinoa seedlings and observed alterations in thylakoid organization (Fig. 10.1). Similarly, Hilal et al. (2004) detected deposition of lignin in epidermal cells of quinoa's cotyledons exposed to UV-B radiations. González et al. (2009b) performed semi-controlled experimental trials on Altiplano varieties 'Cristalina' and 'Chucapaca' to determine their responses to varying intensities of UV-B and observed that glucose, fructose, and sucrose levels differed in foliage and cotyledons of both the cultivars, based on UV-B treatments. These reports are beneficial for understanding the flexibility of plant metabolic pathways required for improving endurance to UV-B rays. In controlled environments, Perez et al. (2015) demonstrated alterations in morphological parameters, for instance, stem diameter, plant length, number of leaves, and area in diverse quinoa cultivars under UV-B radiations. In a different study, Prado et al. (2016) investigated the influence of UV-B radiations on photosynthetic and defense-related pigments along with soluble sugars in five varieties of quinoa from varied geographical origins and witnessed enhancement in the levels of UV-B-absorbing pigments in all five varieties. The researchers suggested that these UV-B-absorbing compounds probably serve as a "chemical shield" protecting the photosynthetic machinery from rays. Reyes et al. (2018) conducted the foremost detailed research on the impact of UV-B on photosynthesis in quinoa and revealed that pigment synthesis, chlorophyll fluorescence, photosynthetic rate, and ROS levels were influenced by diverse exposure and time interval of UV-B. Hence, quinoa can maintain diverse metabolic processes based on UV-B levels.

10.3.4.2 Frost

Frost is of large importance in Andes, particularly in the southern region of Bolivia and Peru, with considerable temperature variations and frost up to 200 days a year during night-time (Jacobsen et al. 2007). Jacobsen et al. (2005) examined diverse genotypes of quinoa exposed to frost conditions and demonstrated that Altiplano cultivars could tolerate −8 °C for a period of 4 h at 2 leaf phases more efficiently compared to Andean cultivars. For example, Altiplano cultivars 'Ayara' and 'Witulla' exhibited 4.17% mortality when exposed to −8 °C for 4 h; while Andean valley variety 'Quillahuaman' exhibited 25% fatality under the same conditions and 50% under −8 °C for 6 h. Moreover, the flowering phase was more susceptible to frost as the investigation reported 56% decrease in productivity in 'Quillahuaman' and 26% in 'Witulla' under temperature of −4 °C for 4 h. The main mechanism behind frost tolerance in quinoa is evasion of ice formation, facilitated by high soluble sugars. Therefore, proline along with soluble sugars, for example, sucrose, can be exploited as indices of frost endurance (Jacobsen et al. 2007). Parallel findings were reported in Altiplano cultivar 'Sajama' exposed to 5/5 °C, in which low temperature stress resulted in the sucrose-starch distribution in cotyledons (Rosa et al. 2009). Furthermore, frost could stimulate various regulatory processes associated with alterations in activities of sucrose synthase, sucrose-6-phosphate synthase and invertase in embryonic axes, and cotyledons during seed formation in 'Sajama' (Rosa et al. 2004).

10.3.4.3 Waterlogging

Changes in soil water levels, either by irrigation or rainfall, can alter growth, development, and yield in quinoa. According to Jacobsen et al. (2006), the occurrence of floods during the rainy season in tropical quinoa decreases its production. This could be due to O_2 deficiency in root zone, decaying of roots (Fig. 10.1), and decreased photosynthesis during high cloud cover, for instance, when years of La Niña incidence occur in Colombia (Fajardo-Rojas 2019). This climatic aspect is of enormous importance, since limited light energy decreases PSII besides the dissipation of energy in the form of heat or fluorescence, thereby lowering the availability of chemical energy required for fixation of CO_2. It can also be ascribed to low uptake of nutrients under waterlogging, which negatively affects the transport of electrons in PSII, facilitating energy losses as heat and fluorescence (Kalaji et al. 2018). Hence, the photosynthetic apparatus gets impaired along with an increase in ROS and denaturation of complexes present in thylakoid membranes. Waterlogging experiments conducted in control conditions (growth chambers) with Altiplano cultivar ‘Sajama’ demonstrated negative effects of waterlogging, including decreased root biomass, photosynthetic pigments, and increased levels of starch and soluble sugars (González et al. 2009a). In Brazil, the field-grown variety ‘BRS Piabiru’ displayed the highest leaf measurements under a water regime of 563 mm. On the other hand, the decline in leaf measurement values was witnessed under 647 mm, suggesting the sensitive nature of quinoa to waterlogging conditions (Jayme-Oliveira et al. 2017). Pre-reap germination in quinoa can be a problematic issue in areas with high rain (Fig. 10.1), particularly when rainfall occurs during the seed-setting period. The sea-level cultivar ‘Chadmo, QQ065-PI 614880’ (originated from the moist region of Chiloe Island in Chile) could be an excellent alternative for such climatic conditions due to its pre-harvest sprouting tolerance coupled with high seed dormancy. This was demonstrated in a relative experiment undertaken in the high rainfall region of Olympia Peninsula of Washington State by Peterson and Murphy (2015). Likewise, conventional varieties cultivated on Chiloe Island could be an additional choice for humid and cold environments. These cultivars are normally grown under 10.6 °C average annual temperature, total rainfall of 1743 mm, and 80% RH. Nevertheless, there are additional factors connected with high rainfall that influence quinoa, particularly during physiological maturity and grain phase, since elevated precipitation promotes pre-germination of seed within inflorescence and yield losses (Garcia-Parra et al. 2020).

10.3.4.4 Nutritional Deficiency Stress

Environmental factors that influence the uptake of nutrients decrease the yield performance of crops. Several nutrients are intricate and involved in plants’ physiological and biochemical processes. Nitrogen (N) constitutes the main nutritional requisites of plants (Fonseca-López et al. 2020). Many studies have indicated that stress because of low N supply in variety ‘UdeC9’ prior to senescence stage induces modifications in PSII, especially in F_v/F_m, quantum yield, non-photochemical quenching (NPQ), and injury to chloroplast (Bascuñán-Godoy et al. 2018). This impairment is ascribed to the least fluorescence yield under dark conditions (F_0) and

F_m, which could be extremely sensitive to alterations in chlorophyll levels at the start of flowering and close to senescence. However, information is scarce to elucidate the supply and uptake of nutrients in quinoa and their correlation with photosynthesis.

10.3.4.5 Heavy Metals

Bhargava et al. (2008) observed accumulation of high levels of heavy metals, viz., nickel (Ni), cadmium (Cd), zinc (Zn), and chromium (Cr) in leaves of 17 quinoa accessions than other species. For example, accessions *C. quinoa* 'Ames 22,158', *C. quinoa* 'PI 478410', *C. quinoa* 'PI 587173', and *C. giganteum* 'CHEN 86/85' accrued the maximum Cd contents; 'Ames 22,156' and 'PI 510536' exhibited the greatest levels of Ni, Cr, and Zn. A different study performed in a polluted metropolitan region 'brownfield' in Vancouver, Canada, concluded Altiplano variety 'Quinoa de Quiaca—PI 510532' as a metal hyperaccumulator (Cd, Pb, and Cu). As a result, quinoa seeds would be unsuitable for human utilization if cultivated in the brownfield region due to elevated contents of metals (Thomas and Lavkulich 2015). Scoccianti et al. (2016) evaluated hydroponically cultured quinoa's physiological responses to varying dosages of Cr and revealed that foliage accumulated lesser Cr contents than roots and stems. Leaves of 'Regalona' variety tolerated non-toxic doses of chromium(III) chloride ($CrCl_3$) by stimulating the buildup of tocopherols and increased tyrosine aminotransferase activity, thereby promoting growth but chloroplastic pigments were unaltered. Fresh biomass and pigments decreased (Fig. 10.1) under higher Cr(III) doses of 5 mM, which became toxic after 7 days of exposure, resulting in oxidative stress with a simultaneous increase in proline levels (Scoccianti et al. 2016). Researchers also observed a decline in chlorophyll a and b and total chlorophyll at maximum Cr(III) dosage, without non-significant alterations in chlorophyll a/b ratio. Quinoa is among one of the few species which could be raised at high altitudes and in conditions of Lake Titicaca. There are rising apprehensions about Lake Titicaca since it is greatly contaminated with heavy metals emanating from natural causes, leftover effluents from mining industries, and metropolitan sewage discharge (Monroy et al. 2014). Thomas and Lavkulich (2015) described that full-grown plants had a higher capability to eradicate metals from the soil compared to young plants; hence, it is likely that at maturity Cr uptake may be higher, and this aspect renders quinoa an appropriate candidate for remediation of metal-polluted soils. However, crop quinoa should not be cultivated on metal-contaminated soils for human food or feedstock since its tocopherols and ROS scavenging features decrease its nutritional value (Scoccianti et al. 2016).

10.3.5 Responses of Quinoa Under Combination of Abiotic Stresses

Heat stress in quinoa has been investigated jointly with other abiotic stresses, for example, salinity, drought, and elevated CO_2 concentration (Yang et al. 2016; Becker et al. 2017; Bunce 2018). A study with 'Titicaca' was performed in cold conditions of 18/8 °C and raised temperatures of 25/20 °C using 3 diverse water treatments (complete irrigation, scarce irrigation, and limited irrigation) which revealed higher negative effects of water stress on physiological characteristics than elevated temperature (Yang et al. 2016). On the contrary, high temperature enhanced chlorophyll fluorescence and contents, stomatal conductance, photosynthesis, and ions in xylem sap, indicating that quinoa can regulate osmotic potential to compensate for the increased transpiration. Similar findings were witnessed regarding stomatal conductance along with photosynthetic rates in Altiplano cultivar 'Achachino' raised at 28/20 °C and sea-level cultivars '17GR (AMES 13735)' and 'QQ74 (PI 614886)' cultivated at 40/24 °C (Becker et al. 2017). Bunce (2017) determined the combined impact of heat stress and elevated level of CO_2 on 2 sea-level cultivars, 'Cherry Vanilla' and 'Red Head,' and a single Altiplano cultivar, 'Salcedo,' at the flower bud opening stage. Findings revealed increased or no effect on harvest index in all varieties exposed to a high temperature of 35/29 °C (day/night). Seed weight declined in 'Cherry Vanilla' when raised at elevated temperature and in optimal CO_2 concentration of 400 μmol mol^{-1}. However, in the other two cultivars, raised temperature and optimal or elevated CO_2 concentration of 600 μmol mol^{-1} resulted in either increased seed biomass or similar to the controls at 20/14 °C. In a different study, Bunce (2018) raised 'Cherry Vanilla' under low (12/6, 20/14 °C) and medium (28/22 °C) climatic temperatures and reported its high adaptability to varied temperatures, based on the carboxylation of Rubisco. Nonetheless, variety's origin also determines its endurance to high temperature. For instance, valley cultivar 'Amarilla de Marangani' generated maximum seed mass at 20 °C day temperature while sea-level variety 'NL-6' yielded the highest seed weight at 30 °C day temperature (Isobe et al. 2012). The firmness of the leaf membrane was evaluated in 6 quinoa cultivars cultivated at 34/32 °C (adapted) and 22/20 °C (non-adapted). Findings demonstrated that Altiplano cultivar 'Illpa' displayed lesser membrane injury following exposure to 50 °C for 64 min under adapted temperature than the same exposure under non-acclimatized conditions (Sanabria and Lazo 2018). Studies have identified quinoa as a C3 plant that responds to CO_2 saturation to a higher extent than C4 plants, indicating its close association with CO_2 level of neighboring environment, thereby resulting in enhanced overall growth and yield based on the cultivar (Bunce 2017). Quinoa exhibits a higher gas compensation point than C4 plants, indicating its positive correlation with increased intercellular CO_2 and nutritional profile (Bascuñán-Godoy et al. 2018). Geissler et al. (2015) argue that an increment in the photosynthetic potential of quinoa results in higher salt tolerance, improves stomatal conductance and decreases oxidative stress. Similarly, among ten quinoa cultivars, those displaying higher photosynthesis and conductances exhibited more yield under drought (González et al. 2011).

A combination of stressors does not always exert negative effects on plants and in a few cases might ameliorate the impacts of individual stresses. Lutts and Lefèvre (2015) demonstrated higher uptake of Cr in quinoa cultivated on saline soil. Salinity augments metal mobility by forming complexes of salt anions with metals and antagonism between salt cations with metals (Lutts and Lefèvre 2015). In addition, NaCl might impact metal absorption through its effect on ionic transporters. For example, Na accretion in quinoa raised on saline and Cr(III) containing soil was lower than controls. The decreased Na^+ (osmoticum) may explain the high expression of glycine betaine and proline biosynthetic genes in the foliage of quinoa plants treated with combination of Cr and NaCl. Cr(III) upregulated the transcript amounts of PHT1;1 (phosphate transporter) in roots but were downregulated in leaves, indicating the involvement of this transporter in translocation rather than uptake (Guarino et al. 2020). Cr(III)-modulated genes were categorized into two groups: (1) genes upregulated more under saline than non-saline conditions, viz., PHT1;1, SULTR3;4b, P5CS, TAT, CqBADH1, and PAL1 and (2) genes upregulated only in response to salinity, namely, SULTR1;1, SULTR3;4a, CAD1, CqDHN1, DHN2, MET2A, and HSP70 (Guarino et al. 2020). Schmöckel et al. (2017) recognized salt-tolerant genes of quinoa and demonstrated their differential upregulation in roots and leaves under 300 mM NaCl, with SULTR3;4b being upregulated in below ground parts and SULTR1;1 along with SULTR3;4a in leaves. Cr(III) significantly upregulated SULTR1;1 and to some extent SULTR3;4a in foliage exposed to salinity, probably because of the association of sulfate and ABA and demand for S compounds under stressful environments (Guarino et al. 2020). Transcript levels of the dehydrin gene can also be induced by metals, such as Cr, and few dehydrins can bind metals (Guarino et al. 2020). Cr(III) and NaCl trigger proline accretion by stimulating the expression of P5CS (Ruiz et al. 2017; Guarino et al. 2020). Expression of PAL1 (phenylalanine ammonia-lyase) enhanced to the same degree in the foliage of NaCl- and/or Cr(III)-exposed quinoa plants, indicating the involvement of this particular enzyme in plant tolerance. In leaves, TAT gene was upregulated only under salinity, whereas in belowground organs both Cr and Cr + NaCl increased TAT expression, indicating this enzyme to be a beneficial indicator of stress in quinoa (Scoccianti et al. 2016; Guarino et al. 2020). The increase in foliar transcript levels of CAD1 and MET2 genes might contribute to the potential tolerance of quinoa to metals, particularly under moderate salinity stress (Guarino et al. 2020).

10.4 Conclusions

Quinoa is regarded as a versatile plant as its seeds and foliage are consumed as human food and biomass as animal feed, or it can be used as a cover crop or phytoremediation tool. Each year, farming land is being lost owing to salinity, temperature extremes, and acute drought, which are described over and over again. As a result, planters have started looking for tolerant species, for example, quinoa that can grow and reproduce well under such harsh environments. Morphological, physiological, and biochemical responses of diverse quinoa cultivars to different abiotic stresses, in the field as well as lab environments, have revealed its adaptability and tolerance potential. This endurance and flexibility appears to be genetically regulated, and novel molecular techniques have eased the complete genome sequencing of quinoa. One of the most notable traits of quinoa is its great tolerance to salt stress. Numerous genes triggering salinity tolerance in quinoa have been discovered through transcriptomic studies which might be of enormous significance in the breeding of salt-tolerant quinoa varieties in the future. In spite of the several latest studies regarding the role and responses of quinoa under abiotic stresses, there are still knowledge gaps. Upcoming research should concentrate on the genetic makeup responsible for quinoa's abiotic stress endurance and its contribution in influencing its chemical makeup. This will enable quinoa breeders to produce new varieties adaptable to diverse environments which in turn would facilitate its global expansion. Taken together, quinoa is an outstanding model for the full exploration of stress tolerance mechanisms and novel genes for improving other plant species.

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Part III

Application of Organic Fertilizers and Phytohormones in Cereals Against Abiotic Stress

Cereals and Organic Fertilizers Under Abiotic Stress

11

Siamak Shirani Bidabadi and Arafat Abdel Hamed Abdel Latef

Abstract

The present chapter attempts to highlight the comprehensive and systematic study of organic fertilizers that mitigated abiotic stresses in cereals such as wheat, soybean, and pulses. Organic fertilizers are potentially one of the most promising alternatives to cope with yield losses caused by abiotic stresses. Organic fertilizers such as vermicompost, green manure, seaweed, and wood ash contain many different compounds that positively affect plant physiology under abiotic stresses. Various research works have been conducted to evaluate the organic fertilizers in improving plant growth when subjected to abiotic stresses. In this sense, this chapter aims to summarize the state of the art regarding various categories of organic fertilizers, their mode of action, and whether they are capable to improve cereals' growth under abiotic stresses.

Keywords

Antioxidants · Biofertilizers · Biostimulants · Environmental stresses · Seaweeds · Vermicomposting

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11.1 Introduction

Abiotic stress caused by climate change, along with a reduction in soil fertility today, poses a terrible threat to the food security of human societies (Nephali et al. 2020). Modern agricultural methods have increased the negative effects of environmental stresses on plant growth. Therefore, adopting a novel sustainable strategy for boosting the plant defense system against abiotic stresses is highly required (Balmer et al. 2015, 2018; Borges et al. 2014; Westman et al. 2019; Nephali et al. 2020). Recently, organic fertilizers have been steadily growing in the agricultural industry and have positioned themselves as one of the key emerging strategies for enhancing plant resistance against abiotic stresses (Shirani Bidabadi et al. 2017). However, the limited fundamental research into the modes of action of many organic fertilizers is among the knowledge gaps that require scientific attention. Elucidation of the biological basis of organic fertilizers function, and a broad mechanism of action at the cellular and molecular levels, is a prerequisite for the development of a scientifically-based biofertilizers industry, leading to an effective exploration and application of formulations in agriculture (Yakin et al. 2016; Fleming et al. 2019). Reviewing of previous findings has shown that organic fertilizers can provide key fundamental knowledge and understanding required to explore novel biostimulant-based strategies for improved crop health and resilience against environmental stresses (Shirani Bidabadi et al. 2017). This chapter represents an overview of plant defense strategies against abiotic stresses and reports on the current application of organic fertilizers. Furthermore, some key aspects in the mechanisms that underlay organic fertilizers-plant interactions under abiotic stresses are discussed.

11.2 Plant Defense System Against Abiotic Stress

Unfavorable environmental factors such as temperature stress, water stress, salinity stress, and heavy metal stress strongly affect the growth and development of plants and lead to a severe reduction in yield and even plant death (Nejat and Mantri 2017; He et al. 2018). Plants are equipped with immune systems to reduce the pressure caused by these environmental stresses when faced with these unfavorable conditions, which increases the plant resistance by reducing the severity of these negative effects (He et al. 2018). Plants are programmed by a complex monitoring network involving upstream signaling molecules including stress hormones, reactive oxygen species, calcium, and downstream gene regulation factors, particularly transcription factors (He et al. 2018). Some of the important defense responses in plant cells are desaturation of membrane lipids, activation of reactive oxygen species (ROS) scavengers, induction of molecular chaperones, and accumulation of compatible solutes. However, these defenses are also programmed by a complex regulatory network involving upstream signaling molecules including stress hormones such as abscisic acid (ABA), auxins (indole acetic acid, IAA), ethylene (ET), cytokinins (CK), gibberellins (GA), salicylic acid (SA), jasmonic acid (JA), and brassinosteroids (BRs) (Slama et al. 2015; Wania et al. 2016; He et al. 2018).

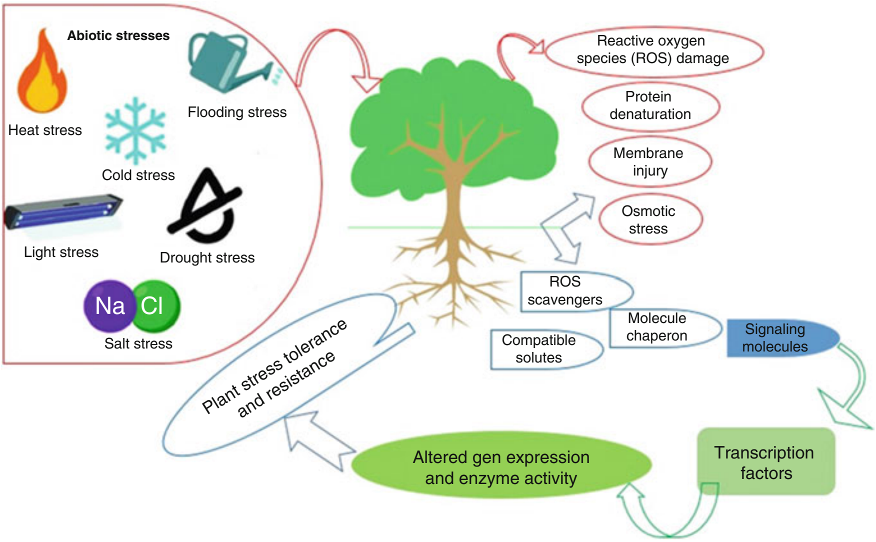

Fig. 11.1 Plant-based defense systems and networks under which these systems are monitored in response to abiotic stresses

Various abiotic stresses cannot only cause cellular disorders but can also trigger secondary stresses, such as membrane damage, ROS damage, protein denaturation, and osmotic stress. Plants are equipped with a series of strategies shown in Fig. 11.1 when faced with these environmental stresses (Fig. 11.1).

Reactive oxygen species-induced lipid peroxidation plays a signaling role, as a small chemical can readily attack different biomolecules encompassing carbohydrates, lipids, proteins, and nucleic acids. Consequently, they lead to oxidative catastrophe including enhanced photoinhibition and membrane lesions, which can be measured by the production of malondialdehyde (MDA) (Guo et al. 2012; He et al. 2018). Plant crop tolerance against abiotic stresses can be acquired via engineering both nonenzymatic (carotenoids, flavonoids, and vitamin E (Gechev et al. 2006; Zhao et al. 2011)) and enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), and several peroxidases, resulting in ROS scavenging system and activation of defense system (Sharma et al. 2012; Shirani Bidabadi et al. 2021). Kong et al. (2017) reported that excessive application of some fertilizers resulted in declining in the ROS scavenging system leading to enhanced stress susceptibility. Notably, glutathione (GHS) not only serves as a bridge between the antioxidant hormonal signaling pathways but is important because it directs defensive responses to abiotic stresses (Perez and Brown 2014; Schwessinger et al. 2015; Shirani Bidabadi et al. 2021). Regarding abiotic stress resistance, the accumulation of wax and alcohol-forming pathway in various plant species have been reported to play a very important role (Bourdex et al. 2011; Borisjuk et al. 2014; Xue et al. 2017). Furthermore, the unsaturation level of fatty acids is an important factor in determining the fluidity of cell membrane when plants encounter abiotic stresses (Mikami and Murata 2003), as membrane fluidity is susceptible to various abiotic stresses (He et al. 2018). Wu et al. (2017) asserted that anionic nanoceria with a low Ce^{3+}/Ce^{4+} ratio at cellular levels protected the photosynthetic machinery from abiotic stresses. On the other hand, some compatible solutes as small organic compounds with electrical neutrality, high solubility, and low toxicity such as raffinose, trehalose, inositol, mannitol, proline, and glycine betaine can even mount up to fairly high concentrations inside the cell with few perturbations. Under stressful conditions, these metabolites may accrue to act as osmoprotectants against dehydration, scavengers of ROS, and stabilizers of proteins and membranes (Ashraf and Foolad 2007; Slama et al. 2015). Mitigation of the negative impact of abiotic stresses by organic fertilizers is performed via the preparation of water and nutrients and plant growth regulators (Van Oosten et al. 2017; Garcia-Garcia et al. 2020; Teklic et al. 2020). Some organic fertilizers contain plant growth regulators which through these compounds improve plant growth under stressful conditions (Lea et al. 2007).

11.3 Main Categories of Organic Fertilizers

With increasing levels of agricultural modernization, sustainable agriculture has also become an important global issue. Organic fertilizers are currently applied for so many crops such as vegetables and fruits. Organic fertilizers refer to compost made from animal waste or animal and plant residues that are rich in natural by-products. In general, organic fertilizers fall into three categories such as animal, plant, and mineral-based manures (Fig. 11.2).

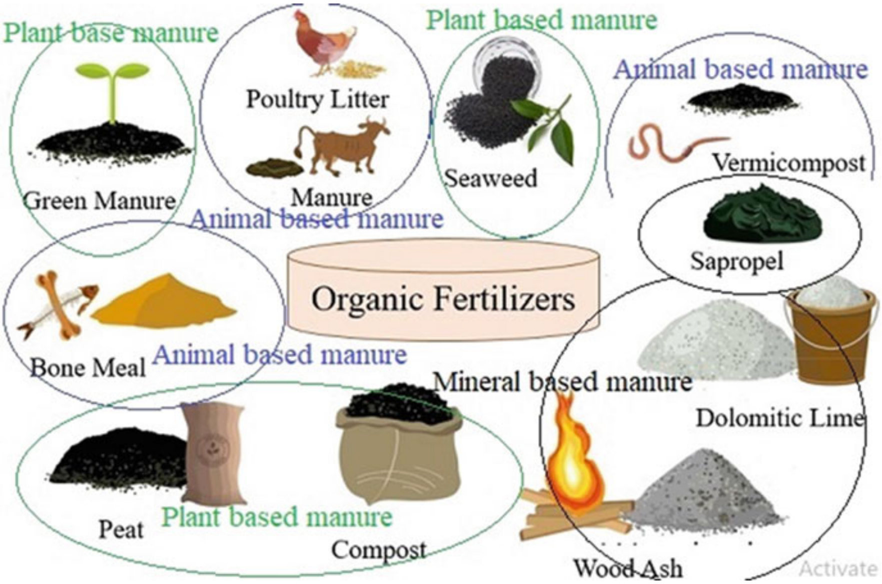

Fig. 11.2 Types of organic fertilizers based on the source from which they are obtained

Organic fertilizer contains a comprehensive range of nutrients, including major elements, trace elements and many physiological active substances, hormones, vitamins, amino acids, glucose, DNA, RNA, and enzymes. Therefore, it is called complete fertilizer. Sapropel is another type of organic fertilizer with a high potential for use in agriculture. In scientific literature, the term "sapropel" has been used mostly in a generic sense for describing organic-rich fine-grained sediments deposited in stagnant water (Emeis and Weissert 2009; Grantina-Ievina et al. 2014). Grantina-Ievina et al. (2014) reported a high level of aerobic heterotrophic bacteria, a high level of yeasts, and a variable level of filamentous fungi with low diversity in sapropel samples. Growth-stimulating activity of sapropel has been reported to be characterized as relatively high when compared to other organic fertilizers (Grantina-Ievina et al. 2013). Sapropel is a rich source of both humic substances and phytohormones (Klavins et al. 2003; Szajdak and Maryganova 2007). The presence of the same compounds in this fertilizer can justify its ability to induce resistance to biological stresses in plants. Application of dolomite as calcium-releasing compound is used to enhance calcium in the plant growth media (Cresswell and Weir 1997). The beneficial effects of mineral-based organic fertilizer dolomite have been previously reported on citrus and vegetable crops (Chen et al. 2006). Wood ash as a result of incomplete combustion of wood, containing a mixture of. oxides, hydroxides, carbonates, and silicates, possesses a high solubility and availability of micronutrients for plants that play very important physiological roles in the formation of chlorophyll, nucleotides and alkaloids as well as in the synthesis of many enzymes, hormones, and vitamins (Ozolincius et al. 2006). The use of wood ash results in enhancing soil fertility by providing nutrients such as calcium, magnesium, potassium, phosphorus, and micronutrients (Chen et al. 2015; Symanowicz et al. 2018). Wood, especially when is associated with nitrogen fertilization, results in improved soil fertility and biological activities and plant growth compared to chemical fertilizers (Saarsalmi et al. 2012). Seaweeds as an important marine resource has been frequently used as a source of organic fertilizers, and its application has been proved to be beneficial for seed germination, seedling development, plant growth and yield improvement, and enhancing plant tolerance to biotic stresses (Zodape 2001; Zhang and Ervin 2008; Raghunandan et al. 2019). Seaweed-based organic fertilizers have been recently commercialized and substituted for conventional synthetic fertilizers (Divya and Niranjana Reddi 2017). These organic fertilizers have been used as soil conditioners, fertilizers, and green manure due to the presence of high amounts of potassium, micronutrients, and growth substances (Divya and Niranjana Reddi 2017). Seaweeds have been reported as a novel source of antioxidants, plant hormones, osmoprotectants, plant nutrients, and other novel bioactive metabolites that improve plant tolerance against abiotic stresses (Ramarajan et al. 2013; Pacholczak et al. 2016; Raghunandan et al. 2019). Seaweeds contain several organic constituents such as polysaccharides, proteins, and fatty acids which improve soil moisture and nutrient, thereby stimulating microorganisms' activity and improving soil texture. Seaweeds facilitate a conducive environment for root growth by enhancing microbial diversity and activities like nutrient mineralization and mobilization (Battacharyya et al. 2015; Raghunandan et al. 2019). Biochemical transformation of organic wastes by naturally occurring or inoculated microbes to organic fertilizer results in compost production (Sawargaonkar et al. 2013; Gopalakrishnan et al. 2020). Compost contains beneficial microbes that help the plants to mobilize and acquire nutrients as well as enhance plant tolerance against biotic and abiotic stresses (Perner et al. 2006; Gopalakrishnan et al. 2020). Another viable and cost-effective technique for the management of livestock manure and production of organic fertilizers is vermicomposting. This technique helps reduce environmental pollution and also provides a healthier substitute for chemical fertilizers where the earthworms' activity results in the decomposition of organic matter and preparing nutrients for plant growth (Obalum et al. 2017; Deepthi et al. 2021; Fatima et al. 2021). Vermicompost directly affects chlorophyll fluorescence and electron transport rate which leads to higher yield and improved tolerance against biotic and abiotic stresses (Meena et al. 2021). The usage of vermicompost leachate has also been reported in several crops by several researchers (Shirani Bidabadi et al. 2016, 2017). Organic manure as an organic fertilizer improves soil microorganisms which has a positive effect on plants grown under biotic and abiotic stresses and provides required plant nutrients (Shariff et al. 2017). Green manures as another fertilizer source could be a promising approach to maintaining sustainable nutrients for crop growth (Kim et al. 2013).

11.4 Organic Fertilizers as Agronomic Tools to Promote Plant Growth Under Abiotic Stresses

Optimal fertilization could be very effective to prevent some of the negative consequences of abiotic stresses. However, chemical fertilizers are not recommended because they may be scarce or even too expensive for small farms. Furthermore, intensive use of these products constitutes a risk for ecosystem stability. Vermicomposting and its processes are recently recommended as attractive alternatives to chemical fertilizers (Shirani Bidabadi et al. 2016, 2017; Mengistu et al. 2017). Studies have demonstrated that the use of biostimulants can boost the plant immune system, leading to enhanced tolerance against abiotic stresses (Van Oosten et al. 2017; Park et al. 2017; Niu et al. 2018). Phosphatase activity of P-solubilizing microbes in soil is stimulated by the organic fertilizers which help to solubilize P, thereby increasing the bioavailable P fraction for plant uptake (Bindraban et al. 2020). Reduced K accumulation by organic fertilizer is due to cationic antagonistic interaction between K and other elements (Ca, Mg, Zn, and Fe) in the cow manure (Dimkpa et al. 2020). Supplementing animal manures such as cattle manure and poultry manure as well as liquid compost to the soil is a promising approach toward sustainable farming of cereals. These organic fertilizers improve soil quality, boost cereal growth, facilitate nutrient recycling, and diminish the necessity for chemical fertilizer (Ghosh et al. 2004; Kumar and Gopal 2015; Liu et al. 2015; Calderon et al. 2017).

11.4.1 The Role of Organic Fertilizers in Enhancing Abiotic Stress in Cereals

Organic fertilizers such as green manure enhance the water storage ability of soils which in turn improve the availability of water for cereals (Lipiec et al. 2006). The biostimulant effects of organic fertilizers could be attributed to the presence of plant growth hormones (Tarakhovskaya et al. 2007). Bradacova et al. (2016) reported that seaweed extract-based biostimulants contained zinc and manganese that improved the tolerance of maize crops against cold stress via enhanced ROS scavenging systems. In another study, Desoky et al. (2016) showed that some seaweeds as organic fertilizers could improve salt stress amelioration in pea plants by increasing antioxidant enzymes, sugar, and proline. Humic acid derived from vermicompost also showed benefits to rice in activating antioxidative enzymatic function and increased ROS scavenging enzymes (Garcia et al. 2012). The growth, nutrient uptake, and grain yield of some cereals such as corn has been reported to be improved by the application of organic fertilizers (Kato et al. 1999). Using compost as an organic fertilizer also is suggested by Raja and Bharani (2012). Compost as biodegradable and nonpolluting fertilizer, while supporting soil microbes to survive, also facilitates cereal growth (Raja and Bharani 2012). Liquid-based organic fertilizers, such as vermicompost leachate, have also reported increase in the seed germination and plant growth in some cereals such as sunflowers and also improve plant responses to abiotic stresses (Srinivasan and Mathivanan 2009; Panda 2013; Shirani Bidabadi et al. 2017). Shukla et al. (2017) investigated the effect of organic fertilizer seaweeds (*Ascophyllum nodosum*) on soybean growth under abiotic stresses. There are several reports about the positive effect of organic fertilizers on various cereals such as wheat (Javaid and Shah 2010), pea (Javaid 2006), *Vigna mungo* (Raja and Bharani 2012), and pulses and oilseeds (Badar and Qureshi 2015), confirming the use of these organic fertilizers as a promising approach to increase the resistance of cereals to environmentally stressful conditions. Supplementing soybean plants with green manure exhibited the highest biomass of the shoot, number, and biomass of pods compared to other treatments (Javaid and Mahmood 2010). However, more comprehensive and systematic investigations of functionality at the molecular level, in cereal plants, are required to further figure out their mechanisms to induce stress tolerance. These approaches may lead to the discovery of plant-target molecules that interact with the bioactive components of organic fertilizers and hence reveal novel regulatory interactions involved in abiotic stress tolerance.

11.4.2 Organic Fertilizers, Beneficial Effects, and Mode of Action

Organic fertilizers as biostimulants (BSs) possessing different compounds with positive effects on plants can be used as one of the most effective alternative methods to increase plant resistance to abiotic stresses, which today, of course, are exacerbated by climate change (Garcia-Garcia et al. 2020). Current knowledge and phenotypic observations demonstrate that organic fertilizers regulate physiological processes in plants to improve growth, mitigate stresses, and boost quality and yield. However, to successfully develop novel organic fertilizer-based formulations, understanding the interaction between plants with organic fertilizers at molecular, cellular, and physiological levels is a requisite (Nephali et al. 2020; Garcia-Garcia et al. 2020). Although few reports exist regarding the role of organic fertilizers in enhancing plant tolerance to certain abiotic stresses, the role of these organic amendments in maintaining or enhancing plant fitness during stress events by increasing plant tolerance and the mechanisms behind these effects is still a matter of intensive investigations. Because of the variable and complex nature of organic fertilizers, it becomes very difficult to determine which of the compounds in fertilizer plays a major role in increasing plant resistance. For example composition of seaweed extract as an organic fertilizer is highly dependent on the method of extraction (Van Oosten et al. 2017). Seaweed possesses some phytohormones, osmoprotectant betaine, micronutrients, vitamins, amino acids, and antibiotics which boost the growth and yield of plant crops under stress conditions (Mathur et al. 2015; Pacholczak et al. 2016). Some possible roles of phytohormones such as melatonin and cytokinin in biofertilizers such as seaweed and vermicompost leachate could be effective in improving the stress tolerance of some seedlings (Wally et al. 2012; Van Oosten et al. 2017). Some recent reports show that melatonin can enhance plant tolerance against some abiotic stresses (Shirani Bidabadi et al. 2020). Application of organic fertilizers such as seaweeds and vermicompost leachate increase water and nutrient uptake in plant resulting in improving plant growth under stressful conditions (Shirani Bidabadi et al. 2017). Shirani Bidabadi et al. (2017) reported that vermicompost leachate (VCL)-based bio-stimulants potentiated the defense response against salt stress in pomegranate. The oxidative stress caused by various abiotic stresses increases cell membrane leakage in plants which is scavenged by enzymatic or nonenzymatic antioxidant activities (Sharma et al. 2012; Shirani Bidabadi et al. 2021). Using some organic fertilizers such as seaweed extract and vermicompost leachate has been reported that mitigate the damaging effects of abiotic stresses on plant crops, and therefore the direct activation of the antioxidative system (catalase, peroxidase, and ascorbate) could be suggested in antagonizing oxidative damage (Shirani Bidabadi et al. 2017). Generally, some recent findings have reported that the phytohormone such as cytokinin, gibberellic acid, and abscisic acid of organic fertilizers helps to support the plant under stress conditions and recover the plants (El-Shoubaky and Salem 2016; Raghunandan et al. 2019). One of the mechanisms through which vermicompost leachate is reported to reduce the negative impact of salinity stress is due to the reduction of Na^+ accumulation (Shirani Bidabadi et al. 2017; Benazzouk et al. 2018). Organic fertilizers contain some bio-stimulants which regulate physiological processes in plants; thereby their growth is promoted, and the negative effects of abiotic stresses are alleviated (Nephali et al. 2020). Paldi et al. (2014) reported the existence of biostimulants in organic fertilizers that are very effective in protecting plant crops against cold stress. Biostimulants possess a multicomponent composition and contain phytohormones or even hormone-like substances, amino acids, betaines, peptides, proteins, sugars, amino polysaccharides, lipids, vitamins, nucleotides or

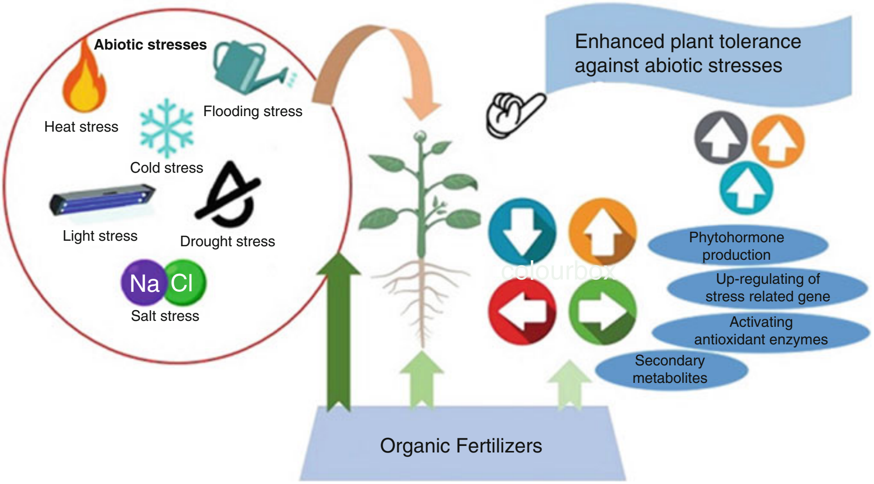

Fig. 11.3 Mode of action of organic fertilizers on the induction of plant tolerance against abiotic stresses

nucleosides, humic substances, beneficial elements, and phenolic compounds (Yakin et al. 2016). They reported that this biostimulant stimulates the phenylpropanoid pathway resulting in an enhanced content of phenol derivatives and anthocyanins and protection of the photosynthetic apparatus. Treating lettuce with some organic fertilizers resulted in greater tolerance to cold, improving its germination, photosynthetic efficiency, and content of carotenoids and vitamin C (Fodorpataki et al. 2019).

Some highlighted mechanisms of action accomplished by organic fertilizers in cereals are graphically presented in Fig. 11.3. Bulgari et al. (2015) asserted that biostimulants must be classified based on their action in the plants or on the physiological plant responses rather than on their composition. Biostimulants based on organic fertilizers contain hormones that act directly on the physiological processes providing potential benefits for growth, development, and/or responses to abiotic stresses (Du Jardin 2012). Most organic fertilizers are added to the rhizosphere and have a positive effect on plant growth, especially under stress conditions by improving plant nutrient uptake. Although most plant biostimulants are added to the rhizosphere to facilitate the uptake of nutrients, many of these also have protective effects against environmental stress such as water deficit, soil salinization, and exposure to suboptimal growth temperatures (Van Oosten et al. 2017). Stimulation of photosynthesis and the downregulation of a plant stress signaling pathway are among the tasks of biostimulants in organic fertilizers (Yakin et al. 2016). Organic fertilizers boost the soil environment to prepare a new condition for the growth of potentially beneficial microbes (Lin et al. 2019). However, understanding organic fertilizers-plant interactions, at molecular, cellular, and physiological levels, must be addressed in the future to develop novel organic fertilizer-based formulations and programs. The knowledge gained from the literature evaluated here helps us to understand the physiological and biochemical basis of organic fertilizers applied to sustainable agriculture in reducing the negative impacts of abiotic stresses.

11.5 Concluding Remarks and Common Features

This chapter provides a general overview of the current knowledge regarding plant defense mechanisms, the categories of organic fertilizers, their beneficial effects, and the mode of action of organic fertilizers. Nowadays, several procedures including traditional and modern breeding techniques have been adopted to induce abiotic stress resistance in plant species. Furthermore, some agronomic management strategies, such as irrigation and grafting, have been implemented to help plants in coping with abiotic stresses, but these techniques are associated with some restrictions or carry high environmental costs. Therefore, a novel technology such as the application of organic fertilizers is required to sustain a growing global population under abiotic stresses although there are still many unclear points that need to be clarified to fully understand the complexity of the plant-organic fertilizer-abiotic stress relationship. Therefore, changing and directing the metabolomics and molecular processes induced by biostimulants of organic fertilizers in plant crops will result in improving growth and enhancing plant immunity under these stressful conditions. A wide array of molecular methods has been applied to distinguish the active compounds found in organic fertilizers including microarrays, metabolomics, proteomics, and transcriptomics methods. These technologies have been applied to biostimulants to explore modifications in gene expression due to organic fertilizers application (Jannin et al. 2013; Santaniello et al. 2013). However, further research on the effects of complex biostimulants existing in organic fertilizers and their components on the complete genome of plants is needed to understand the mechanisms of action involved in growth responses and stress mitigation.

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Cereals and Phytohormones Under Salt Stress

12

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Abstract

Cereal crops are occupying a dynamic part in nourishing the whole population of the world. The development and production of these cereal crops are poorly affected when exposed to different environmental abiotic stresses, among which salinity stress plays a major role. Plants that respond to salt stress involve various complex physiological, molecular, as well as biochemical changes in the plant system. Phytohormones play a crucial role in acquiring some adaptational reactions in a plant's system when exposed to salinity. Gibberellins (GAs), ethylene (ET), cytokinins (CKs), salicylic acid (SA), jasmonates, abscisic acid (ABA), and brassinosteroids (BRs) are important plant hormones that respond to salinity stresses via their signalling attributes. The cellular disturbances caused by salinity stress are potentially removed by exogenous phytohormones in plants.

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Phytohormones extensively regulate some specific genes to deal with saline conditions. In this chapter, the collective information is mentioned which is focused on the role of phytohormones along with the involved genes in the alleviation of salinity stress in cereal crops.

Keywords

Abiotic stress · Cytokinin · Ethylene · Gibberellin · Salicylic acid · Salinity

12.1 Introduction

Due to climate changes in the present scenario, the plants are facing a diversity of abiotic stressors in the field. Abiotic stress variables such as drought, cold, soil salinity, high temperature and flood have a significant impact on worldwide cereals productivity. Soil salinity is one of the most damaging abiotic stresses, causing a reduction in cultivable land, crop productivity, and quality and it is recognised as one of the most susceptible threats to human and plant health (Shrivastava and Kumar 2015). The principal and the main cause of salinity is weathering of parental rocks because it releases various types of salt in excess amounts, mainly calcium chloride ($CaCl_2$), sodium chloride (NaCl), and magnesium chloride ($MgCl_2$), as well as sulphate ($SO_4{}^{-2}$) and carbonate ($CO_3{}^{-2}$) in small amounts, all of which accumulated on agricultural land (Singh et al. 2015). In addition, poor disposal of metropolitan wastes and the overuse of various chemical manure are both lethal sources of saline stress (Chen et al. 2010). Besides this, there are some other causes of salinity contamination in soil and water bodies such as the direct release of water containing a large amount of salt from the factories manufacturing dyes, paints, and pigments. It enhances negative health effects in humans and animals. Salt stress has been proven to inhibit morphology in sensitive species, as well as photosynthesis, protein synthesis, and respiration (Mustafa et al. 2014). Extreme production of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide anion ($O_2{}^{\bullet -}$), and hydroxyl radicals ($HO^{\bullet}$) are significant biomarkers of salinity-mediated oxidative destruction in plants, notably in mitochondria and chloroplasts. Salinity produces a disproportion in cellular ionic flow due to variations in Na^+/K^+ ratio and Na^+ and Cl^- ion acquisition inside cells, which has a negative influence on plant morphology by producing osmotic stress (Subramanyam et al. 2011). Cereals are grasses that belong to the Poaceae family, often known as the Gramineae family, and are grown for the grain's edible component. They are the principal food crops grown across the world. Wheat, millet rice, maize, barley, oats, and sorghum are the most important cereal crops. These cereals are grown for the endosperm, germ, and bran, which are edible components of their caryopsis (Giordano et al. 2021; Kumari et al. 2021). Salt stress in maize produces several biochemical and physiological changes, including ionic imbalance, cellular homeostatic disturbance, respiration, and nitrogen

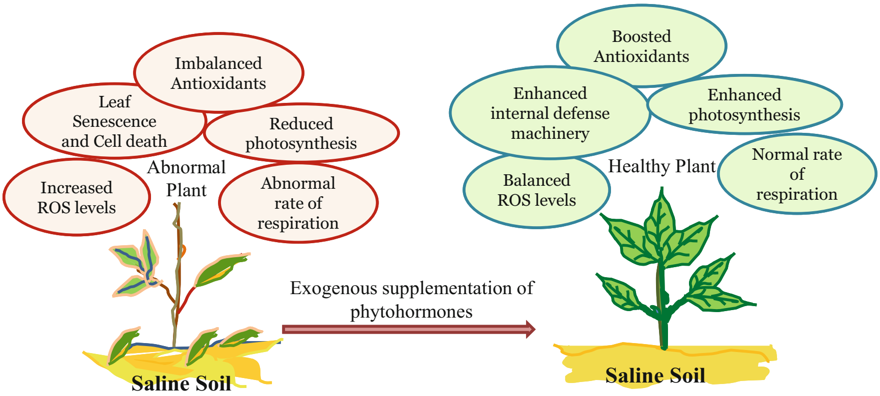

Fig. 12.1 Systemic representation of negative influences of salinity stress and positive impacts of exogenous phytohormones in plant system

assimilation (Davani et al. 2017). When wheat plants are exposed to saline soil, growth and health, as well as their productivity, are hampered enormously. The increased concentration of salt ions in the irrigated water has a substantial adverse impact on wheat yield (Srivastava 2017). Scientists developed several methods to alleviate salt stress in cereal crops by using different phytohormones, signalling molecules, etc. Previous reports suggested that sodium nitroprusside (SNP, used as a source of NO), trehalose, silicon (Si) ion and silica nanoparticles, manganese sulfate ($MnSO_4$) and many others can alleviate salinity stress in cereals crops (Rahman et al. 2016; Abdel-Haliem et al. 2017; Adamu et al. 2018). But the usage of exogenous phytohormones is the most accepted and considered a reliable method among all. Studies demonstrated that the application of phytohormones can potentially enhance the rate of photosynthesis, boost the antioxidant defense machinery as well as reduce the ROS contents and also normalize the rate of respiration in salinity-stressed plants (Verma et al. 2020) (Fig. 12.1). The use of salicylic acid (SA) in rice plants could help to lessen the harmful consequences of salt-mediated stress regulation via physiological mechanisms. Exogenous SA supplementation potentially reduces the dangerous outcome of salinity on maize growth and yield (Tahjib-Ul-Arif et al. 2018). Likely, wheat seedlings treated with exogenous jasmonate and NaCl had significantly higher levels of antioxidant enzymes (Qiun et al. 2014). By analyzing above facts, it is considered that the exogenous supplementation of phytohormones is the best method to alleviate the negative impacts imposed by a saline environment. Thus, in this chapter, various strategies of different phytohormones in the mitigation of salt stress have been well demonstrated. Along with this, collective studies have also been mentioned regarding metabolic and genetic approaches mediated by hormonal homeostasis to amplify salt stress tolerance in cereal crops.

12.2 Influence of Phytohormones on Plant Growth Exposed to Salt Stress

12.2.1 Effect of Auxin (IAA) on Plants Exposed to Salt Stress

Indole acetic acid (IAA) is an abundant and native auxin that is required for plant development regulation. It regulates vascular tissue growth, the dominance of apical soot tips, cell elongation, etc. in plants (Wang et al. 2001). IAA is mainly produced in young leaves, apical meristem, seeds, and developing fruits and is also produced in the dividing tissue of the young branch. IAA is produced from tryptophan amino acids. It also aids the plant's defense mechanisms against high salt concentrations. In a previous study, it was demonstrated that the rice seedlings when exposed to NaCl had an extensively decreased level of IAA (Batool et al. 2016). The impact of seed priming with auxin on sprouting, productivity, nutritional and mineral quality, and physiological parameters in *Triticum aestivum* L. plants growing under saline conditions was investigated (Javid et al. 2011a, b). A previous study by Batool et al. (2016) reported that auxin enhanced the growth, total dry weight, carotenoids, and total chlorophyll pigment content in salt-exposed *Oryza sativa* plants. In another study, it was found that under the saline condition in *Oryza sativa*, exogenic application of 15 mg IAA/L potentially enhanced the oxidative defense machinery, ion accretion, entire soluble protein, and entire soluble sugars to provide sufferance against salt stress (Saedipour 2016). In salt-stressed *Triticum aestivum* L., the exogenic use (seed priming) of 0.0009.84 mol/L of auxin enhanced the salt tolerance as well as the yield along with the CO_2 assimilation rate, phenolic, and protein contents (Iqbal and Ashraf 2013). In the salt-stressed *Triticum aestivum* L. plant, the seeds were primed with 200 ppm IAA, which improved the growth and yield through a tolerance mechanism (Guo et al. 2018). According to Saedipour (2016), the foliar spray of 15 mg/L IAA alleviates the salinity stress and improved the oxidative defense mechanism along with ion accumulation, total soluble protein, and sugar in the *Oryza sativa* plant. Similarly, in *Triticum aestivum* L., the salt stress is alleviated by the use of 5.7 mg/L IAA, which enhances the physiological parameters along with the growth and productivity (Abdoli et al. 2013).

12.2.2 Impact of Cytokinin (CK) on Plants Exposed to Salt Stress

Cytokinin's major role is to control growth, development, and uptake in meristems by promoting division in cell development and tissue differentiation. Cytokinin is produced by the plant in both bound and free arrangements, but the former is the physiologically active form. Free cytokinins are produced by insects, several disease-causing bacteria, and nematodes, which are associated with higher plants (Kieber 2002). Crown gall cells, for example, grow in vitro without the input of hormones; these cells include IPT genes for cytokinin synthesis. In entire plants, the root apical meristems are the primary sources of free cytokinin production (Ha et al. 2012). Cytokinins play an essential role in biology by controlling shoots and roots' cell division, wherever some aspects related to the cell cycle contribute to differentiation and aging. CK plays a role in shoot differentiation, nutrient mobilization, apical dominance promotion, cell division process, anthocyanin biosynthesis, chloroplast development, and photomorphogenesis during physiological and developmental actions in plants (Fahad et al. 2015). According to studies, CK has many roles in plant growth by regulating particular functions such as chlorophyll production and amino acid translocation. CK effects are being studied in depth under harsh environmental conditions since they not only regulate its metabolism but also activate the production or collection of other phytohormones that regulate a variety of other metabolic activities, including stress resistance induction. (Keshishian et al. 2018). It was reported that under different abiotic environmental stresses, the concentration of cytokinin rises extremely and it is plant- and cultivar-specific and under a stressed condition, it participates strategically in increasing stress tolerance capacity (Moura et al. 2017). Improved stress resistance in several plant species exposed to different abiotic environmental stresses was determined to be due to endogenous increases in cellular levels of CK, and the stress resistance was related to the enhancement in numerous physiological indicators (Merewitz et al. 2011). In the *Triticum aestivum* plant, a cellular level of CK (i.e., about 3, 5, 7 nmol) was found to be effective for increased growth, antioxidative defense mechanisms, physiological processes, chlorophyll content, and (Nishiyama et al. 2012). Exogenous administration of CK is also viewed to be beneficial in increasing stress tolerance in a diversity of crop plants and the effective concentration is species-specific or types of stress (Ali et al. 2015; Soleymani and Taheri 2015). Exogenous seed priming with cytokinin has been shown to boost the ability of numerous seed sprouting processes in salt-stressed *Sorghum bicolor* L. plants (Ismail 2003). Application of exogenously applied CK is known to trigger seed sprouting and growth and production in different plants. When CK was given by foliar application to *Zea mays* and *Oryza sativa* at 100 mg/L and 205.4 mg/g, respectively, seed germination and biomass production were found to be enhanced (Davani et al. 2017). Wheat plants produced after being primed with 100, 150, or 200 mg/L of cytokinin showed enriched growth and grain yield under salt-stressed conditions (Iqbal et al. 2006). Exogenous cytokinin at concentrations of 200, 400, and 600 mg/L promoted the synthesis of carbohydrates and polysaccharides along with the formation of photosynthetic pigments (Sadak et al. 2013).

12.2.3 Impact of Gibberellins (GAs) on Plants Exposed to Salt Stress

Gibberellin, a potential phytohormone plays an important role in plant growth and development by promoting fruit set and seed germination, enhancing stem growth in dwarf and rosette plants, regulating the transition from juvenile to adult phases, stimulating floral initiation and sex determination. Foliar spray of gibberellin is found very effective for crop breeding as well as in the regulation of fruit production, malting barley, and increasing sugar production in sugarcane. Gibberellins belong to a vast family of diterpene acids produced in three stages by the terpenoid pathway and controlled via a wide range of enzymes and genes. The manufacturing of terpenoid precursors involves ent-kaurene in plastids, oxidation mechanisms in the organelle endoplasmic reticulum to generate GA_{12} and GA_{53}, and additional gibberellins through GA_{12} or GA_{53} in the cytoplasm as the final step of biogenesis. GA is usually biosynthesized in the apical tissues, which are highly sensitive to various influences like light, temperature, and so on. Auxin may also increase gibberellin production in higher plants (Hedden and Sponsel 2015). Gibberellins are also known to govern a number of biochemical and physiological processes, including cell extension and division, enhancing cell wall extensibility, and regulating cell cycle kinase transcription in intercalary meristems. GAs have been discovered in some plants that are subjected to various abiotic stimuli; it improves stress resistance and performs a key function in the upgrading of several physiological parameters. According to AlBalawi and Roushdy (2018), foliar spray of 10^{-2} M GA is effective in salt-stressed *Zea mays* L. plants, and it improves plant growth, transport, iron uptake, and nutrient utilization. In salt-stressed *Triticum aestivum* L., the exogenous application of 100 ppm of GA improves the biosynthesis of photosynthetic pigments and growth and enhances the nutritional quality (Chauhan et al. 2018). According to Rahman et al. (2017), it was mentioned that the externally added GA (5–20 mmol) improved the growth, yield, productivity, and nutrient quality in *Oryza sativa* L. plants that suffer from salt-induced stress. In salt-stressed *Triticum aestivum* L., the foliar spray of 200 mg/L GA improved reducing sugar content, protein content, pigment biosynthesis, and catalase (CAT) as well as peroxidase (POD) activities (Rahdari and Hoseini 2015). In an experiment, Chauhan and Kumar (2015) found that exogenous (seed priming) by 6 μmol GA alleviates salt stress and increases nutrient uptake, yield, and productivity. GA also alleviates NaCl-induced rice growth suppression by modulating certain salt-regulated proteins, demonstrating GA's salinity stress-moderating effect in rice plants (Wen et al. 2010). GA_3 priming produces changes in ion uptake and demarcation (among aerial shoots and underground roots), as well as hormonal balance, which improves wheat grain output under saline circumstances (Iqbal and Ashraf 2010). The foliar spray of 100 ppm GA_3 enhanced the growth and biosynthesis of photosynthetic pigments and also increased the nutritional values in plants (Chauhan et al. 2018). The seed pretreatment with 150 ppm GA_3 alleviates salinity-induced stress in *Zea mays* L. and improves chlorophyll biosynthesis, growth, and yield (Mohamed and Mahmoud 2018). In another study, it was found that the foliar spray of 5–20 mmol GA_3 alleviates salinity stress in *Oryza sativa* L. and similarly improves the growth and nutrient homeostasis (Rahman et al. 2017). These findings recommend that the application of GA_3 to crop plants cultivated in a saline environment can improve salinity stress tolerance attributes.

12.2.4 Effect of Ethylene on Plants Exposed to Salt Stress

The gaseous phytohormone was the first to discover ethylene as a natural plant product that is generated automatically during plant metabolism in a variety of agricultural plants (Gane 1934; Egea et al. 2018; Kim et al. 2018). Ethylene is formed in all compartments of higher plants, and the production rate depends upon the stage of development, environmental condition, and tissue type. The meristematic region and nodal areas of growing leaves are the active sites for ethylene production. The 1-aminocyclopropane-1-carboxylic acid (ACC) plays an intermediary in the alteration of methionine to ethylene, and the amino acid methionine is a possible precursor of ethylene production (Egea et al. 2018; Kim et al. 2018). The ethylene concentrations that are effective for biological responses frequently extend the fruit's storage life. Plants' ethylene biosynthesis is stimulated by their developmental status, environmental factors such as floods, cold, temperature, or drought challenges, other phytohormones such as auxin, and physical and chemical harm. The rate of ACC (1-aminocyclopropane-1-carboxylic acid) and ethylene biosynthesis in the abscission zone increases as fruit matures, and this progression is mostly governed via auxin phytohormone (Iqbal et al. 2017a, b; Egea et al. 2018; Kim et al. 2018). Functionally enhanced ethylene production shows the plant response to salt stress, which has been further studied widely through exogenous application. Increasing the expression of ROS scavenger enzymes is a chief factor (Peng et al. 2014). The internal rise of ethylene concentration at basic cellular levels indicates the increased stress tolerance in a range of plants under several abiotic pressures, and the stress resistance was based on improvements in many physiological and biochemical indicators. In *Oryza sativa* L., endogenous ethylene is effective in salt stress tolerance and enriches the activities and responses of antioxidant enzymes, chlorophyll cumulation, as well as ion cumulation (Lee and Yoon 2018).

12.2.5 Role of Brassinosteroids (BRs) Under Salt Stress Conditions

Brassinosteroids (BRs) are steroids that govern particular development and metabolic processes, and they are recently discovered in plants as plant hormones. Many physiological processes in plants are triggered by them, including stem elongation, seed germination, immunity, and a variety of developmental and reproductive functions. Brassin, a floral extract from *Brassica napus* helps in stem elongation and cell division when sprayed on internodes of bean plants. The first revealed BR was termed "brassinolide," which was segregated from 40 kg of bee collected from *Brassica rapa* pollens (Oklestkova et al. 2015). The key precursor for BR biosynthesis is campesterol, which has been elucidated by numerous Japanese scientists and then demonstrated through the production of BR in *Arabidopsis thaliana,* tomatoes, and peas (Fujioka and Sakurai 1997). Plant tissue has signal transduction genes that are necessary for its sustained biosynthesis. Experimentally, the loci of BR synthesis in plants have yet to be determined. BR biosynthesis and signal transduction genes are found in an extensive range of plant organs, as well as a short range of hormonal activity, which is responsible for one widely held belief that BRs are synthesized in all tissues (Ali et al. 2020). BRs have a variety of functions in plants under various biotic and abiotic stressors. Improvements in several physiological parameters, mainly total phenolic contents, total chlorophyll and carotenoids, were used to improve tolerance against stress in plants growing under diverse abiotic stressful environments, and attainment of stress tolerance was based on an increase in endogenous levels of brassinosteroids. The endogenous level of 10^{-5} M concentration of brassinosteroid was found very effective in a saline environment for the *Oryza sativa* plant, which protected the plant from oxidative damage by improving the growth and accumulating N-containing compounds like amino acids and vitamins (Sharma et al. 2017). Another study in *Sorghum bicolor* depicted that the use of foliar application of 2 and 3 μmol brassinosteroid alleviates salt stress (Vardhini 2012). Similarly, the foliar spray of 50, 100, and 200 mg/L brassinosteroid eases the salt-induced stress in *Triticum aestivum* L. and improves the growth and production of the plant (Eleiwa et al. 2011).

12.2.6 Impact of Jasmonates on Plants Exposed to Salt Stress

Jasmonates, which comprise methyl jasmonate (MeJA) and its liberated acids, jasmonic acid (JA), are significant cellular regulators and play roles in seed germination, ripening, underground root growth, fertility, fruit formation, and senescence in plants (Wasternack and Hause 2002). Biosynthesis of jasmonic acid occurs in leaves, but some evidence regarding the JA biosynthesis mechanism in roots has also been found. Furthermore, cellular organelles including chloroplasts and peroxisomes are thought to be the major spots of JA production (Cheong and Choi 2003). Jasmonic acid is a well-known and naturally found plant growth regulator, which is involved in the modification and maintenance of higher plant growth and development in response to various environmental situations. It has been observed that JA biosynthesis is a difficult and quick process that is catalyzed by a range of enzymes that originate abundantly in leaves and that respond to environmental stimuli by becoming active, such as lipoxygenases (LOX) and allene oxide synthase (AOS) (Wasternack and Song 2016). JA takes part in plant growth and development by improving photosynthetic activities, reducing stomatal opening, and improving cell division; thereby, JA can convey its substantial structural and biochemical functions in the enhancement of resistance to various abiotic stimuli (Fugate et al. 2018). Because of its role in regulating diverse abiotic stresses, jasmonic acid is an important plant hormone. However, it also decreases abiotic stress by performing as a signalling molecule and influencing cellular-level metabolic activities. Endogenous increment, which is based on increases in physiological parameters like plant water relations and production of fresh biomass, promotes plant stress tolerance (Attaran et al. 2014; Fugate et al. 2018). In *Oryza sativa* L. the foliar spray of jasmonic acid (i.e., 10–20 μmol) enhances the plant growth by upregulating the POD and ascorbate peroxidase (APX) enzyme activities, K^+ concentration, and chlorophyll content in salt conditions (Mahmud et al. 2017). According to Kang et al. (2005), JA concentrations were shown to be much lower in salt-sensitive plants than in salt-resistant plants, but it was also discovered that exogenous JA applied afterward can assist salt-stressed rice seedlings cope.

12.2.7 Impact of Salicylic Acid (SA) on Plants Exposed to Salt Stress

Salicylic acid (SA) is a well-known phenolic component that is known to manage various physiological activities in plants, comprising growth, photosynthesis, nitrate metabolism, ethylene production, heat generation, and flowering (Hayat et al. 2010). It is generated from phenylalanine in plants by two altered pathways: the shikimate-phenylpropanoid pathway and the isochorismate pathway, both of which are catalyzed by phenylalanine ammonia-lyase (Chen et al. 2009). Chorismate is a likely precursor in both of these processes. In the phenylalanine ammonia-lyase (PAL) pathway, isochorismate transforms to cinnamic acid, which is further hydroxylated into ortho-courmarate or benzoic acid. Finally, benzoic acid is hydroxylated to produce SA as an ultimate product (Metraux 2002). In another pathway, the enzyme isochorismate synthase (ICS) catalyzes the changes of chorismate to isochorismate, which further transforms to SA by the enzyme isochorismate pyruvate lyase (IPL) (Serino et al. 1995). SA plays an important role in seed germination, fruit yield, photosynthesis, stomatal conductance, nutrient uptake, and balancing of antioxidant enzymes; thereby, SA significantly regulates to improve the resistance against abiotic environmental stresses (Vlot et al. 2009). Several studies have discovered that SA plays a key role in modifying plant responses to abiotic stressors like drought, salt, temperature, and heavy metal stress (Khan et al. 2015). In *Triticum aestivum* L., the foliar application of 0.25 and 0.5 mmol SA enhanced the growth, soluble protein content, and biochemical and physiological parameters under saline conditions (Suhaib et al. 2018). Similarly, Alamri et al. (2018) conveyed that the foliar spray of 100 μmol SA improved the germination, seedling height, total chlorophyll, and total carbohydrate content in salt-stressed *Triticum aestivum* L. plant. Exogenic application of SA potentially improves the growth and development of barley plants growing under salinity stress by increasing photosynthetic rate and maintaining membrane stability (El-Tayeb 2005). Likewise, SA improved the persistence of maize plants at the time of salinity stress and reduced Na^+ and Cl^- accumulation inside the cell (Gunes et al. 2007). During salt stress, it was found that lipid peroxidation and cell membrane penetrability were enhanced and these damaging effects were alleviated by SA treatment (Horvath et al. 2007). Under the saline condition, the endogenous level of SA in rice seedlings was found to be amplified, which shows the role of SA in the interior defense mechanism and also explains the involvement of SA biosynthetic enzyme, benzoic acid 2-hydroxylase, in salt stress alleviation (Sawada et al. 2006). Under salinity, the SA treatment resulted in the accumulation of both ABA and IAA in wheat seedlings (Sakhabutdinova et al. 2003). These outcomes indicated that SA plays a major role in mitigating salinity stress by modulating internal defense systems in plants.

12.2.8 Role of Abscisic Acid (ABA) Under Salt Stress Conditions

ABA, a typical plant stress hormone, has been discovered in all parts of the plant, from the underground root cap to the aerial apical bud. Coleoptiles, seed germination, as well as GA-induced α-amylase production are all inhibited by ABA. The carotenoids are likely precursors of ABA biosynthesis in the terpenoid pathway where ABA is produced. In the terpenoid pathway, 6-hydroxymethyl plays a role in the change of carotenoids to ABA (Fernando and Schroeder 2016; Ratnayaka et al. 2018). The ABA is thought to operate like moderator molecules in a plant that respond to a number of stressors, such as water scarcity and salinity stress. ABA is a key internal signal that allows plants to withstand harsh conditions like salinity stress (Keskin et al. 2010). In the study of Zhang et al. (2006), it was depicted that plants generate a proportionate rise in ABA content in response to salt-induced stress, which is usually linked to leaf or soil water potential, showing that salt-induced cellular ABA accumulation is caused by a water deficit, not by specialized salt effects. Wang et al. (2017) demonstrated that in *Triticum aestivum* L. the exogenic use of 1 mmol ABA enhanced the antioxidant defense system and thereby enhanced the growth and production during the saline condition. An exogenous spray of 0.05 M ABA alleviates the salt stress in *Oryza sativa* L. by maintaining increased levels of proline and chlorophyll, as well as by boosting CAT and APX enzyme activities (Kibria et al. 2017). A foliar spray of 100 mol of ABA increased the contents of polysomes in *Hordeum vulgare* that suffer from salinity stress (Szypulska and Weidner 2016). A study by Gurmani et al. (2013) revealed that seed priming with 10^{-5} M ABA potentially enhances the growth, dry weight, stomatal conductance ability, and net assimilation rate and also decreases the Na^+ concentration in the leaf blades of *Oryza sativa* L. plant at the time of salinity stress. Endogenous application of 0.1 mmol of ABA enhanced the glutathione and lipid peroxidase levels in the salinity-stressed *Zea mays* L. plant (Kellos 2008). Similarly, a foliar spray of 0.5 mmol ABA enhances the chlorophyll and carotenoid contents and antioxidant enzyme activity, thereby improving the leaf area, total biomass, and membrane stability in *Triticum aestivum* L. (Agarwal et al. 2005). By considering the above facts, it is depicted that ABA has a substantial role in whole plant reactions against salt stress by utilizing various ways.

12.3 Genetic Approaches Mediated Hormonal Homeostasis to Enhance the Salt Stress Tolerance in Crop Plants

IAA is a plant hormone associated with the auxin family (Aoi et al. 2020). Saline conditions can cause a notable drop in IAA concentrations in *Oryza sativa, Triticum aestivum,* and *Zea mays* plants (Zhang and Li 2019; Ji et al. 2020). It has been described that the exogenic application of auxin might ameliorate the salinity in several crops, including wheat (Khalid and Aftab 2020). The auxin-mediated TaIAA gene family demonstrates variable appearance at the time of inorganic ion absorption in wheat plant roots (Talboys et al. 2014). In salt stress conditions by preventing H_2O_2 accumulation, growth and expansion in a wheat plant are regulated by an auxin-responsive gene TaSAUR75 (Guo et al. 2018).

Cytokinins, the important class of plant hormone that encourages cell division in the underground roots and apical shoots of plants, are of two types: (a) phenylurea type and (b) adenine type, where the main form is adenine-type plant hormones, which are classified as isopentenyl adenine (iP), cis-zeatin (tZ) and trans-zeatin (cZ), and dihydrozeatin and its riboside (Quamruzzaman et al. 2021). Cytokinin comeback factors (CRFs) in the ERF-VI subfamily, induced by CKs completely regulate the osmotic stress resistance (Quamruzzaman et al. 2021). According to Quamruzzaman et al. (2021), overproduction of CK by modifying stress-mediated genes, appearance shows negative effects in plants; for example, true leaf appearance and primary root formation under stress situations are inhibited by upregulation of cytokinin biosynthetic gene AtIPT8 (adenosine phosphate–isopentenyl transferase 8) (Quamruzzaman et al. 2021).

Gibberellins, which belong to a broad group of tetracyclic di-terpenoid carboxylic acid derivatives and whose most prevalent form is Gibberellic acid, have a variety of physiological roles, including stimulating organ growth by accelerating cell division and cell elongation (Gao and Chu 2020). Endogenous GA content was found to be reduced due to salinity stress, which further promoted the plant's hypersensitivity to salt (Liu et al. 2018; Lv et al. 2018). Different environmental and hormonal signalling is regulated by DELLA family protein, which is a chief GA-repressor. For example, plant growth is inhibited by restricting GA signalling under salt stress conditions by DELLA protein-SLR1 (Quamruzzaman et al. 2021). Excessive expression of some other GA catabolism-allied genes like OsMYB91 (Zhu et al. 2015) (Table 12.1) in rice reduces the growth and shows improved tolerance to salt stress related to wild plants. A potential GA-neutralising protein, OsCYP71D8L, plays a substantial role in regulating the stress responses and growth process, which causes improved resistance to salinity in rice (Zhou et al. 2020). The reduction of GA signaling under salt stress conditions is directly connected with the salt stress tolerance capacity in plants. Excessive salt exposure also severely diminishes the enzyme-related activities and tends to create a nutritional imbalance in plants. In wheat, TaEXPB23 transcript expression was upregulated by salt-induced stress but down-regulated by GA.

Brassinosteroids, the plant growth regulators, are primarily polyhydroxylated and sterol-derived. Multiple developmental, physiological, molecular, and biochemical processes including cell division, seed germination, and cell elongation, regular demarcation of vascular tissues, senescence, development of underground root and aerial shoots, reproduction, and photo-morphogenesis are regulated by BRs. Plants require BRs to acquire adaptation to different types of abiotic and biotic environmental stresses (Ahammed et al. 2015; Ahanger et al. 2018). The molecular mechanisms underlying how BRs regulate the expression of those genes which are expressed perfectly in response to abiotic stress in plants and also modulate stress responses (Quamruzzaman et al. 2021). At the cell surface, BRs bind to a leucine-rich duplicate receptor kinase (BRI1) family, triggering an intracellularly active signal transduction cascade that alters the expressions of a number of genes complicated in a variety of tasks, including salt stress adaptation. In rice, transcript stages of the brassinosteroid receptor (OsBRI1) were critically inclined by EBL and its grouping with saline conditions (Quamruzzaman et al. 2021). Moreover, by the mixture of salt and EBL, the salt-reactive gene (SalT) was marginally expressed.

Table 12.1 Hormone-mediated responses in different plants by involving various functional genes during salinity stress situations

Phytohormones	Plant	Gene involved	Hormone-mediated effect on functional gene	References
Auxins	Wheat	TaSAUR75 gene upregulated	By preventing H_2O_2 aggregation under salt stress, growth and development is regulated	Guo et al. (2018)
GAs	Rice	OsMY891	Enhanced tolerance to salt stress compared to wild plants	Zhu et al. (2015)
SA	Wheat	GPX1, GPX2	Improve tolerance to salt stress, by upregulation of transcript levels of genes as well as enhancement in enzyme activities of the ASH-GSH cycle	Quamruzzaman et al. (2021)
ABA	Rice	Expression of OsP5CS1 and OsP5CR genes raised	Increased plant performance by triggering proline accumulation	Quamruzzaman et al. (2021)
	Wheat	TaCIPK29	Plant shows higher K^+/Na^+ ratio, increased activity of POD and CAT	Quamruzzaman et al. (2021)
	Wheat	Enhanced WESR1 and WESR2	Improving intercellular K^+/Na^+ ratio and chloroplast function	Quamruzzaman et al. (2021)
	Wheat	TabHLH1	Promote stomata closure and increases biomass production	Yang et al. (2016)
Ethylene	Wheat	Overexpression of TaERF1	Salt stress tolerance increased	Quamruzzaman et al. (2021)
	Wheat	TaLTP1	Elevate transcripts of the lipid transfer protein gene	Quamruzzaman et al. (2021)

Salicylic acid, a phenolic molecule, serves as a basic growth regulator in the body. It controls how plants respond to different stress conditions (Gururani et al. 2015).

Abscisic acid is a stress hormone that supports the plant's ability to cope with several kinds of stresses (Wani and Kumar 2015; Zhu et al. 2017). In several de novo plant compartments such as flowers, soil-covered roots, aerial leaves, and stems, ABA is synthesized (Quamruzzaman et al. 2021). ABA is an endogenous signalling molecule that allows plants to persist in tough environments, such as salinity conditions (Vishwakarma et al. 2017). Cellular levels of ABA rise in response to salt stress, aiding plant tolerance to salinity by reducing ROS formation (Balusamy et al. 2019). Application of 100 μM ABA solutions exogenously to rice plants has increased plant performance by raising the expression of the OsP5CS1 and OsP5CR (Table 12.1) genes by triggering proline accumulation (Quamruzzaman et al. 2021).

Salt and abscisic acid-induced wheat LEA (late embryogenesis abundant) protein DHN-5 confers salt and osmotic stress resistance, and Dhn-5 transgenic plants have increased germination rates and leaf area and improved growth. Greater K^+ concentration in leaves and osmotic regulation created by an active addition of proline could explain the transgenic plant's higher salinity tolerance (Quamruzzaman et al. 2021). TaCIPK29, a novel supporter of the CIPK (calcineurin B-like protein-interacting protein kinase) gene family, has been recognized in wheat. After treatment of ABA and NaCl, TaClPK29 transcription level increased, and TaClPK29 transgenic plant showed a greater K^+/Na^+ ratio and boosted the activities of POD and CAT during salt stress conditions (Quamruzzaman et al. 2021). A salt-resistant wheat mutant, RH8706–49, cloned a novel, ABA-inducible TaSC gene that acts in a CDPK pathway, improving endogenous K^+/Na^+ proportion and function of the chloroplast. Initial salt stress-reactive genes WESR1 and WESR2 were also enhanced in wheat (Quamruzzaman et al. 2021) by exogenous ABA treatment. Plant adaptation to osmotic stressors is mediated by an elementary helix-loop-helix wheat genetic factor (TabHLH1). Under salt and ABA treatment, this gene is linked to endorsing the stomatal closure and enhancing biomass production.

Ethylene, an active gaseous signalling molecule, is known as a stress-reactive hormone in higher plants (Yu et al. 2020). Due to saline conditions, ethylene as well as its direct precursor ACC (1-aminocyclopropane-1-carboxylic acid) increases rapidly inside the cellular compartments (Zapata et al. 2017). Increased ethylene production causes salt-sensitive phenotypes in numerous plants, including rice, *Arabidopsis*, rice, pepper, spinach, beetroot, and lettuce (Zapata et al. 2017). In the tolerance of abiotic stress, mainly in salinity, ethylene-related response factors (ERFs) work as key regulators. Salinity induces the transcription of the wheat ERF gene (TaERF1) and excessive expression of this gene triggers stress-related genes, increasing salinity stress resistance in transgenic plants (Quamruzzaman et al. 2021). When compared to normal wheat seedlings, TaERF3-overexpressing transgenic lines had dramatically improved the tolerance against water scarcity and salt stress (Rong et al. 2014). Salt and ethephon treatment elevated the transcripts of the lipid transfer gene (TaLTP1) (Table 12.1) in wheat (Quamruzzaman et al. 2021). Ethylene also activates a variety of early response genes involved in the stimulation of ribosomal proteins, chaperoning synthesis, ROS scavenging, and the carbohydrate metabolite pathway (Ma et al. 2020).

12.4 Metabolic Approaches Mediated Hormonal Homeostasis to Enhance Salt Stress Tolerance in Crop Plants

Salt-induced stress causes an interruption in many metabolic and physiological processes, ultimately reducing crop output, depending on the intensity and period of the stress (Gupta and Huang 2014). Wheat, rice, and maize are three primary cereal crops that account for more than half of human daily calorie intake and are characterized as salt-sensitive species (Quamruzzaman et al. 2021). Salt tolerance is induced by phytohormones by raising the action of ROS scavenging enzymes, which maintains ROS at a harmless level during an abiotic stress situation. PGRs showed the potential to alleviate symptoms influenced by environmental factors such as their cellular absorption, the required concentration at which they are activated, and the physiological capacity of the plant (Quamruzzaman et al. 2021). Plants are harmed by salt stress because it inhibits growth, seed germination, and plant development, as well as flowering and fruiting. The high sodium concentrations in salty soil hinder the water uptake and nutritional absorption in plants (Gong 2021). The prime stresses, like osmotic stress and ionic stress, are caused by water scarcity and nutritional imbalance. These primary stresses cause oxidative stress, which in turn can lead to a cascade of secondary stresses (Zhao et al. 2021). Salt stress causes a variety of biochemical, molecular, and physiological changes in plants, and it obstructs plant growth by decreasing photosynthesis, which reduces available resources and inhibits cell division and expansion (Van Zelm et al. 2020). Salt stress disturbs the development of light-harvesting complexes and controls the state transition of photosynthesis (Chen and Hoehenwarter 2015). Importantly, by distorting glycation under salt stress conditions, enzyme activities or protein strengths of crucial photosynthetically active enzymes like ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and others are negatively affected (Zhao et al. 2021). Sugar signalling and sugar levels, such as sucrose, fructose, and glycolysis, are also affected by salt stress. Various abiotic environmental stresses hinder plant growth and development; to reduce the effects of these stresses, seed priming with IAA has been described as very effective (Rhaman et al. 2021). IAA priming boosts cell division, photosynthetic activity, and glucose translocation, resulting in lateral root initiation, blooming, and strong stand formation (Rhaman et al. 2021). Cell division, apical dominance, underground root formation, stomatal behavior, and chloroplast development are only a few of the many aspects of plant growth and development that are regulated by CKs (Schaller et al. 2014). It is commonly established that the application of CKs promotes agricultural productivity. For example, cotton yield increased by 5–10% with the application of CKs (Rhaman et al. 2021).

Exogenously administered CKs have also been shown to promote *Epipremnum aurum's* net photosynthesis, net C-assimilation, and dry matter accumulation, leading to higher plant growth (Di Benedetto et al. 2015). Exogenous administration of CKs, on the other hand, improved rice growth and yield. Priming with CKs boosts the photosynthetic rate, enhances membrane stability, and keeps the steady ionic levels in plants, as well as increases chlorophyll (*Chl*) biosynthesis and biomass accumulation. Wheat seeds primed with kinetin showed endogenous lower levels of ABA and higher accumulation of IAAs, which ultimately improved the seed germination and provided salt stress tolerance (Rhaman et al. 2021). In the study of Sepehri and Rouhi (2016), it was noticed that antioxidant enzyme activities were boosted and oxidative damages were lessened, which ultimately improved the seedling indices and the germination of old groundnut (*Arachis hypogaea* L.). However, the precise mechanisms by which priming with CKs reduces abiotic plant stress have yet to be studied. It plays an important function in stomatal mobility and inhibits ABA-induced stomatal closure when applied exogenously (Rhaman et al. 2021). However, the effects of seed priming with CKs on stomatal motility are still unexplored. Abiotic environmental stresses such as salt, drought, cold, heat, and heavy metals limit adequate nutrient intake and photosynthesis, resulting in reduced plant growth (Hasanuzzaman et al. 2020). Externally added GAs can markedly enhance the plant's growth and development by reducing abiotic stresses. By preserving comparative water content, boosting the antioxidant mechanism system, and preserving chlorophyll concentrations, exogenic administration of GA improves wheat (*Triticum aestivum*) plant development and alleviates drought-mediated cellular oxidative damage (Moumita et al. 2019). Exogenous addition of GA_3 in tomato (*Solanum Lycopersicum*) plants enhanced their adequate leaf water content, stomatal density, and *Chl* pigment content by alleviating salinity stress (Jayasinghe et al. 2019). Seed priming with GAs (50 M) enhances the rate of seed germination, plant growth, and biomass output in *Leymus chinensis* (Ma et al. 2018). Similarly, seed retreatment with GAs improved the age and frequency of seed germination as well as the growth, yield, and yield-contributing features of wheat, maize, and lentil (Shineeanwarialmas et al. 2019). More research is needed, however, to find out the internal mechanisms and cellular changes after GA priming in abiotic stress alleviation. According to Wei et al. (2015), under alkaline stress, priming of rice seeds with ABA (10 μM and 50 μM) enhanced the growth and survival rate, biomass accumulation, and underground root formation. Increased salinity stress tolerance and enhanced growth of rice, wheat, and sorghum plants were observed after seed priming with ABA (Rhaman et al. 2021). SA, a phenolic plant hormone, regulates many physiological, molecular, and biochemical processes in plants, including vital photosynthesis, respiration, transpiration, and ion transport (Rhaman et al. 2021).

12.5 Conclusions and Future Perspective

Salinity is one of the dominating abiotic stresses for cereal crops all across the world. Increased salinity affects the crops by creating water stress, oxidative stress, and ion toxicity, which ultimately causes the reduction of plant growth and its development. Cereal crops are vulnerable to salinity stress and saline conditions because the salinity stress diminishes the overall plant development and yield. Plants tolerate salinity stress through changes in their metabolic pathways and physiological parameters. There are many proteins, signalling molecules as well as phytohormones, and many other mechanisms that are potentially involved in mitigating salinity-induced stress. In this chapter, we have discussed the role of phytohormones in mitigating salinity stress. Much progress has been made in understanding the potential role of phytohormones in cereals under salt-induced stress. However, more research is still needed to fully comprehend the specific mechanism of action for stress tolerance in challenging environments. With the gene level study, knowledge of the role of phytohormones in cereals under salt stress became more convenient. Despite the fact that many studies have been done in this area, there are still a lot of studies that are needed to clearly understand the plants' behavior under such unfavorable environmental conditions. This chapter will help in increasing the awareness of the role of phytohormones and involved genes in cereal crops to alleviate salinity stress.

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Cereals and Phytohormones Under Drought Stress

13

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Abstract

Climate change is expected to amplify drought frequency and intensity, with a significant alteration of the ecosystems. It affects the livelihoods, communities, and productivity of many important crops globally, including cereals. These crops are vulnerable to drought stress due to disturbed growth, nutrient acquisition, and cell functioning and biochemistry, which decrease yields and grain quality. Thus, understanding plants' drought stress tolerance mechanisms could be an effective strategy for ensuring continuous productivity.

Drought stresses plants and associated factors (e.g. soil microorganisms), inducing adjusted responses involving plant-soil signalling via phytohormones. The coordination of plant responses to drought by phytohormones is of great interest owing to the plants' sessility, and their subsistence relies mainly on their aptitude to quickly regulate their growth and physiology processes and to alleviate drought stress effects. Phytohormones are typically involved in these processes. Research interest has recently been focused on understanding phytohormones' multiple functions that are critical regulators of plant functioning, including cell expansion and division, endogenous level of metabolites, and gene expression. Phytohormones, especially abscisic acid (ABA), salicylic acid (SA), jasmonate (JA), ethylene (ET), auxin (IAA), cytokinins (CKs), brassinosteroids (BRs), gibberellins (GAs), and strigolactones (SLs) are known to be involved in plants' tolerance to drought. Some reduce water loss through regulating stomata opening, while others induce root development, accumulation of osmolytes, and antioxidant enzymes to protect plant cells from stress-related damages. Some of these signalling molecules could be either produced by plants suffering from water deficiency or induced by the presence of microorganisms. Besides, they could also be exogenously applied to vegetative tissues and soil. Despite several studies on phytohormone effects, their mechanisms and possible crosstalk are still a subject of debate. Thus, this chapter presents an overview of the different roles of phytohormones in regulating cereals' adaptive responses to drought stress severity and the potential factors to alter their effectiveness in mitigating this constraint in cereals.

Keywords

Drought stress · Phytohormones · Cereal crops · Tolerance · Signalling pathways

Abbreviations

13-LOX	13-Lipoxygenase
9'-c-n	9'-Cis-neoaxanthin
α-LeA	α-Linolenic acid
AAO	ABA Aldehyde oxidase
ABA	Abscisic acid

ACC	1-aminocyclopropane-1-carboxylic acid
ACO	1-aminocyclopropane-1-carboxylic acid oxidase
ACS	1-aminocyclopropane-1-carboxylic acid synthase
AMF	Arbuscular mycorrhizal fungi
AOC	Allene oxide cyclase
AOS	Allene oxide synthase
APX	Ascorbate peroxidase
BA	Benzyladenine
BR	Brassinosteroid-Insensitive receptor
BRs	Brassinosteroids
CAT	Catalase
CCD	Carotenoid cleavage dioxygenase
CDK	Cyclin-dependent kinase
CDPK	Calcium-dependent protein kinase
Ch	Chitosan
CKs	Cytokinins
CKX	Cytokinin oxidase/dehydrogenase
CP	Cytochrome P450
CPKs/CDPKs	Calcium-dependent protein kinase
CPS	Copalyl diphosphate synthase
DMAPP	Dimethylallyl pyrophosphate
DREB/CBF	Dehydration-Responsive Element Binding proteins/C-repeat Binding Factor
EDS	Enhanced disease susceptibility
EIL	Ethylene insensitive-like protein
EL	Electrolyte leakage
EPS	Exopolysaccharides
EPS1	Enhanced *Pseudomonas* susceptibility 1
ERF	Ethylene response factor
ET	Ethylene
ETR	Ethylene receptor
F_v/F_m	Photosystem II efficiency
GA2ox	Gibberellin 2-oxidases
GAs	Gibberellins
GB	Glycine betaine
GPX	Glutathione peroxidase
GR	Glutathione reductase
GST	Glutathione S-transferase
HSP	Heat shock proteins
IAA	Indole-3-Acetic acid
IC	Isochorismate
ICS	Isochorismate synthase
iP	N^6-(Δ^2-isopentenyl)-adenine
IPA	Indole-3-pyruvate
IPT	Isopentenyl transferase

JA	Jasmonic acid
JA-Ile	Jasmonoyl isoleucine
JAZ	Jasmonate ZIM-domain
JIH	Jasmonoyl-l-isoleucine hydrolase
JMT	Jasmonic acid carboxyl methyltransferase
LEA	Late embryogenesis abundant
MAPKKK/MPK	Mitogen-activated protein kinase
MDA	Malondialdehyde
MeJA	Methyl jasmonate
MJE	Methyl jasmonate esterase
NCED	9-cis-epoxycarotenoid dioxygenase
NCEI	Neoxanthin synthase
NPR	Non-expressor of pathogenesis-related gene
NSY	Neoxanthin synthase
NXS	Neoxanthin synthase
OPDA	(cis)-12-oxophytodienoic acid
OPR	12-oxophytodienoate reductase
PAL	Phenylalanine ammonia-lyase
PEG	Polyethylene glycol
PGPF	Plant growth-promoting fungi
PGPR	Plant growth-promoting rhizobacteria
POD	Peroxidase
PP2C	2C protein phosphatase
ROS	Reactive oxygen species
SA	Salicylic acid
SDR	Short-chain dehydrogenase/reductase-like
SLs	Strigolactones
SOD	Superoxide dismutase
SWE	Seaweed extract
TAA	Tryptophan aminotransferase of *Arabidopsis*
TF	Transcription factor
Trp	Tryptophan
tz	Trans-zeatin
WUE	Water use efficiency
ZEP	Zeaxanthin epoxidase enzyme

13.1 Phytohormones: Key Mediators of Cereal Responses to Drought Stress

Alarming environmental challenges have mounted and become more evident due to exacerbating water scarcity, industrialization, and extreme weather events. According to FAO (2018), up to 60% of the global population will suffer from water deficiency by 2025. Drought has recently received great importance since it is among the critical constraints that control and reduce the agricultural production of global crops (Iqbal et al. 2020; Meza et al. 2020). This constraint results in wide morphological, biochemical, and genetic disturbances and changes in plants and subsequently affects development, productivity, and yield (Ullah et al. 2018a; Boutasknit et al. 2021; Lahbouki et al. 2022). Thus, the impact of droughts threatens complex global food security and may reduce agricultural yields, including cereals (up to 10% decrease) (Lesk et al. 2016; Fu et al. 2021). To address this global issue, research in agriculture has targeted improving genetic resources and agricultural practices to enhance water use efficiency (WUE) (Haile et al. 2020; Ahluwalia et al. 2021). Additionally, this worrying scenario requires the urgent implementation of sustainable measures to improve crop yield and quality. Increasing attention has been focused on applying beneficial biostimulants to minimize the effect of drought.

Cereal crops, mainly rice, wheat, maize, sorghum, barley, and pearl millet provide more than 50% of the population's caloric requirements, particularly in developing countries in South Asia, sub-Saharan Africa, and Latin America (Olugbire et al. 2021). Cereal crops are known as an excellent source of total calories (48%) and total protein (42%) that contribute to more than two-thirds of dietary energy intake worldwide (Curiel et al. 2020). Cereals have been considered staple foods for most human populations for about 10,000 years due to specific characteristics such as ease of growth, development, storage, and transport (Wendin et al. 2020). In addition, cereals are classified as essential materials for producing animal feed and biofuels (Olugbire et al. 2021). However, cereal crops have experienced yield losses of up to 40% globally in wheat and maize caused by drought stress effects (Daryanto et al. 2016; Fu et al. 2021). Cereals are mostly grown in (semi-) arid areas and are often exposed to intense and prolonged drought episodes. Hence, understanding drought-responsive mechanisms in cereals and molecular signalling pathways is a time-demanding task.

Phytohormones are considered regulators of plant growth and development since they act through several pathways such as additive, synergistic, or antagonistic pathways to enhance growth under normal and stressful conditions (Sadiq et al. 2020; Li et al. 2021). These molecules also develop potential phenological and biochemical processes to keep the cells' relative water content (RWC) and water potential constant (Yadav et al. 2021). In response to drought stress conditions, several processes are elaborated by various phytohormones, such as abscisic acid (ABA), which plays a significant role in stomatal behaviour by responding to water deficiency (Li et al. 2021). Other phytohormones intervene in coordinating plant responses under drought conditions to different degrees, namely, salicylic acid (SA), jasmonic acid (JA), ethylene (ET), auxins (IAA), cytokinins (CKs), brassinosteroids (BRs), gibberellins (GAs), and strigolactones (SLs) (Tardieu et al. 2018; Ilyas et al. 2021; Yadav et al. 2021). These molecules act as chemical regulators of plant responses to multiple environmental stresses. Once the perception of the stress signal is established, a series of chemical reactions are released and activated in a network of interactions to enhance specific protective mechanisms, including stomatal closure, osmolyte accumulation, and antioxidant defense, in an attempt to escape water deficiency (Gupta et al. 2020; Yadav et al. 2021).

13.2 Correlations Between Phytohormones and Drought Stress Tolerance in Cereals

Phytohormones have essential roles in controlling multiple plants' acclimatization processes in response to water deficiency. ABA is the primary hormone that strengthens plant water stress tolerance via many processes such as stomatal movements, root expansion, and stimulation of ABA-dependent pathways (Cardoso et al. 2020; Nawaz and Wang 2020; Wang et al. 2021a). Additionally, JA, SA, ET, IAA, GAs, CKs, SLs, and BRs are also necessary to meet the challenges of water deficiency. These molecules commonly are in cross-talk to ensure plant survivability under drought stress (Ullah et al. 2018a). Various investigations have highlighted the impact of water stress on phytohormones and vice versa, usually concluding that there is a high correlation between drought stress and phytohormone production. For instance, Bano et al. (2012) compared the effects of ABA and drought stress application at pre-sowing and 55 days after sowing in two drought tolerance contrasting wheat varieties. The drought-resistant variety developed a great defense mechanism to mitigate reactive oxygen species (ROS) effects through stimulation of the antioxidant enzyme activity. Under water deficiency, ABA induced a significant increase in superoxide dismutase (SOD) and peroxidase (POD) activity, with a significant decrease in this activity in re-watering. For both wheat cultivars, ABA treatment significantly enhanced RWC under drought conditions. Furthermore, the sensitive variety was more responsive to ABA treatment and showed low concentrations of endogenic ABA.

On the other hand, the tolerant cultivar presented a great recovery from water stress at re-watering. In addition, the grain weight was significantly improved by ABA treatment for tolerant cultivars under water deficiency (Nayyar and Walia 2003; Bano et al. 2012). Drought stress decreased GA and IAA and increased ABA and proline in two wheat cultivars (Bano and Yasmeen 2010). ABA and benzyladenine (BA) application at the anthesis stage induced osmoregulation by proline production. BA was more effective at the early stages of grain filling, while ABA was more effective at the later stages (Bano and Yasmeen 2010).

Similarly, leaf GA and IAA content significantly decreased under drought stress (Xie et al. 2003). The correlation analyses between yields, starch, and protein content in grains and levels and ratios of four hormones indicated that the changes were associated with IAA and GA reduction and ABA increase, especially in grains. The overall results of these studies suggested that the varying concentrations of endogenic hormones under post-anthesis drought conditions could alter grain starch and protein content by regulating the activity and processes of the enzyme, which might be attributed to synthesis decrease (Xie et al. 2004) or a degradation decrease (Davenport et al. 1980) of IAA and GA. Foliar application of glycine betaine (GB) improved drought tolerance and yield of maize and sorghum, but not wheat

(Agboma et al. 1997). In contrast, drought significantly decreased maize and sorghum's grain numbers and yields. Foliar application of GB minimally enhanced biomass production in the three crops and significantly increased maize ($P = 0.001$) and sorghum ($P = 0.003$) grain yield.

13.3 Hormones' Signalling for Drought Stress Response and Tolerance

The evolution has enabled plants to develop multiple strategies to manage water scarcity. They have established mechanisms, including altered molecular, biochemical, and physiological processes (Bhargava and Sawant 2013; Seleiman et al. 2021). Such response mechanisms occur via plant hormone signalling pathways (Ilyas et al. 2021). Phytohormones are indispensable molecules that participate in various biological processes. Besides, they are vital to stress signalling pathways. The abiotic stress signalling in plants depends on the nature, intensity, and length of exposure.

In the signalling cascade, phytohormones are instrumental in orchestrating plant development, growth, and tolerance mechanisms (Tiwari et al. 2017; Tardieu et al. 2018; Jogawat et al. 2021).

Here, we will focus on the signalling pathways related to each of the nine hormones involved in drought tolerance in cereals.

13.3.1 Abscisic Acid (ABA)

ABA is a sesquiterpenoid phytohormone often labelled as "stress hormone" due to its discrete association with plant abiotic stress mitigation (Zhao et al. 2021). Therefore, this molecule is the hormone of abscission and is probably the most studied of plant hormones (Chen et al. 2021b). ABA is formed via the carotenoid pathway (Fig. 13.1). Zeaxanthin is transformed to all-trans-violaxanthin by antheraxanthin. This reaction is activated by the zeaxanthin epoxidase enzyme (ZEP; EC 1.14.13.90) (Agrawal et al. 2001), followed by the conversion of trans-violaxanthin to 9-cis-violaxanthin and 9-cis-neoxanthin. Neoxanthin synthase (NXS; EC 5.3.99.9) is involved in these reactions (North et al. 2007). The final reaction to ABA production takes place in chloroplasts and is catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED; EC 1.13.11.51) (Iuchi et al. 2001). The first-ever NCED gene was studied in the maize *vp14* mutant and is activated under water deficiency in the course of seed maturation (Tan et al. 1997). ABA orchesters diverse physiological functions and developmental phases, such as seed development and dormancy (Sano and Marion-Poll 2021), stomatal opening (Hasan et al. 2021), embryo morphogenesis (Kruglova et al. 2021), and biosynthesis of storage lipids and proteins (Ali et al. 2022). Furthermore, ABA is also implicated in controlling the expression of genes implicated in the ABA signalling pathways (Some et al. 2021). The role of ABA as a crucial messenger in mitigating stress

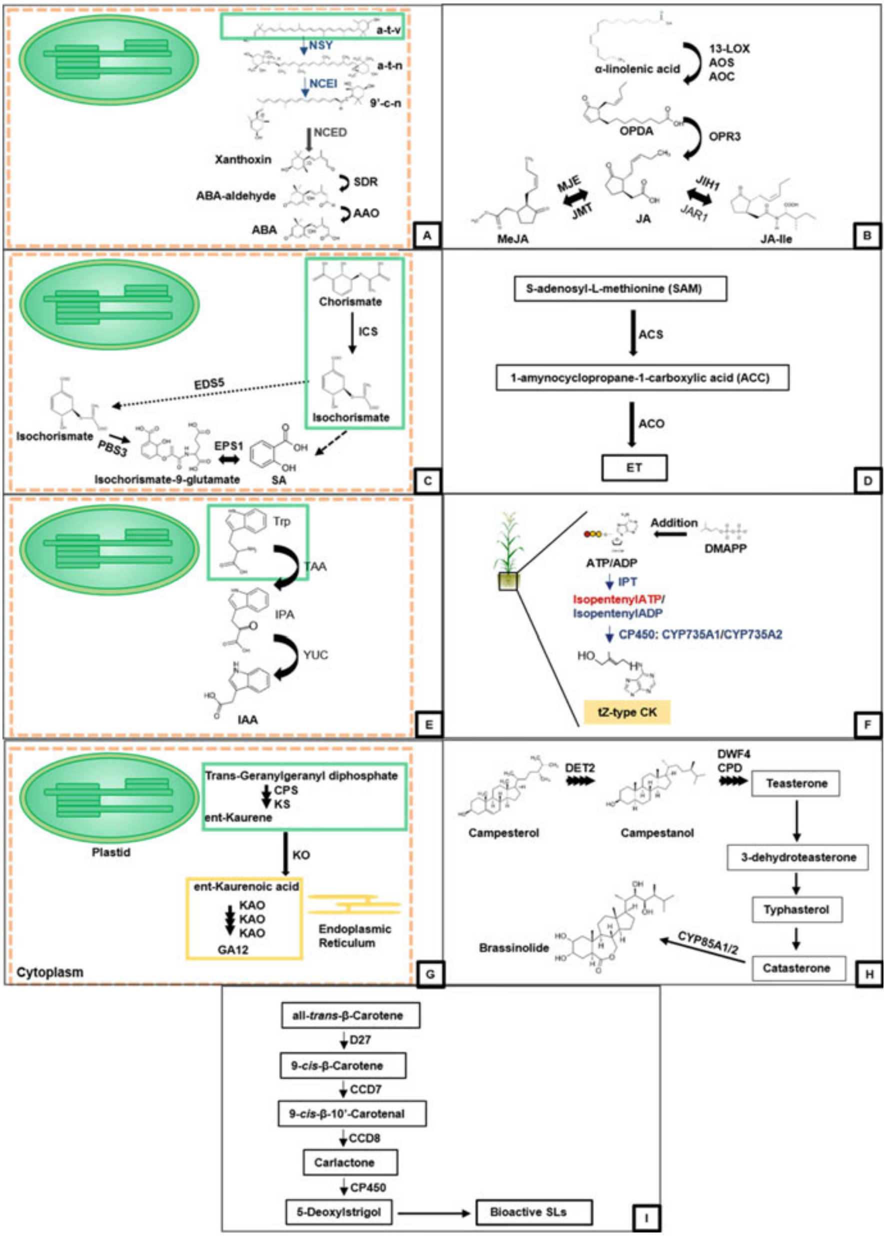

Fig. 13.1 Schematic diagrams of the major plant hormone generation and signalling pathways. (**a**) Abscisic acid, (**b**) jasmonates, (**c**) salicylic acid, (**d**) ethylene, (**e**) indole-3-acetic acid, (**f**) cytokinins, (**g**) gibberellins, (**h**) brassinosteroids, and (**i**) strigolactones. *13-LOX* 13-lipoxygenase, *9’-c-n* 9’-cis-neoaxanthin, *AAO* ABA aldehyde oxidase, *ACO* 1-aminocyclopropane-1-carboxylic acid oxidase, *ACS* 1-aminocyclopropane-1-carboxylic acid synthase, *AOC* allene oxide cyclase, *AOS* allene oxide synthase, *a-t-n* all-trans-neoxanthin, *a-t-v* all-trans-violaxanthin, *CCD* carotenoid cleavage dioxygenase, *CP450* cytochrome P450, *CPS* copalyl diphosphate synthase, *D27* dwarf27, *DET2 DEETIOLATED2* gene, *DMAPP* dimethylallyl pyrophosphate, *DWF4* dwarf4, *EDS5* enhanced

and improving plant tolerance has received much attention (Wilkinson and Davies 2002). To cope with drought stress, cellular ABA content tends to rise, leading to the plant hormone binding to the receptors of pyrabactin resistance (PYR/PYL/RCARs), which inactivates type 2C protein phosphatases (PP2Cs) (Siodmak and Hirt 2021). The protein kinases, SnRK2s, are auto-stimulated after dissociation from PP2Cs, which triggers ABA responses. In addition, calcium-dependent protein kinases (CDPKs) play a role in ABA signalling. CDPKs were described in rice (29 CDPKs), wheat (20), and maize (35) (Schulz et al. 2013). Under drought stress, implicated signalling pathways and gene expression levels (more than 10% of protein-encoding genes) are de-regulated in response to increased endogenous ABA levels (Nemhauser et al. 2006; Canales et al. 2021), which results in limiting water loss through the reduction of leaf expansion and stomatal opening (Wilkinson et al. 2012). Another attribute to ABA resides in its implication in robustness and development of root architecture (Wilkinson et al. 2012; Benderradji et al. 2021). In addition, ABA interferes in synthesizing dehydrins and Late Embryogenesis Abundant (LEA) proteins (Sun et al. 2021). Tolerance is indeed conferred on plants owing to the upregulation by ABA of production of osmoprotectants, maintenance of cell turgor, and stimulation of antioxidant defense (Chaves et al. 2003). In a study conducted by Dominguez and Carrari (2015) on drought-tolerant Zhengdan 958 and drought-sensitive Xundan 20 maize hybrids, exogenous S-ABA helped mitigate drought stress by enhancing *Asr1* (ABA, stress, ripening) gene expression levels.

13.3.2 Jasmonates (JAs)

JAs are a group of hormones formed by cyclopentanone that include free jasmonic acid (JA) (the most common form) and methyl jasmonate (MeJA) (Fig. 13.1). These plant hormones are very abundant across different plant species. JAs are crucial for plant development and survival. They are required for senescence, flowering, fruiting, direct and indirect defense responses, and secondary metabolism (Wu et al. 2008; Fahad et al. 2015). JAs are synthesised from α-linolenic acid (α-LeA) through the galactolipase (Li et al. 2021a). JA formation is initiated by oxygenation of 13-lipoxygenase, the 13(S)-hydroperoxy-octadecatrienoic acid is transformed to an epoxide by a 13-allene oxide synthase and cyclized to the

Fig. 13.1 (continued) disease susceptibility 5, *EPS1* enhanced *pseudomonas* susceptibility 1, *ICS* isochorismate synthase, *IPA* indole-3-pyruvate, *IPT* isopentenyl transferase, *JA-Ile* jasmonoyl isoleucine, *JIH1* jasmonoyl-l-isoleucine hydrolase 1, *JMT* jasmonic acid carboxyl methyltransferase, *KAO* ent-kaurenoic acid oxidase, *KS* ent-kaurene synthase, *MeJA* methyl jasmonate, *MJE* methyl jasmonate esterase, *NCED* 9-cis-epoxycarotenoid dioxygenase, *NCEI* neoxanthin synthase, *NSY* neoxanthin synthase, *OPDA* cis-oxo-phytodienoic acid, *OPR3* 12-oxophytodienoate reductase 3, *PBS5* phosphate-buffered saline 5, *SDR* short-chain dehydrogenase/reductase-like, *TAA* tryptophan aminotransferase of *Arabidopsis*, *Trp* tryptophan, *tz* trans-zeatin cyclopentenone (cis)-12-oxophytodienoic acid (OPDA) by an allene oxide cyclase. In this step, the enantiomeric structure of the naturally occurring (þ)-7-iso-JA ((3R,7S)-JA) is established (Wasternack et al. 2013). JAs act as a plant defense activator when subjected to abiotic stresses, including drought (Pauwels et al. 2009; Seo et al. 2011). JA ZIM-domain (JAZ) proteins play a significant role in the JA signalling pathway. JAI3/JAZ proteins bind to transcription factors (TFs) under normal conditions. Under stress conditions, however, JA and its derivatives accumulate, and JAZ proteins degrade, leading to the activation of TFs, which upregulate the genes implicated in stress responses (Liu et al. 2017; Han and Luthe 2021). Furthermore, JA induces the development of roots and ROS scavenging and the closure of stomata via the JA precursor, OPDA (Wang et al. 2021b). Allagulova et al. (2020) indicated that dehydrins might participate in the methyl jasmonate (MeJA)-induced protecting effect in wheat plants subjected to drought stress. Treated plants with 0.1 μM of exogenous MeJA decreased membrane structure lesions. Furthermore, TADHN dehydrin transcripts and dehydrin protein expression increased during dehydration.

13.3.3 Salicylic Acid (SA)

SA is a naturally occurring phenolic compound implicated in pathogenesis-associated protein expressions (Chen et al. 2012). It plays a crucial role in regulating plant growth (Bernal-Vicente et al. 2018), ripening and development (Changwal et al. 2021), and in triggering plants' responses to abiotic stresses; including drought (Miura et al. 2013), salt (Khodary 2004), and heat (Fayez and Bazaid 2014). Two routes are involved in the biosynthesis of SA: the isochorismate (IC) and the phenylalanine ammonia-lyase (PAL) pathways, with the IC pathway being the major one (Fig. 13.1) (Uppalapati et al. 2007). While low concentrations of SA can increase the antioxidant machinery, high concentrations can lead to cell death and vulnerability under abiotic constraints (Prakash et al. 2021). SA triggers the expression of genes encoding chaperones, heat shock proteins (HSP), antioxidants, and genes involved in the biosynthesis of cytochrome P450 and secondary metabolites, sinapyl alcohol dehydrogenase, and cinnamyl alcohol dehydrogenase (Jumali et al. 2011).

SA responses to the environment occur through the nonexpressor of pathogenesis-related genes, *NPR1*, expressing *PR* genes (Maier et al. 2011). Activated genes like *WRKYs* and *TGAs* improve plants' tolerance against biotic and abiotic stresses (Chen et al. 2012; Ullah et al. 2018b). SA content in barley roots was enhanced ca. 2x under water stress (Bandurska 2005). SA-inducible pathogenesis-related genes *PR1* and *PR2* were incited in response to water deficits (Miura et al. 2013). NPR1 protein acts as a regulator of the SA-controlled signalling pathway, especially under pathogen infection. SA accumulation implicates antimicrobial NPR1 proteins in the defense process, leading to the import of monomeric NPR1 to the nucleus, where it binds with SA and generates a conformational change that conducts to the C-terminal activation domain that triggers transcription. Another work on two wheat varieties, drought-tolerant Kundan and drought-sensitive Lok1, subjected to 75 and 50% reduction of RWC and recovery, revealed that SA-induced thioredoxins activated defense responses against ROS, leading to drought tolerance (Sharma et al. 2017).

13.3.4 Ethylene (ET)

ET constitutes a simple hydrocarbon gaseous molecule that acts as a plant hormone. ET is implicated in specific stages of plant growth and development, particularly fruit ripening (Liu et al. 2021), flower senescence (Naing et al. 2021) and the abscission of petals and leaves (Yang et al. 2021). The primary precursor of ET is 1-aminocyclopropane-1-carboxylic acid (ACC) (Fig. 13.1). ACC synthase is the enzyme that catalyzes the conversion of *S*-adenosyl-L-methionine to ACC, which is later converted to ET by the action of ACC oxidase (Bleecker and Kende 2000). One of the prominent roles of ET is the regulation of drought tolerance in plants. APETELA2/Ethylene-Responsive Element-Binding Protein (AP2/EREBP) genes have been found to respond to drought (Dong et al. 2021). The expression of *GmERF3*, an ethylene response factor (ERF), was shown to be induced under drought and salt stresses, conferring tolerance to plants (Zhang et al. 2009; Ilyas et al. 2021). Another ERF gene, *AtERF019*, acted positively in delaying senescence (Scarpeci et al. 2017), whereas transgenic plants have shown improved tolerance to drought by lowering transpiration rate and regulating stomatal regulation aperture and cuticle-thinning.

Environmental stress leads to ET accumulation, which improves the survival of plants under adverse environmental conditions (Gamalero and Glick 2012; Salazar et al. 2015). *SUB1A*, an ethylene-response-factor-like gene and an ETS2 Receptor Factor present in limited rice accessions, attributed submergence tolerance to rice (Xu et al. 2006; Fukao et al. 2011). Genotypes with the *SUB1A* gene could recover after desubmergence via the establishment of new leaves (Fukao et al. 2006). These findings suggest that *SUB1A* also may help the process of enduring several abiotic stresses. Under drought stress, *EIN2* downstream signalling components are kept inactive by the action of a Raf-like kinase and critical negative regulator of ET, *CTR1* kinase-dependent phosphorylation (Eppel and Rachmilevitch 2016). Besides, Dubois et al. (2013) highlighted *SIERF5*, *AtERF5*, and *AtER6* as central regulators of salt and drought stresses. It is worth mentioning that *AtERF6* stimulates the expression of different osmotic stress-responsive genes such as *STZ*, *MYB51*, and *WRKY33*.

13.3.5 Auxins

Indole-3-acetic acid (IAA) is the most common phytohormone of the auxin family involved in signalling and several aspects of plant growth and responses to environmental conditions (Jin et al. 2021). Auxins are deemed as the first phytohormones to be characterized (Masuda and Kamisaka 2000), being IAA the most abundant and versatile (Zhao 2010), yet the mechanisms governing IAA biosynthesis, transport, and signalling pathways are still to be elucidated (Wang et al. 2015). This is due to the complexity of the process itself. Available data suggest that the amino acid tryptophan (Trp) acts as a precursor or the major IAA precursor (Fig. 13.1). The conversion of tryptophan to IAA has also been reported (Bartel 1997). Coleoptile tips excised tissues with ^{14}C-Trp-seeds (kernels) of maize (*Zea mays* L. cv. Golden Cross Bantam 70) have shown label incorporation, demonstrating the conversion of tryptophan into IAA (Koshiba et al. 1995). Moreover, IAA can release from IAA conjugates through the hydrolysis of IAA-amino acids, IAA-sugar, and IAA-methyl ester (Bartel 1997; Qin et al. 2005).

IAA acts as a plant growth regulator. It induces cell elongation (Rayle and Cleland 1992), differentiation of cell and vascular tissues (Ding and Friml 2010; Casanova-Sáez et al. 2021) and axial elongation (Campanoni and Nick 2005). It acts as a mediator of apical dominance (Booker et al. 2003). The role of IAA extends to influencing gametogenesis (Zhao 2010), embryogenesis (Cheng et al. 2007), seedling growth (Hu et al. 2017), vascular patterning (Berleth et al. 2000), and flower development (Cheng and Zhao 2007).

IAA plays an integral part in plant adaptation to drought, heavy metal, salinity, and fungal stresses by increasing root and shoot growth at the transcriptional level (Yuan et al. 2013; Tiwari et al. 2020). In tobacco, it has been shown that auxin-inducible glutathione S-transferase (GST), PjGSTU1 from *Prosopis juliflora* confers drought tolerance (George et al. 2010; Cicero et al. 2015). In *Arabidopsis*, increased endogenous levels of IAA-inducing drought tolerance were attained by the activation of flavin monooxygenase encoding genes involved in the tryptophan-dependent IAA biosynthesis pathway (Niyogi and Fink 1992). Similar results were obtained by overexpressing *YUCCA7* in *Arabidopsis* (Lee et al. 2012). Induction of the *OsGH3–2* gene encoding an enzyme for IAA activation in rice subjected to water deficit exhibited drought resistance (Ahammed et al. 2013). Furthermore, the *OsPIN* gene family, particularly *OsPIN2* and *OsPIN5b,* was upregulated under drought stress (Lu et al. 2015) and *TLD1/OsGH3.13*—an IAA amino synthetase encoding gene—overexpression stimulated LEA, leading ultimately to drought tolerance (Rao et al. 2014).

13.3.6 Cytokinins (CKs)

Natural forms of CKs occur as N^6 substituted adenine derivatives, with distinct substitutions attached to the N^6 position of the adenine ring (Fig. 13.1). N^6-(Δ^2-isopentenyl)-adenine (iP), trans-zeatin (tZ), cis-zeatin, and dihydrozeatin are the most common forms. The significant derivatives are tZ, iP, and their sugar conjugates (Sakakibara 2021). CKs are biosynthesized in roots. The addition of the prenyl group derived from the prenol phosphate, named dimethylallyl diphosphate, to the N^6-terminus of ADP/ATP constitutes the first step catalyzed by isopentenyl transferase (IPT), a multigene family that is encoded in most plants

(Kakimoto 2001; Sakakibara 2021). Cytochrome P450 enzymes, CYP735A1 and CYP735A2, participate in the hydroxylation of the isoprenoid side chain, which converts the resulting iP-ribotides into tZ-type CKs (Wheeldon and Bennett 2021). CKs then move the xylem upward to other plant parts, functioning as long-distance messengers to regulate plant growth and development (Aloni et al. 2006; Dun et al. 2006). Prominent roles include cell division (Riou-khamlichi et al. 1999), sink/source relations and nutrient uptake (Roitsch and Ehneß 2000), phyllotaxis (Reinhardt 2004), and gametophyte and embryonic development (Wybouw and De Rybel 2019).

CKs regulate protective responses in plants under abiotic stresses from roots to shoots (Wu et al. 2021). The local stress sensed by roots might implicate changes in the levels of CKs in different plant organs, leading to the plant's drought adaptation, thanks to an enhanced apical dominance stimulated by reduced CK levels (O'Brien and Benková 2013). It has been reported that deregulation of CKs (up- or downregulation) leads to drought tolerance. Enhanced endogenous CK levels were registered in transgenic plants expressing an *IPT* gene, resulting in delayed senescence by suppressing drought-induced leaf senescence. Overexpression of CK oxidase/dehydrogenase (CKX; EC. 1.5. 99.12), which catalyzes CK breakdown, improved drought tolerance possibly due to endogenous plant hormone concentration reduction (Prerostova et al. 2018).

A suggested model, under environmental stresses, revealed that *IPT* gene expression decreases, leading to a decrease in CKs accumulation. Consequently, the triggered expression of stress-responsive genes, following the alleviation of the inhibitory effect of CK signalling, leads to an enhanced plant tolerance. Results displaying altered activity of CK metabolic enzymes in mutant and transgenic cells and tissues corroborate it (Nishiyama et al. 2011). CKs are believed to negatively regulate the branching and growth of roots (Tessi et al. 2021). CKs are degraded under drought stress, thereby enhancing primary root growth and branching (Werner et al. 2010). Batool et al. (2019) reported that two wheat (*Triticum aestivum* L.) genotypes, Heshangtou and Longchun 8275, were subjected to a cascade of water deficit treatments ranging from 80 to 45% reduced CK concentration and closed stomata, resulting in less gas exchange. These changes improved antioxidant machinery and osmotic regulation, leading to enhanced WUE. Altogether, these findings pointed out the CK implication in the root-to-shoot signaling process under environmental stress.

13.3.7 Gibberellins (GA)

GAs form a large group of naturally tetracyclic diterpenoid carboxylic acids based on their ent-gibberellin carbon skeletal structure. GAs range from GA1 to GA136 and are present in 128 vascular plant species (Sponsel and Hedden 2010). The biosynthesis of GAs occurs in the plastid from trans-geranylgeranyl diphosphate, via the methylerythritol phosphate pathway (Kasahara et al. 2002), through the plastid-localized sequential action of two terpene cyclases (Fig. 13.1). The following step is the oxidation by cytochrome P_{450} monooxygenases, which occurs in the endoplasmic reticulum, and then by soluble 2-oxoglutarate-dependent dioxygenases (Yamaguchi 2008). The dioxygenases involve the GA 20-oxidase and GA 3-oxidase families of isozymes, whereas the GA 2-oxidases (GA2ox), another class of dioxygenases, lead to the formation of inactive products in order to enable GA turnover. Drought tolerance is promoted by reducing the endogenous GA level in plants (Colebrook et al. 2014; Zhou et al. 2020). *Arabidopsis* gibberellin methyl transferase1 (*AtGAMT1*) gene was shown to encode an enzyme that catalyzes the methylation of active GA—generating GA methyl esters—resulting in drought tolerance improvement. The overexpression of the *SiDREB* gene was shown to suppress GA biosynthesis genes and increase drought tolerance (Nir et al. 2014; Ullah et al. 2018b).

Besides, *GA2ox* genes are considered to be the most receptive genes to abiotic stress (Ben Saad et al. 2020; Li et al. 2021b). A previous study suggested that restrained plant growth due to exposure to abiotic stress can be partially mediated by DELLA (Asp-Glu-Leu-Leu-Ala) protein—a negative regulator of GA signaling—acting downstream of the GA receptor (Yoshida et al. 2014). Upregulation of specific *GA2ox* genes by dehydration-responsive element binding proteins/C-repeat binding factor (DREB/CBF) family belonging to APETALA2 (AP2) family TFs regulates the expression of stress-responsive genes (Martin et al. 2021). The most significant role of GAs under abiotic stress appears to be associated with cell elongation, as they stimulate DELLA proteins to regulate gene expressions under water scarcity (Krugman et al. 2011). The genotypes of wheat drought-resistant, Y12-3, and drought susceptible, A24-39, subjected to 7-day drought stress, showed shifts in the expression of gibberellin-related genes.

13.3.8 Brassinosteroids (BRs)

BRs are a group of polyhydroxy steroidal plant hormones. Over 70 BRs have been characterized in plants. The most bioactive BRs are brassinolide, 28-homobrassinolide, and 24-epibrassinolide, and they are ubiquitous in the whole plant (Bajguz and Hayat 2009). The first steps in the biosynthesis of BRs are arguably the conversion of campesterol into campestanol, which is later converted to castasterone (Fig. 13.1). These reactions can occur via early or late C-6 oxidation. Finally, castasterone is transformed into brassinolide, which is the first isolated brassinosteroid. Further investigation into the BRs biosynthesis pathways revealed transformations between teasterone and typhasterol via 3-dehydroteasterone. Available data indicates that early and late C-6 oxidation pathways occur in many plants (Hu et al. 2021). BRs act in stem and root growth (Wei and Li 2016), floral initiation (Clouse 2008), and the development of flowers and fruits (Ali et al. 2021). BRs can mitigate abiotic stresses such as high-temperatures (Chen et al. 2021a), salinity (Vázquez et al. 2019), drought (Farooq et al. 2009; Chen et al. 2021b), flooding (Wani et al. 2016), metals/metalloids (Kour et al. 2021), and organic pollutants (Ahammed et al. 2013) by modulating antioxidant machinery components. BRs bind to BR-Insensitive 1 (BRI1) Leucine-Rich Repeat (LRR)-RLK family members on the plasma membrane in response to environmental stress. A ligand elicits BRI1 to act together with the co-receptor BRI1 Associated Receptor Kinase 1, primordial for early BR signalling events (He et al. 2000; Anwar et al. 2018). This is followed by the initiation of a signalling cascade of phosphorylation governing multiple BR-regulated gene expression through BRI1-EMS-SUPPRESSOR1 (*BES1*) and Brassinazole Resistant1 (*BZR1*) TFs (Fàbregas et al. 2018). *WRKY* TFs were implicated in plant growth and response to water deficit stress. *AtDWF4* gene confers better growth, yield, and tolerance against drought in *Brassica napus* (Sahni et al. 2016). Farooq et al. (2009) corroborate the role of BRs in rice subjected to 50% field capacity (FC) water limitation after exogenous application of BRs, 28-homobrassinolide and 24-epibrassinolide, which the cv. Basmati showed drought tolerance by modulating leaf water economy and growth promotion.

13.3.9 Strigolactones (SLs)

SLs are a group of terpenoid lactones that are derived from carotenoids (Fig. 13.1). They play a crucial role in developing the overall root architecture (Xu et al. 2021). SLs play a crucial role in the germination of seeds and plant-microorganism interactions (Mitra et al. 2021). Treatment of strigolactone-response mutant (MAX2) *Arabidopsis thaliana* seedlings with GR24 (a synthetic and biologically active strigolactone) did not repress the lateral root formation, suggesting that the negative effect of strigolactones on lateral root formation is MAX2-dependent (Kapulnik et al. 2011). While SLs are synthesized and exuded essentially in roots, they can be produced in other plant parts (Bradley and Lumba 2021). Moreover, cytochrome P450 and MAX (more axillary growth) genes were displayed to operate SL biosynthesis (Yoneyama and Brewer 2021). A new class of Fe-containing protein, D27, was also identified as an SL biosynthetic element (Lin et al. 2009).

SLs are generally influenced by environmental stimuli and act on shoot and root architecture depending on nutritional conditions (Raza et al. 2021). SLs act in drought acclimatization in plant shoots, while their biosynthesis is suppressed in roots. Since SLs are transported acropetally, their downregulation can indicate affected shoots (Visentin et al. 2016). SLs act as signalling molecules in nodulation during the legume-rhizobium interactions (Soto et al. 2010; Foo and Davies 2011). In barley, the *HvD14* gene has been shown to encode α/β hydrolase implicated in SL signalling and is an orthologue to *D14* described in rice. All these results highlight the potential of SLs to mitigate drought stress (Marzec et al. 2020).

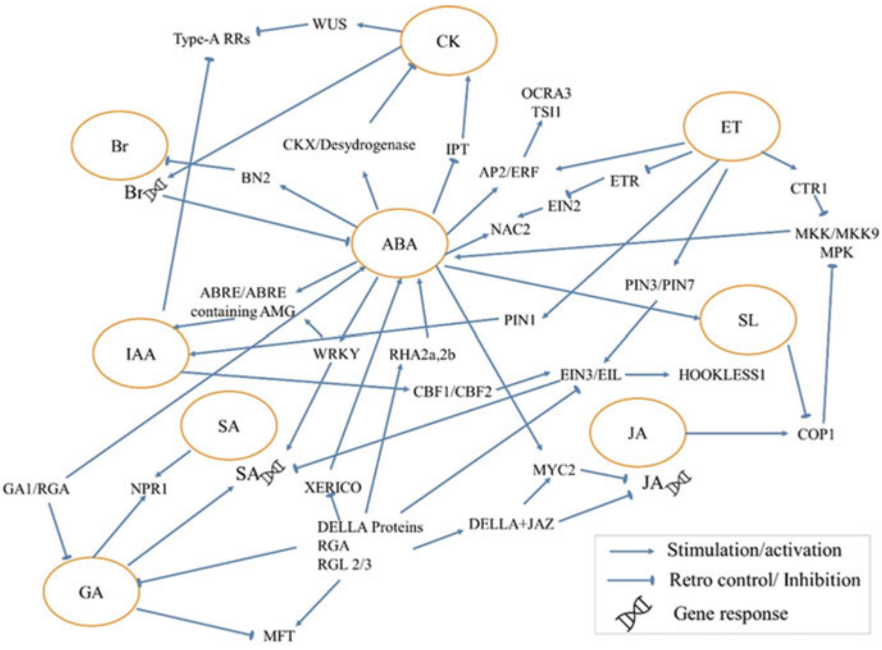

Fig. 13.2 Schematic presentation of potential crosstalk between phytohormone signalling in cereals under drought stress conditions. ABA is the key operating phytohormone against drought stress due to its ability to adapt to stress signals and address downstream stress responses. Stress adaptation regulation is directly controlled by synergistic/antagonistic crosstalk between ABA and other phytohormones. *CDK* cyclin-dependent kinase, *CKX* cytokinin oxidase/dehydrogenase, *COP1* E3 ubiquitin ligase constitutive photomorphogenic 1, *CTR1* constitutive triple response, *EIL* ethylene insensitive-like protein, *EIN2* membrane protein ethylene insensitive 2, *ERF* ethylene response factors, *ETR* ethylene receptor, *HOOKLESS* ethylene response gene, *MAPKKK/MPK* mitogen-activated protein kinase, *MFT* mother of FT and TFL1, *MYC2* helix-loop-helix (bHLH) transcription factor, *NPR1* non-expressor of pathogenesis-related gene 1, *PIN1/3/7* efflux proteins PIN FORMED 1/3/7, *RHA2A-E3* ubiquitin-protein ligase, *Type A RR* response regulator, *WUS* homeodomain transcription factor Wuschel

13.4 Hormone Signalling Crosstalk in Cereal Under Drought Stress Conditions

ABA, JA, ET, and SA are primal actors in drought stress mitigation, where ABA plays a leading role in controlling osmotic stress (Lata and Prasad 2011) (Fig. 13.2). GA, BRs, IAA, SLs, and CKs also act with stress-related gene factors and other phytohormones to sustain plant growth under drought stress. Increasing ABA level under water deficiency was closely linked with ABA-gene activation (Du et al. 2010), thereby inducing drought resistance through stomatal closure and osmolyte accumulation (Tiwari et al. 2017). SA and JA were also shown to be critical factors in water stress signalling based on their increase during this stress and their overall beneficial controlling role in drought resistance mechanisms such as stomatal closing (Savchenko et al. 2014; Tiwari et al. 2016). JA or MeJA (methyl-JA) is converted into an active form JA-Ile ((+)-7-iso-Jasmonoyl-L-isoleucine) after their exogenous supplementation to plants. JA-Ile gets bounded by the SCF-COI complex receptor, which has the COI1 (coronatine insensitive1) F-box protein (Fonseca et al. 2009). This action induces the degradation of JAZ (Jasmonate ZIM-domain) repressors, leading to the JA response gene activation by MYC2 (helix-loop-helix transcription factor 2) (Thines et al. 2007). In the absence of JA, JAZ blocks MYC2, which is then incapable of activating JA-inducible gene transcription. During the stress response, GA in interaction with SA and its exogenous supplementation induced the *NPR1* expression and SA-related genes implicated in SA effect.

ABA also regulates the BR signalling pathway through *BIN2* or its upstream components via the protein phosphatase 2C (*PP2C*) gene family (Zhang et al. 2009). Under drought stress, ABA also restrains BR-induced responses in plants (Divi et al. 2010). CKs regulate the drought stress responses that reduce the biosynthesis and transport of CKs (Tran et al. 2010). Both auxins and BRs, with the presence of MeJA, activate ACO (1-aminocyclopropane-1-carboxylic acid oxidase) enzymes that increase ethylene production (Arraes et al. 2015).

13.5 Factors Modifying the Phytohormonal Activity in Conferring Drought Tolerance in Cereal

Plants are deeply influenced by environmental factors such as light, temperature, infection by microorganisms (beneficial or pathogenic), low nutrients, precipitation, and contamination with metals. These external stimuli affect phytohormone levels in all plant tissues. Therefore, phytohormones are considered a challenge that limits an accurate understanding of plant physiology changes and reaches the mechanistic insight of the implication of phytohormones in regulating drought stress tolerance. Nevertheless, applying natural and chemical substances, minerals, organic amendments, and beneficial microorganisms is the most effective approach for inducing the resistance of plants to drought stress.

13.5.1 Substances, Minerals, and Organic Amendments

Applying priming agents such as injuries or exogenous substances could prepare the plant to respond faster and more effectively against future stresses. A recent study reported that primed wheat plants with polyethylene glycol (PEG) solution maintained higher water potential, increased net photosynthetic rate and proline and GB levels for better dehydration resistance, and activated ABA receptor *PYL4* gene that regulates stomatal closure (Wang et al. 2021a) (Table 13.1). The application of other polymers, such as chitooligosaccharides, chitosan (Ch) and Ch nanoparticles, stimulated plant growth and alleviated water stress in cereals (Zou et al. 2015; Behboudi et al. 2018; Hafez et al. 2020; El Amerany et al. 2020; Almeida

Table 13.1 Effect of external stimuli on phytohormones and drought tolerance in cereals

Factors	Plant species	Effects	Reference
PEG priming	Wheat	Induction of phytohormone signalling (ABA), stress *defense*, and cell elongation gene expression	Wang et al. (2021a)
Zinc foliar application	Maize	Increased IAA and GA level Higher RWC and antioxidant enzyme activity (CAT and SOD)	Moghadam et al. (2013)
Formulated Fertilizer Synergist: 18% N + 2.7% P + 8.3% K + urease and nitration inhibitors + bioactive substances	Rice	Induction of ABA accumulation in roots and leaves Net photosynthetic rate improvement	Wang et al. (2007)
Humic acid	Rice	Increase of endogenous ABA level in leaves and roots	García et al. (2014)
Arbuscular mycorrhizal fungi *Rhizophagus irregularis*	Maize	Decreased ABA content in roots	Li et al. (2016)
Rhizophagus irregularis, strain EEZ 58 + salicylic acid	Maize	Increased IAA, SA, JA, and JA-ile levels in roots	Quiroga et al. (2018)
Glomus microaggregatum, *Rhizophagus irregularis*, *Funneliformis mosseae*, *F. geosporum*, and *Claroideoglomus claroideum*	Rice	Increased IAA and ABA levels in leaves	Chareesri et al. (2020)
PGPR *Azospirillum lipoferum* strain USA 59b	Maize	Enhanced ABA and GA level increased plant length, leaf area, shoot and root dry biomasses	Cohen et al. (2009)
Azospirillum sp.	Wheat	IAA produced by bacteria enhanced plant growth and yield plant water potential and content adjustment	Arzanesh et al. (2011)
Pseudomonas fluorescent (*Ps fluorescent*) strain 153 and 169 and Ps putida strain 4 and 108	Maize	Improved GA, IAA, Cks, and ABA in plant tissue Increased proline content in leaves	Ansary et al. (2012)
Rhizobium leguminosarum, *Mesorhizobium ciceri*, and *Rhizobium phaseoli* (MR-2)	Wheat	IAA produced by bacteria improved plant growth and drought tolerance index	Hussain et al. (2014)
Rhizobacteria (*Bacillus pumilus* (*B. pumilus*); *Ps* sp.; *B. cereus*; *Proteus* sp.; B. *pumilus* + *Ps* sp.; *Proteus* sp. + *Ps* sp.) applied individually or combined with L-tryptophan	Maize	Increased IAA, ABA, and GA levels in leaves Higher osmotic potential, protein, and photosynthetic pigment content	Yasmin et al. (2017)
Azospirillum lipoferum + *Ps putida* + super absorbent polymer	Maize	Increased ABA level and proline Downregulation of the antioxidant enzymes (CAT and GPX)	Moslemi et al. (2011)

et al. 2020). Polymers' effects are due either to their structures containing free amino groups-NH_2 that could interact with ROS or to their ability to decrease the concentration of malondialdehyde (MDA) and electrolyte leakage (EL) and to improve the photosynthetic efficiency, diameter of vascular bundle, RWC, and antioxidant enzymes (i.e., POD, SOD, and CAT) activity (Hidangmayum et al. 2019; El Amerany et al. 2020). However, the effects of these polymers on hormone levels in cereals have not yet been investigated. Zhang et al. (2018) reported that the exogenous supplementation of Ch improved ABA, CKs, and GA levels under drought stress conditions but reduced IAA in white clover (*Trifolium repens* L.).

The application of mineral nutrients (i.e., zinc and ZnO nanoparticles) either to leaves or roots and organic amendments (i.e., formulated fertilizer synergist, biochar, vermicompost, humic acid, and compost) has been commonly applied in agriculture to increase seedling growth and to alleviate drought stresses in cereals (Wang et al. 2007; Moghadam et al. 2013; García et al. 2014; Sun et al. 2020; Ding et al. 2021). Their effects are related to the modulation of phytohormone levels implicated in stress tolerance (Table 13.1). The mineral imbalance in the soil (starvation or accumulation) negatively affected the hormonal interaction between the above-ground and underground parts of plants (Battal 2004). It has been shown that phosphate starvation increased ABA production in roots and inhibited the translocation of CKs from roots to shoots of barley plants, which therefore inhibited roots extension and vacuolar invertase activity and reduced ATP content (Werner et al. 2008; Vysotskaya et al. 2016; Vysotskaya et al. 2020). The excess supply of phosphate increased the ethylene response, which reduced the acquisition of other nutrients (Fe, Zn, Mn, Ca) and the number of meristematic cortical cells and inhibited the growth of the primary root (Shukla et al. 2017).

Organic amendments are considered essential components of soil organic carbon and are well known as biostimulants that may achieve phytohormone-like effects to stimulate nutrient absorption (Canellas et al. 2020). For instance, the application of humic acid to rice seedlings activated plasma membrane H^+-ATPase and increased the activity of calcium-dependent protein kinases (CPKs/CDPKs) implicated in phytohormone production and signalling (Ramos et al. 2015; Xu and Huang 2017). Additionally, the application of seaweed extract (SWE) that contains osmoprotectants (i.e., GB) and phytohormones mixtures (IAA, GA, and CKs) decreased the oxidative damage of wheat grown under limited water supply by inducing the biosynthesis of ascorbate and CAT (Kasim et al. 2015). Shemi et al. (2021) reported that the individual application of GB, Zn, or SA increased the growth of maize seedlings under drought conditions due to their ability to stabilize chlorophyll pigments, maintain water equilibrium, decrease ROS and MDA content, and increase gas exchanges, RWC, and antioxidant enzymes (SOD, CAT, POD, glutathione reductase (GR), and ascorbate peroxidase (APX)). Although there is scarce information about SWE functioning to alleviate drought, they could positively affect the expression of genes responsible for host hormonal biosynthesis, like auxin (Ali et al. 2021).

13.5.2 Beneficial Microorganisms

Other strategies plants adopt to deal with (a)biotic stresses, especially drought, are interaction with beneficial soil microbes, including plant growth-promoting fungi (e.g. arbuscular mycorrhizal fungi (AMF)) and rhizobacteria. Significantly, the 'cry-for-help' strategy suggests that plants recruit beneficial microorganisms to resist environmental stresses by changing their root exudation chemistry (Rizaludin et al. 2021). These microorganisms have been described as effective biofertilizers for host plant growth-boosting, encompassing all the dynamic processes of growth, metabolism, and defense (Ait-El-Mokhtar et al. 2020; Anli et al. 2020; Ben-Laouane et al. 2021; Boutasknit et al. 2020; El Amerany et al. 2020; Hossain and Sultana 2020).

13.5.2.1 Plant Growth-Promoting Fungi (PGPF)

PGPF are nonpathogenic saprotroph fungi that have shown increasing interest in recent years due to their benefits, especially in promoting crop production and potentiating tolerance against stresses (Hossain and Sultana 2020; Cornejo-Ríos et al. 2021). These fungi could alter the physiology and biochemical processes of the host plants through various strategies, including the conversion of the insoluble phosphate to a soluble form, mineralization of organic substrate, production of enzymes, volatile compounds (i.e., sesquiterpenes and diterpenes), and phytohormones (Hossain and Sultana 2020). Several studies reported that *Trichoderma atroviride* ID20G application to maize seedlings reduced the injurious effects of water stress by stimulating photosystem II efficiency (F_v/F_m), pigment contents, and antioxidant enzyme activity (Guler et al. 2016). While no report related to phytohormone changes in cereals under water deficiency, either *Phoma glomerata* LWL2 or *Penicillium* sp. LWL3 application to cucumber seedlings mitigated water deficit by impairing polyphenol oxidase activity and reducing glutathione and endogenous SA, JA, and ABA levels that could impact GAs and IAA secretion (Waqas et al. 2012).

Arbuscular mycorrhizal fungi (AMF) could form symbiotic interactions with more than 70% of terrestrial plants (Cosme et al. 2018). Many reports showed that AMF-inoculated plants increased height, number and length of lateral roots, leaf area, number of flowers and fruits, and dry matter production (Elhindi et al. 2017; Boutasknit et al. 2021; Vosnjak et al. 2021). For instance, the plant weight of rice was ten times higher in *Glomus intraradices* inoculated plants than in non-inoculated plants (Ruíz-Sánchez et al. 2011). Moreover, the mutualistic relationship between plants and AMF is regulated by phytohormones. Some SLs are involved even before physical contact between the fungi and the host plants, whereas others are accumulated only at a late stage of mycorrhization (i.e., CKs) (Mitra et al. 2021). In addition, some phytohormones are accumulated to regulate root system architecture and fungal development (i.e., IAA, ABA, and JA) (Akiyama and Hayashi 2006; Hause et al. 2007). In rice, the overexpression of *OsNAC14*, a TF that is implicated in drought stress tolerance, induced SL biosynthesis (Shim et al. 2018). Nevertheless, the effect of CKs on the establishment of mycorrhization and water stress tolerance is still not well understood; specific authors pointed out that the accumulation of these hormones was positively correlated with the photosynthesis rate increase and fungal growth (Werner et al. 2001). Inoculation of *Catalpa bungei* with *Rhizophagus intraradices* reduced the content of zeatin in well-watered plants and those exposed to water deficiency (Chen et al. 2020). These findings showed that mycorrhization rate and the level of other hormones, IAA and ABA, were not adversely affected. Also, the level of phytohormones might vary between plant cultivars. For instance, in maize, while cv. B73 inoculated with *R. irregularis* reduced ABA levels, however, PR34B39 cv increased them (Table 13.1). Furthermore, a metabolomic study revealed that the inoculation of durum and bread wheat roots with *Funneliformis mosseae* under drought stress increased the levels of brassinosteroids (6 alpha-hydroxy-castasterone and brassinolide-23-O-glucoside), hydrolyzable abscisic acid (D-glucopyranosyl abscisate), a hormone similar to IAA (indole-3-acetyl-methionine), gibberellins (gibberellin A29-catabolite and gibberellin A34-catabolite), and jasmonate derivative (tuberonic acid glucoside) in roots (Bernardo et al. 2019).

13.5.2.2 Plant Growth-Promoting Rhizobacteria (PGPR)

The PGPR are beneficial bacteria that positively influence the growth and yield of different crops (Oleńska et al. 2020). They could fix and convert atmospheric N to ammonia, transform soil macromolecules into easily available compounds for plants, solubilize soil phosphate, release organic acids, and produce exopolysaccharides (EPS) and phytohormones (i.e., CKs, IAA, GA_3, and zeatin) to alleviate drought stresses (Martínez-Viveros et al. 2010; Vardharajula et al. 2011; Zaheer et al. 2019). EPS are organic polymers made by bacteria to contact the host plants (Naseem et al. 2018). Despite the vital role of EPS in drought stress tolerance, their role in modulating phytohormone levels is unknown. A previous study showed that applying one or multiple rhizobacterial strains, individually or combined with either L-tryptophan or super absorbent polymer, significantly increased plant performance (Table 13.1). This positive effect is due to increased osmotic potential, proline and sugar content, antioxidant enzyme activity, ABA, GAs, CKs, and IAA levels (Table 13.1).

13.6 Metabolic Engineering of Phytohormones: New Strategies in Cereal to Mitigate Drought Stress

Using the most tolerant plant species to water stress and increasing cereal resistance through making crosses between inbred lines or applying a transgenic approach are considered the best-applied strategies for improving cereal productivity and minimizing land consumption of freshwater resources (Parmar et al. 2017). These advanced lines are characterized by deregulating genes of interest and stimulating regulatory factors (proteins) involved in the biosynthesis of metabolites, especially phytohormones, to ensure drought tolerance.

13.6.1 Breeding

Developing new drought-tolerant cereal lines using natural breeding becomes an important strategy. This technique provides changes in plant traits and creates plants with desirable characteristics based on crossing lines selected based on their high WUE or lines with contrasting phytohormone levels (Bruce et al. 2002). Despite the applicability of this approach to a broad type of plant species, however, it did not meet the general need yet, owing to the long time it takes to minimize linkage drag through phenotypic screening. Successful findings were reported in maize. For example, Pekić et al. (1995) reported that crossing maize lines “Polj17” (high ABA level) x F-2 (low ABA level) increased yield and ABA level in both leaves and kernels and reduced transpiration in the offspring compared to the parents. Moreover, the maize inbred line “RIL70”, from crossing Ph4CV × F9721, was more tolerant to stress than parental lines due to its ability to detoxify stress signals through increasing photosynthetic rate, cell wall biosynthesis, and the early expression of aquaporin-related genes. Min et al. (2016) reported that ABA level and *bZIP* gene expression involved in ABA synthesis and *ABRE* TFs were induced in the “RIL93” line (drought-sensitive) compared to the “RIL70” line.

13.6.2 Genetic Engineering

Genetic engineering is of the utmost importance for cereal growers since it offers a fast and exact way to attain the same objective as breeding crops for certain desirable traits in one generation rather than multiple. To achieve this goal, new cultivars are created by employing wild genes involved in drought tolerance, selecting marker-assisted breeding, and isolating trait locus genes (Khan et al. 2019). Plants could alleviate the deleterious effects of drought stress by stimulating the expression of TFs, i.e., *NAC*, *MYB*, *bZIP*, *HDG*, and *WRKY*, that activate phytohormone biosynthesis genes at the transcriptional level and deregulate the expression of stress-related genes (He et al. 2016; Shim et al. 2018). In rice, Shim et al. (2018) reported that overexpression of *OsNAC14* induced SL biosynthesis and diminished DNA damage and the expression of drought-responsive marker genes (*OsDIP1*, Dehydration Stress-Inducible Protein 1, and *OsRbcS*, Small Subunit of Rubisco). Overexpression of *OsMYB6* in rice could play a pivotal role in minimizing drought stress injuries because it elevated the expression of the NAC gene (*SNAC1*) (Tang et al. 2019). Overexpression of *OsHBP1b* in rice plants boosted plant growth and development and increased callose and antioxidant enzyme levels (Das et al. 2019).

Transgenic wheat plants over-expressing *AtHDG11* and *TaWRKY2* showed better growth than wild type plants. These transgenic plants are characterized by lower stomatal density, higher WUE, and accumulation of osmotically active molecules (i.e., proline, chlorophyll, and sugars, CAT, and SOD) to detoxify ROS molecules (Li et al. 2016; Gao et al. 2018). Exogenous application of phytohormones, such as BRs, induced *OsDof12*-type TFs in rice plants; however, the overexpression of *OsDof12* in plants negatively regulated BRs signalling genes and affected plant cell architecture (Wu et al. 2015). Overexpression of *JERF1*, involved in ET biosynthesis, in rice exhibited better shoot and root development and a higher level of ABA (Table 13.2).

13.7 Conclusion and Future Perspectives

Drought stress is a constant factor that alters cereals' growth, physiology, and metabolism. Substantial progress has been achieved recently to understand the mechanisms and the role of signalling molecules, such as phytohormones, on plant growth and yield and plant tolerance to environmental stress. As phytohormones upregulate various plant functioning processes, they can control the same traits to manage the adaptation of plants to stressful conditions. Under drought stress, the growth and development of plants are controlled by phytohormones including CKs, IAA, ET, GAs, ABA, JAs, BRs, SA, and SL through signalling cross-talk pathways orchestrated by ABA. These compounds are implicated in the drought adaptation process through stimulating stomatal closure, increasing WUE, metabolite adjustment, and expression of TFs and stress-responsive genes. The phytohormones' cross-talk under water deficiency is carried out at different levels such as hormone activation, transcriptional activation, gene expression, and developmental variations. Despite the significant role of phytohormones in alleviating drought stress, their production and signalling pathways may be hindered owing to the vast difference in plant physiological characteristics and the duration and severity of stress. Therefore, many methods and technologies have been used to retrieve cereals from the negative impact of drought and deregulate the phytohormone concentration involved in tolerance to improve the yield. Selection of drought-tolerant species, exogenous application of minerals and organic amendments, inoculation with beneficial microorganisms (AMF, PGPF, and PGPR), and use of natural breeding/genetic engineering are factors and techniques that could help to boost cereals under future environmental stresses. With the development of omics-based research in recent decades, many gaps still need to be investigated, especially in the molecular mechanisms related to the cross-talk among phytohormones at cellular and transcriptional levels and their transport systems, receptors, mediators, and targets in plants. These aspects are highly complicated, particularly under drought stress. It is worth mentioning that genome-wide studies targeting phytohormone signalling responses under adverse environmental situations are needed and will significantly contribute to a better understanding of hormone interaction with the crosstalk network and developing ultimately effective strategies for improving cereal stress tolerance.

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Table 13.2 Example of phytohormones metabolic engineering for drought stress tolerance in cereals

Hormone	Gene	Gene function	Expression	Plant species	Effects	Reference
ET	*JERF1*	ET response factor proteins	Upregulation	Rice	Reduction in water loss Increase in seedlings fresh weight, root length, proline level, biosynthesis of ABA and its enzyme genes (*OsABA2* and Os03g0810800)	Zhang et al. (2010)
	ACC synthase	ET biosynthesis	Downregulation	Maize	Higher kernel number and grain yield	Habben et al. (2014)
ABA	*LOS5*	ABA biosynthesis	Upregulation	Maize	Reduction in water loss and MDA and H_2O_2 Increase in stomatal closure, root system, antioxidative enzymes activity, ABA level, and the expression of *NCED1* gene	Lu et al. (2013)
	AtNCED6	ABA biosynthesis	Upregulation	Barley	Downregulation of endogenous *HvNCED* better assimilation of water	Seiler et al. (2014)
	OsWRKY5	Inactivate ABA biosynthesis	Downregulation	Rice	Downregulation of endogenous *OsWRKY5* improve drought tolerance in rice	Lim et al. (2021)
Auxin	*TLD1*	IAA biosynthesis	Upregulation	Rice	Dwarf-like phenotype Higher tiller number and IAA-amino acid conjugate	Zhang et al. (2009)
	OsPIN3t	Auxin efflux carrier	Upregulation	Rice	Increase root development and drought tolerance	Zhang et al. (2012)
	OsIAA6	Regulation of auxin biosynthesis	Upregulation	Rice	Increase plant growth, F_v/F_m, and tiller number Reduction of *DIP1* (dehydration marker) transcript	Jung et al. (2015)
CK	*IPT*	CK biosynthesis	Upregulation	Rice	Up regulation of ABA, CK-O-glucosyltransferase, and BR-insensitive1-like precursor genes Down regulation of JAZ1, PP2C7, auxin-induced protein 5NG4, and ethylene-responsive TF genes	Peleg et al. (2011)
	AtCKX1	Vacuole-targeted CK dehydrogenase	Downregulation	Barley	Increase the number of lateral roots and yield and maintain higher level of water content	Pospíšilová et al. (2016)

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Cereals and Phytohormones Under Temperature Stress

14

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Abstract

Temperature stress causes noticeable yield losses in cereals. The rate of cereal growth, determining grain production, is affected by temperature stress. Therefore, high temperature tolerances are urgently needed to ensure food security for this explosive population. Phytohormones affect tolerance to temperature stress and regulate the growth and development of cereals. The changes in phytohormonal levels protect yields through reinforcing responses to temperature stress and salvaging the expression of growth promoters. Changing phytohormones associated with signaling mechanisms in cereals can lead to alleviating heat stress. Transportation of hormones and their interactions are applied by cereals to cope with temperature stress. An accurate understanding of the interactions between temperature stress responses, growth processes, and hormone signaling may result in the mechanisms under which cereals optimize growth and yield under high and low temperatures. In this chapter, the latest literature data regarding the growth regulation by phytohormones in cereals under temperature stress have been analyzed and summarized.

Keywords

Chilling stress · Heat stress · Maize · Plant growth regulators · Rice · Wheat

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14.1 Introduction

Temperature is considered a primitive agent affecting plant growth and development and affects cereal crops belonging to the *Poaceae* family, as the most economically important group of plants (Fitter and Hay 2002; Zrobek-Sokolnik 2012; Hatfield and Prueger 2015; Tiwari et al. 2020; Sadura and Janeczko 2022). In the tropics, the daytime temperature even exceeds 60 °C, and instead, in the polar and cold regions, the temperature is below −70 °C (Kai and Iba 2014). Therefore, temperature stress in cereals could be categorized into three types depending on the stressor, which may be high, chilling or freezing temperature stress (Zrobek-Sokolnik 2012; Kai and Iba 2014). Winter cereals suffer from frost, and tropical zone-grown cereals are damaged because of high temperatures, leading to noticeable yield losses. Each cereal crop has its ideal temperature range for growth, which is called the optimum temperature of plant growth. This optimum temperature varies from species to species. When the temperature either drops below the optimum range or surpasses it, it can affect a cereal's growth (Sadura and Janeczko 2022). The development of temperature stress can be induced by a high or low temperature and may depend on the duration of the exposure, the rate of temperature changes, and the plant growth stage at which stress exposure occurs (Zrobek-Sokolnik 2012; Kai and Iba 2014). The mechanisms by which cereals can withstand low temperatures, especially during winter are very complex. Fowler et al. (2014) used some equations describing acclimation, vernalization, dehardening, and damage because of low-temperature stress to establish a model for the survival of cereals. However, to overcome temperature stress, cereals apply certain adaptive strategies, which involve hormonal activities. Recent research has shed light on the formation of a stress resistance mechanism that combines the perception and transduction of external signals and the subsequent triggering of specific metabolic processes (Janni et al. 2020; Kosakivska et al. 2022). To tackle abiotic stresses such as temperature, cereals apply some adaptive strategies such as combining morphological, physiological, and biochemical responses which are mostly involved in phytohormones (Kosakivska et al. 2022). Cereal growth involves several biochemical reactions that are affected by temperature, and thereby they are facilitated to acclimate to temperature stress, and one of these facilities is that plant crops are equipped with phytohormones (Fitter and Hay 2002; Kosakivska et al. 2022). Phytohormones are among the most important plant components regulating different plant functions, which can equip the cereals to survive under temperature stress (Kosakivska et al. 2022). Some important phytohormones such as auxin, abscisic acid, ethylene, cytokinins, gibberellins, jasmonates, salicylic acid, brassinosteroids, and strigolactones may be responsible for toleration against temperature stress. Most of the abovementioned hormones enhance plant resistance to temperature stress by activating different signaling pathways (Sadura and Janeczko 2022). In this chapter, the focus is on cereals' responses and adaptation to temperature stress, endogenous phytohormone biosynthesis, and their role in cereals' growth under stress.

14.2 Cereal Responses and Mechanisms of Tolerance to Cold Stress

The mechanism underlying the interaction between low-temperature stress and cereals remains unclear. This chapter attempts to address low temperature tolerance as a potential contributor to the success of plant species. One of the most destructive effects of low-temperature stress is that it results in severe membrane damage, which is noticeably due to dehydration during low-temperature stress (Yadav 2010). Low-temperature stress lowers the capacity and efficiency of photosynthesis in some cereals such as rice by modifying gas exchange, pigment content and chloroplast development and also decreases chlorophyll fluorescence (Farooq et al. 2009). When subjected to temperature stress, the metabolism in plants is modified in two steps. First, plants attempt to balance their cellular metabolism that is altered due to rising or falling temperatures. In the second step, this modified metabolism in response to temperature stress has resulted in an enhanced tolerance of plants (Fernie et al. 2005; Yadav 2010). One aspect of temperature stress is cold stress, which precedes either chilling (0–15 °C) or freezing (<0 °C) and adversely affects the growth and agricultural productivity of cereals (Guo et al. 2018; Liu et al. 2018). Cold stress negatively affects the stability of proteins and lowers the activities of some antioxidant enzymes that scavenge reactive oxygen species (ROS), which is followed by photo-inhibition, impaired photosynthesis, and membrane damage (Ruelland et al. 2009). During freezing stress, ice nuclei form and grow as ice crystals, which spread into the apoplast where they induce water efflux, leading to cell dehydration (Pearce 2001; Dai et al. 2007). Cold stress resulted in degradation of starch granules in mature pollen grains, inhibition of pollen germination, weak pollen tube elongation, and finally pollen sterility of rice (Shinada et al. 2013). Ji et al. (2011) asserted that cold stress enhanced ABA levels in spikelets of rice. The mechanisms of cold acclimation of plant crops are related to several gene-signaling pathways and the production of cold-responsive (COR) proteins (Sanghera et al. 2011; Park et al. 2015). The COR proteins regulate proteins that are responsible for controlling signal transduction and functional proteins such as dehydrins, antifreeze proteins (AFPs), molecular chaperones, lipid-transfer proteins, and detoxification enzymes. This controlling process leads to modifying the cellular structures and compositions (Grennan 2006; Yamaguchi-Shinozaki and Shinozaki 2006). Dehydrins are a group of glycine-rich proteins that notably accumulate to prevent cell dehydration in response to cold stress (Kosová et al. 2007). Some metabolites act as signal molecules to regulate cold stress response and initiate COR gene expression (Svensson et al. 2006; Zhu et al. 2007). Soluble sugars are among the cell metabolites that regulate plant acclimation to cold stress (Rekarte-Cowie et al. 2008). Phytohormones may affect sugar metabolism during cold acclimation. This modification in sugar metabolism results in the up-regulation of genes encoding enzymes such as β-amylases and sucrose synthase in response to low temperatures (Gibson 2004; Kaplan and Guy 2004; Rekarte-Cowie et al. 2008). Zhu et al. (2007) asserted that chloroplasts may also have an important role in sensing temperature changes. They reported that the difference in the light energy harvested and the energy dissipated through metabolic activity might create an energy imbalance, leading to inducing high photosystem II excitation pressure, resulting in the generation of ROS in cold stressed plants. ROS itself may also act as a signal for cold stress, albeit studies show that ROS could have a dual role in plant metabolism as both toxic and signal molecules (Mittler et al. 2004; Hung et al. 2005; Ouellet and Charron 2013). It has been reported that ROS signals can activate redox-responsive proteins, Ca^{2+} and Ca^{2+}-binding proteins (Mittler et al. 2004; Chinnusamy et al. 2007). The major location for the perception of temperature change has been reported to be the plasma membrane (Wang et al. 2006). At the cellular level, microtubules and microfilaments are responsible for transducing signals. During this signal transduction process, the Ca^{2+} channels are modulated following membrane rigidification (Thion et al. 1996; Orvar et al. 2000). It has been reported that phospholipid D conjoins the cytoskeleton and plasma membrane structurally and acts as a signaling link between these compartments (Hong et al. 2008). Dhonukshe et al. (2003) reported that phospholipid D regulates the interaction between the cytoskeleton and plasma membrane via Ca^{2+} channels under cold stress conditions. Indeed, Ca^{2+} as a second messenger in plants affecting the signaling network may be regulated by phytohormones in response to cold stress (Dodd et al. 2006; Klimecka and Muszyńska 2007; Ray 2017). Different kinds of enzymes involved in respiration and the metabolism of carbohydrates, lipids, proteins, antioxidants, and molecular chaperones and antioxidant enzymes that scavenge oxidative stress are activated during cold stress acclimation of plant crops (Heidarvand and Amiri 2010). Plants respond to temperature stress by regulating membrane lipid composition, stress-related transcription factors, metabolite synthesis, and detoxification pathways (Kai and Iba 2014). Other enzymes involved in the metabolism of lignins, osmolytes, and starch and the biosynthesis of sterols and oligosaccharides have also an important role in response to cold stress (Renaut et al. 2006). Some proteins have been reported to have an important role in photosynthesis, photorespiration, primary and secondary metabolism, signal transduction, redox homeostasis, and nucleotide processing, which are created during cold stress exposure (Yan et al. 2006). However, while the mechanisms of cold acclimation and freezing tolerance have been extensively studied in cereals and have been efficient in engineering cold tolerance in these crops, further studies are needed to clarify potential genes that play a major role in expressing tolerance against cold stress to sustain agricultural productivity under climate changes. Here we attempt to review some of the major findings on cold stress effects on plant physiology, mechanisms, and hormonal regulations.

14.3 Role of Phytohormones in Plant Development Under Low-Temperature Stress

Plants can tolerate low temperatures by modifying cell membrane composition and activating ROS scavenging systems due to phytohormonal modifications (Fig. 14.1). C-repeat-binding factors (CBF) are known as a genetic pathway induced by low temperature, which activates promoters through the C-repeat (CRT) cis-element.

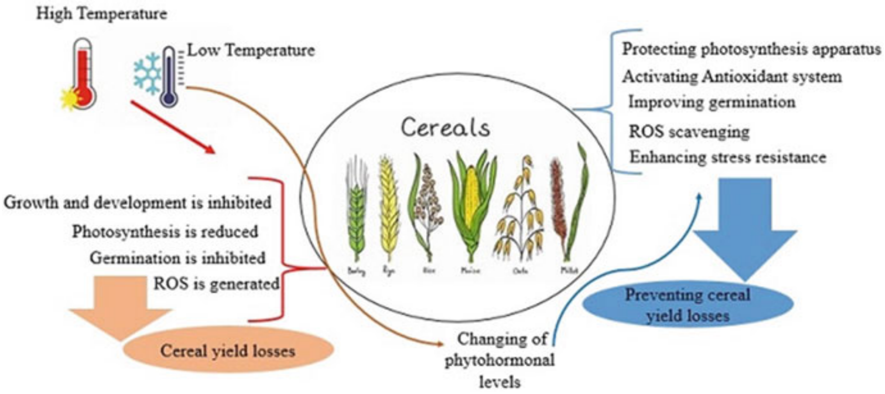

Fig. 14.1 Cereal responses to changing phytohormone levels under temperature stress

Also Ca^{2+} acts as a major signalling event during low-temperature incidence, which activates many enzymes, such as phospholipases and calcium-dependent protein kinases. Interestingly activating these signalling pathways leads to modifications in the transcriptome. However, some phytohormones, such as abscisic acid, brassinosteroids (BRs), auxin, salicylic acid, gibberellic acid, cytokinins, and jasmonic acid, have major roles in controlling plant growth under low-temperature stress. These phytohormones can even alleviate important processes involved in tolerance to low-temperature stress in plants (Khan et al. 2017; Sadura and Janeczko 2022). Sadura and Janeczko (2022) asserted that the sugar metabolism in winter rye, barley, and maize is controlled by BRs, leading to acclimation to low temperatures. Discovering the processes involved in gene controlling in future studies could provide new strategies for improving tolerance to low-temperature stress alleviated by phytohormones (Khan et al. 2017; Sadura and Janeczko 2022). The exogenously applied BR to cereals such as winter rye and winter wheat results in enhanced frost tolerance, while cold tolerance in maize and tolerating a high temperature in rice (Sadura and Janeczko 2022). Auxin may have a major responsibility in controlling all aspects of the growth and development of plants, but its role under low-temperature stress is yet to be dissected in detail. Interestingly, the low temperature (4 °C) prevented gravitropic response of inflorescence and roots gravity in *Arabidopsis* although this response was returned to the first state when transferred at room temperature (Wyatt et al. 2002; Nadella et al. 2006; Rahman 2013). There is also a report on the interaction between auxin and brassinosteroids (BRs) in regulating cell elongation in shoots and roots (Hardtke et al. 2007). BRs have been reported to confer tolerance in plant crops against temperature stress (Khan et al. 2015). Exogenously applied BRs prior to low-temperature stress reduced the ion leakage in cold stressed plants and increased the antioxidant defense system in chilling stressed plant crops (Janeczko et al. 2007; Xi et al. 2013; Ahammed et al. 2012; Khan et al. 2015). Janda et al. (1999) reported that exogenously applied SA mitigated the harmful effect of low temperatures in maize plants. He et al. (2005)

also showed that salicylic acid (SA) improved plant tolerance to chilling and heat stress. Moreover, other studies reported the positive effects of SA in low temperature tolerance of winter wheat and barley (Tasgin et al. 2006; Mutlu et al. 2013). Gibberellins, BR and ABA have an important role in gaining tolerance to low temperatures in cereals (Sadura and Janeczko 2022). GA has also been reported to have a critical role in the low temperature tolerance of cereal crops (Khan et al. 2017). Higher starch and mannitol content in GA-treated plants showed that the application of GA inhibited the use of starch and mannitol for sucrose, which resulted in the rapid enlargement of differentiated tissues in the cold, which caused the rosette to break (Ogasawara et al. 2001; Khan et al. 2017). The application of the GA quenched low temperature-induced male sterility rice (Sakata et al. 2014). Veselova et al. (2005) reported that cold stress reduced the content of cytokinins due to the induced activity of cytokinin oxidase. Methyl jasmonate (MeJA) also has been reported to be beneficial in improving the cold stress tolerance of cereal crops (Qi et al. 2005; Zhao et al. 2013). In terms of molecular studies, the JA signaling pathway has an important role in the cold stress tolerance of plant crops by modifying the CBF signaling pathway (Hu et al. 2013). However, the alleviative effect of GA on cold stress is because of improved antioxidant activity and a higher ratio of unsaturated to saturated fatty acids (Gao et al. 2016). In a general conclusion, it can be stated that a detailed analysis of hormonal interventions in cereals under cold stress will increase our understanding in the future of how such important crops adapt to changes under cold stress.

14.4 Plant Responses and Mechanisms of Tolerance to Heat Stress

Heat stress caused by global warming is a major abiotic stress that restricts plant growth and development and also threatens the yield of wheat, rice, and maize worldwide. Therefore, the plants’ response to heat stress has been a concern of researchers (Lobell et al. 2011; Asthir 2015; Kothari and Lachowiec 2021; Zhao et al. 2021). Peng et al. (2004) reported that the grain yield of some important cereals, such as rice, decreases by 10% for each degree Celsius increase during the growing season. Other field studies report a 2% decrease in wheat yield due to heat between 1980 and 2015 (Daryanto et al. 2016). Here, we review recent progress in the hormonal regulation of the cereals’ response to heat stress. We also attempt to summarize advances in the understanding of the hormonal regulation underlying plant–heat interactions. Finally, the challenges and opportunities of future research regarding cereals’ response to heat stress will be discussed. The mechanisms by which cereals respond to heat stress are of great interest. Heat stress negatively affects some physiological activities of plants such as photosynthesis, respiration, transpiration, membrane thermostability, and osmotic regulation (Bita and Gerats 2013; Hemantaranjan et al. 2014; Zhao et al. 2021). Reduced leaf tissue water content and root conductance are one of the major consequences of plants exposed to heat stress (Machado and Paulsen 2001; Morales et al. 2003). This water loss under heat stress could be due to an increased rate of transpiration, leading to impaired physiological processes in plants (Huang et al. 2012). Heat stress negatively affects the activity of some enzymes such as nitrate reductase, which are responsible for an efficient nutrient metabolism (Klimenko et al. 2006). The chlorophyll biosynthesis in plants is also negatively affected by heat stress. The reduced accumulation of chlorophyll because of heat stress could be also attributed to the deactivation of different enzymes (Dutta et al. 2009). Photosystem II is one of the processes in cereals' cells that is seriously damaged by heat stress (Camejo et al. 2005; Fahad et al. 2016). The activities of the source and sink are reduced under heat stress, which significantly affects plant growth (Taiz and Zeiger 2006). As shown in Fig. 14.1, the generation of ROS due to heat stress exposure has been reported (Liu and Huang 2000; Wahid et al. 2007). Enhanced ROS accumulation caused by heat stress leads to membrane damage, which results in decreasing tolerance to heat stress. Therefore the stability of the membrane is an important criterion in conferring tolerance to heat stress in plants (Abdul-Razack and Tarpley 2009; Zhao et al. 2021). Working on some cereal crops such as rice, Farooq et al. (2008) asserted that to cope with oxidative stress, plants responded by the activation of an antioxidant defense system which may be enzymatic or nonenzymatic. The recruited antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), and peroxidase (POX), by plants, is a developed mechanism by which plants can detoxify ROS and enhance heat tolerance (Jespersen 2020). Under transient or mild heat stress, plants modify the rate of respiration and transpiration to adjust water loss and heat dissipation. The levels of soluble sugars and proteins are also changed during heat stress to control osmotic pressure within the cell (Wang et al. 2020). Phytohormones may be involved in all of these processes and changes and may play key roles. Phytohormones as natural defense molecules in plants enhance levels of antioxidants under heat stress. These plant growth regulators assist plants to acclimatize to heat stress by boosting growth, development, source/sink transitions, and nutrient allocation (Fahad et al. 2015). The phytohormone-induced amelioration of heat tolerance stress in plants has been evaluated by Chhabra et al. (2009). They asserted that indole acetic acid (IAA), GA, and kinetin/abscisic acid (ABA) were effective for mitigating the effects of heat stress.

14.5 Role of Phytohormones in Plant Development Under High-Temperature Stress

Some phytohormones, such as auxin, gibberellic acid (GA), abscisic acid (ABA), cytokinins (CTKs), ethylene (ET), salicylic acid (SA), brassinosteroids (BRs), strigolactone (SL), and jasmonic acid (JA) have a very important role in regulating plant growth in response to heat stress (Wani et al. 2016; Sharma et al. 2019; Kothari and Lachowiec 2021). Heat stress affects root development, stomatal movement, pollen development, photosynthesis, osmolyte accumulation, and curtailing ROS accumulation. Various phytohormones released by heat stress regulate the abovementioned physiological processes and help cereals to adapt to heat stress (Sakata et al. 2010; Li et al. 2014; Wu et al. 2017; Jegadeesan et al. 2018; Rezaul et al. 2019; Raza et al. 2020; Kothari and Lachowiec 2021). Changes in auxin biosynthesis gene(s) and exogenous supplementation of auxin have resulted in mitigating the negative effects of heat stress on rice (Zhang et al. 2018; Wu et al. 2019). Activating the antioxidant system, protecting photosynthetic apparatus, or maintaining stay green and delayed senescence during heat stress have been attributed to CTKs (Zavaleta-Mancera et al. 2007). Heat stress prevented CTK transport from roots to shoots of rice plants due to the enhanced activity of CTK oxidase/dehydrogenase (Wu et al. 2017). Cheikh and Jones (1994) reported that improved heat stress tolerance of plants could be attributed to the balance between ABA and CTKs. In an interesting study, Zhang et al. (2017) found that exogenously applied melatonin significantly ameliorated the perennial ryegrass under heat stress by increasing CTKs biosynthesis and restricting ABA biosynthesis. Noticeably, the mechanism by which ABA regulates plant water status is due to regulating stomatal aperture closure during water stress (Daszkowska-Golec and Szarejko 2013). However, the mechanistic role of ABA in contributing to heat stress tolerance in cereals must be further addressed in the future (Zhang et al. 2017). Supplementation of heat-stressed plants with ABA also enhanced their resistance via producing various proteins and osmolytes (Robertson et al. 1994). The increased activity of ascorbate peroxidase and multiprotein bridging factor 1 proteins resulted in an enhanced tolerance of plants against heat stress, which was due to increased ABA levels (Zandalinas et al. 2016). Enhanced levels of ABA in plants result in enhanced tolerance against heat stress by enhancing H_2O_2 activity and activating the antioxidant system (Li et al. 2014; Rezaul et al. 2019). Induced heat stress tolerance in plants mediated by GA_3 was due to enhanced invertase activities which resulted in an increased grain skin activity (Asthir and Bhatia 2014). Barba-Espin et al. (2014) reported that α-amylase biosynthesis was not influenced by heat stress during barley seed germination, but treatment with GA_3 resulted in cell death of GA_3-induced aleurone layers and was correlated with higher endogenous H_2O_2 and lipid peroxidation. For the first time, Wilen et al. (1995) reported the involvement of brassinosteroids (BR) in inducing high temperature tolerance. The application of BRs to heat stressed plants resulted in enhanced chlorophyll content, photosynthetic activity, stomatal conductivity, and filled seed numbers (Thussagunpanit et al. 2015). BR-mediated regulation of heat tolerance in plants is due to improved photosynthetic efficiency by maximizing the carboxylation rate of Rubisco, improved the efficiency of photosystem II photochemistry, enhanced chlorophyll content, stomatal conductivity, membrane stability, and proline content, reduced lipid peroxidation, activated antioxidant mechanisms, and maintained redox homeostasis (Cao and Zhao 2008; Ogweno et al. 2010; Hayat et al. 2010; Kaur et al. 2018; Kaya et al. 2019). Chlorophyll content, photosynthesis, and photochemical activity of PSI under high-temperature stress are also improved following exogenously applied BRs (Zhang et al. 2014). BRs minimize ROS activity and maintain plant cellular redox homeostasis by activating antioxidant and glyoxalase mechanisms under heat stress (Hussain et al. 2019). Divi et al. (2010) reported that the alleviation of heat stress in plants may be due to the crosstalk of BRs with MeJA, ABA, ET, and SA signaling pathways. Activating antioxidant mechanisms, accumulating osmoprotectants, and inducing excessive H_2O_2 generation have been reported that might be due to SA under heat stress (Wang et al. 2014; Kohli et al. 2018; Kaya et al. 2020). The alleviative effect of SA on heat stress has been reported by Khan et al. (2013). This action of SA takes place through its effect on increasing chlorophyll, improving photosynthesis, activating nitrogen assimilation, and increasing proline content. Exogenous applied SA results in improved photosynthetic activity of plants by improving net photosynthesis rate, Rubisco and PSII efficiency, soluble protein, and sugar content. The positive effects of SA on the abovementioned physiological processes ultimately increase resistance to heat tolerance (Kousar et al. 2018; Galani et al. 2016; Pirnajmedin et al. 2020; Wassie et al. 2020). SA mitigates the negative effect of heat stress by activating the antioxidant defense system in various plant species (Li 2015; Khanna et al. 2016; Zhang et al. 2017; Janda et al. 2020). Proline, betaine, and trehalose accumulation and enhanced antioxidant activity in plant crops under heat stress have also been attributed to the synergistic effect of SA and H_2S (Li 2015; Li et al. 2015). Strigolactones (SLs) are a group of terpenoid lactones boosting abiotic stresses such as heat stress tolerance by improving antioxidant defense system, plant architecture, mainly shoot branching and mesocotyl, hypocotyl, internode, and root elongation (Jia et al. 2014; Van Ha et al. 2014; Hu et al. 2018; Sharifi and Shirani Bidabadi 2020; Shirani Bidabadi and Sharifi 2021). Exogenously applied SLs have been reported to boost root elongation through the up-regulation of cell division and cell-cycle-related genes including PCNA, CycD2, and CDKB, and down-regulation of the auxin receptor TIR1 gene and transport genes including PIN1, PIN2, and PIN5 to plants, leading to regulated heat stress tolerance (Hu et al. 2018). Supplementation with MeJA in heat-stressed plants resulted in a reduced electrolyte leakage in stressed cells (Clarke et al. 2009). The positive effects of MeJA on mitigating heat stress in plants have been attributed to the enhanced activity of cell-cycle-related genes and diminished activity of auxin transport-related genes (Hu et al. 2019). High temperatures significantly reduce the biosynthesis, transport, and signaling of IAA related genes in cereals, leading to decreased levels of auxin, which in turn leads to changes in the morphological and physiological changes of vegetative and reproductive organs and sterility of spikelets (Gupta et al. 2017; Sharma et al. 2018). Although much research has been done so far on hormonal regulations in plants under temperature stress, extensive future research on the contribution of phytohormones to heat stress tolerance could advance our understanding of the mechanistic role of phytohormones, especially newly discovered ones, in heat stress tolerance in plants.

14.6 Concluding Remarks

Temperature stress has created many restrictions on the growth and development of plants and caused great concern for global food security (Wahid et al. 2007). Among all the solutions studied for the development and introduction of heat-resistant plant crops, the role of plant hormones in mitigating the negative effect of heat stress is noteworthy. Exogenously applied phytohormones could boost plant performance by regulating important physiological processes such as photosynthesis by detracting from photoinhibition, lowering lipid peroxidation, and activating the antioxidant defense system under heat stress (Sharma et al. 2019). However, the molecular mechanisms by which phytohormones contribute to physiological adaptations in plants, such as reducing oxidative stress under temperatures, need greater attention. Phytohormones control different physiological regulatory pathways and processes related to temperature stress. Phytohormones can also activate the signaling of the various regulatory gene(s) under temperature stress. Interaction among phytohormones also plays a critical role in regulating the temperature response in plants; however, understanding the complete molecular mechanisms under which phytohormones regulate temperature tolerance remains unclear. As the role of phytohormone signaling and crosstalk in regulating plant growth in response to temperature stress is complicated, it is also worth further investigation. Furthermore, the ingestion of regulatory genes that are activated by phytohormones in response to temperature stress needs further research.

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Cereals and Phytohormones Under Heavy Metal Stress

15

Ishta Bhardwaj and Neera Garg

Abstract

This book chapter addresses the contribution of phytohormones in the moderation of heavy metal (HM) stress in cereal crops. Cereals like rice, wheat, rye, corn, barley, oat, and millet are stapled foods in different areas around the world, contributing to about half of human energy necessities. HMs such as Fe, Mn, Co, Cu, Ni, Zn, Cd, Hg, and As are accrued in soils for a long time via sewage disposal and industrial waste. Though some of them are essential micronutrients accountable for many steady processes in plants, however, their excess can have deleterious effects and can directly impact the growth, physiology, and metabolism of the plant. The central defense system stimulates the signalling actions, dependent on the type of metalloid stress, which further leads to cascade events, involving activation of kinases and production of reactive oxygen species along with the accumulation of phytohormones. Phytohormones are chemical messengers imparting tolerance to HM stress in plants, letting them sustain healthy growth and progressive developments in the life cycle. The well-designed phytohormone signalling systems and their cross-talk with each other render them perfect candidates for facilitating defense responses. Moreover, their exogenic supplementation along with alteration of the endogenic concentrations via specifically aiming at their biosynthetic and signalling machineries is an effective method of imparting defensive safeguards to cereal crops in order to tolerate stressful environments. Henceforth, the present book chapter primarily analyses the concrete advances in the contributions of plant hormones to the moderation of metal/metalloid stress in cereal crops.

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Cereals · Phytohormones · Heavy metals · Signalling · Defense systems

15.1 Introduction

Cereals are the chief suppliers to global food demand, fulfilling more than half of the whole human calorie necessities and the sustainable accessibility of good value cereal grains is a crucial step to mention the highly important issue of food security. Agronomic crops, mainly cereals (*Triticum aestivum*, *Zea mays*, *Oryza sativ*a, *Hordeum vulgare, Avena sativa, Sorghum bicolor,* etc.), are cultivated in a large area, and their exposure to heavy metal (HM) stress results in numerous physiological, biochemical, and molecular changes, subsequently triggering oxidative injury and interfering with the usual metabolic functions (Basu and Rabara 2017). Currently, metal(loid) (Cd, Cu, Cr, Fe, Ni, Pb, Zn, As, Sb) accumulation is one of the most serious environmental concerns owing to their toxicity to crops and subsequently pose risk to humans. Since this chapter is dedicated to the role of phytohormones in cereal crops under HMs pollution, it is worth noting that few metals are essential for the growth of plants, but within reasonable limitations, because their high dosages are reported to be injurious. HMs are reported to negatively affect the cell membrane permeability, biosynthesis of organic compounds, and growth and developmental parameters of cereals, which ultimately lead to lowered genetic potential and decreased yield (Munzuroglu and Geckil 2002).

Two main strategies imparted by plants to tolerate (HM) stress are avoidance and tolerance. The earlier strategy involves exclusion and chelation of HMs with proteins containing sulfhydryl (–SH) groups, accretion of amino acids, and compartmentalization, which are going to hinder the uptake of heavy metals. However, the synthesis and stimulation of antioxidative defense response (enzymatic and non-enzymatic) and increased transcription of genes combating stress are included in the tolerance mechanisms (Hall 2002). The avoidance mechanisms are preferred by plants over tolerance mechanisms to alleviate HM stress. Perception of stress signals and their transduction in a synchronized manner involves the participation of plant hormones, that is, phytohormones. Identification and depiction of the pathways behind the HM stress tolerance imparted by phytohormones have been employed with the help of diverse scientific tools such as screening of mutants, proteomics, microarray analysis, and bioinformatics.

15.1.1 Importance of Phytohormones in Cereals Under HM Stress

Phytohormones comprise a broad spectrum of signalling molecules found in minute concentrations, performing central roles by easing growth and developmental processes, evolving sink and source relations and also guiding different signal

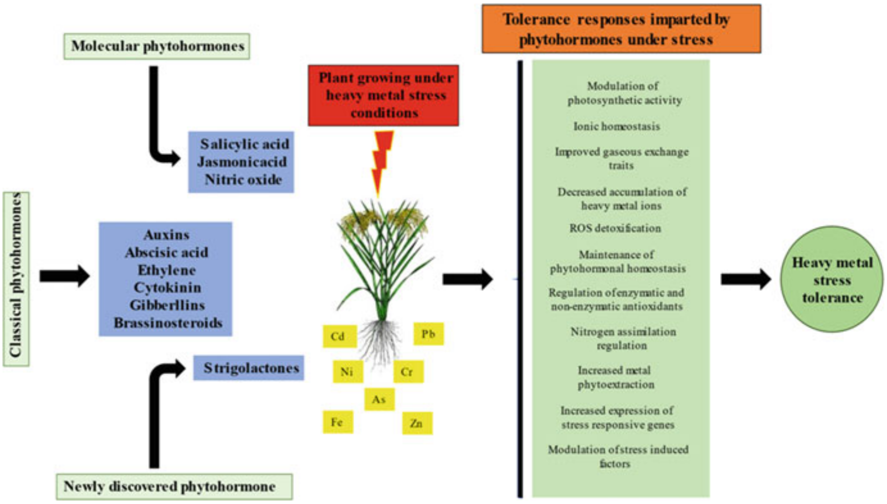

Fig. 15.1 Phytohormones facilitated heavy metal stress tolerance in plants

transduction pathways, allowing the plant to acclimatize under different environmental stresses (Wani et al. 2016).

Phytohormones are going to either act locally at the site of their synthesis or be transported to another location in plants, having an impact on practically every facet of growth and development. However, the mechanism of action is going to differ from hormone to hormone. It has been reported that sometimes a solitary hormone is regulating multiple processes at a time and sometimes multiple hormones are regulating a single process through cumulative actions. There are mainly three classes of phytohormones: (1) classical phytohormones (auxin (AUX), ethylene (ET), cytokinin (CK), gibberellins (GA), abscisic acid (ABA), brassinosteroids), (2) molecular phytohormones (salicylic acid (SA), jasmonates (JAs), nitric oxide (NO)), and (3) newly discovered strigolactones (Fig. 15.1) (Smith and Li 2014). Different stages of plant life are controlled by phytohormones and are considered vital for plants to withstand heavy metal stress.

Recently, environmental and biological scientists are developing various potential strategies and alternatives to mitigate the hostile effects of heavy metal pollution in agronomic systems in order to satisfy the worldwide demand for food. Amongst them, the exogenous application of phytohormones is a promising technique for modifying the developmental patterns in plants and helping them to re-establish land polluted by contaminants in agronomical crop management practices (Piotrowska-Niczyporuk et al. 2012). However, adequate evidence regarding the exact participation of phytohormones in modifying the functioning of HM stress receptive signalling mechanisms is not available. In this context, the current chapter primarily evaluates the main conceptual progress on the interactions/roles of phytohormones in HM stress mitigation in cereal crops and their future prospects.

15.2 Classical Phytohormones Under Heavy Metal Stress

15.2.1 Auxins

Auxins (AUX) are a commonly found, versatile signalling molecule and phytohormone that plays critical functions in the majority of the preliminary growth facets of plant life. AUX synthesis occurs in the meristematic regions of the roots, shoot, and newly developing leaves and is then further mobilized over longer distances to different segments of the plants (Jiang et al. 2021). Auxin is typically produced by a tryptophan (Trp)-dependent pathway which has determinedly recognized the role of L-tryptophan (Trp)-an aromatic amino acid acting as the pioneer of AUX synthesis. However, the Trp-independent pathway for auxin synthesis was discovered after concluding that the mutant defectives in Trp-synthesis were still synthesizing auxins and it was later proposed that the Trp-independent IAA production was facilitated by cytosolic indole synthase (INS) through the production of indole from indole-3-glycerol-phosphate (Wang et al. 2015). The IPyA pathway has been recognized as the principal route for IAA production in cereal crops, where Trp is firstly deaminated to IPyA by TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1 (TAA1) proteins. YUCCA flavin-comprising monooxygenases, is the main enzyme, catalysing the crucial step involving the decarboxylation of IPyA into indole-3-acetic acid (IAA). The chief naturally occurring forms of AUX in plants are IAA, indole-3-butyric acid (IBA), 4-chloroindole-3-acetic acid, and phenylacetic acid (PAA) (Ludwig-Müller 2011). However, the biosynthetic content of auxins is modified in plants by reversible and irreversible couplings to sugars, amino acids, peptides, and proteins. These couplings of auxins are quite impressive in altering the bioactive hormone pool in plants under diverse environmental stresses.

In addition to the de novo biosyntheses of free IAA, it can also be formed as a result of release from coupled forms (loaded pool) or IBA by peroxisomal β-oxidation. The accessibility and accretion of bioactive auxin in cells are crucial for generating an auxin gradient which is regulated by transport of AUX through phloem transport which is a non-directional, extended transport along with cell-to-cell carriage systems over a short distance with a slow and directional flow (Zažímalová et al. 2010). Auxin curbs metalloid stress by controlling the formation of reactive nitrogen and oxygen species in several subcellular sections of root cells such as peroxisomes, plastids, cytoplasm, and mitochondria, and also increases the activity of antioxidative enzymes (Piacentini et al. 2020). On coming in contact with harmful concentrations of metalloids, the appropriate content of auxin is sustained through realteration of the active pool either by inactivation/degradation or by transport to long distances for improved flexibility during hostile conditions. Praveen and Gupta (2018) reported changed regulation of genes involved in AUX synthesis and circulation in rice when exposed to arsenic (As) stress, which led to reformed root system morphology. As has destructively affected the regulation of LAX3, YUC6, and PIN1, leading to diminished synthesis and localization of AUX, which has subsequently resulted in the uneven quiescent centre (QC) and abnormal

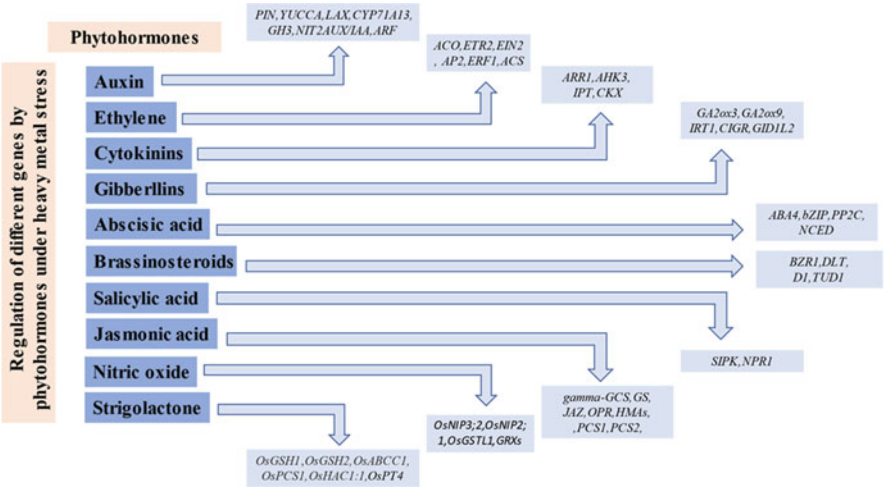

Fig. 15.2 Schematic representation of genes/proteins involved in phytohormonal responses to heavy metal stress conditions. Auxin (PIN: pin-formed; YUCCA: YUCCA flavin monooxygenases;; LAX: like-AUX1; CYP71A13: cytochrome P450 monooxygenase 71A13; GH3: gretchen hagen 3; NIT2: nitrilase 2; AUX/IAA: auxin/indole-3-acetic Acid ARF: auxin response factors), ethylene (ACO: 1-amino-cyclopropane-1-carboxylate oxidase; ETR2: ethylene receptor 2; EIN2: ethylene-insensitive 2; AP2: apetala 2; ERF1: ethylene response factor1; ACS: 1-aminocyclopropane-1-carboxylate synthase), cytokinins (ARR: arabidopsis response regulator; AHK3: arabidopsis histidine kinases 3; IPT: isopentyl transferase; CKX: cytokinin oxidase), gibberellins (GA2ox: gibberellin-2-oxidase; IRT1: iron-regulated transporter 1; CIGR: chitin-inducible gibberellin-responsive; GID1L2: gibberellin insensitive dwarf1 L2), abscisic acid (ABA4: abscisic acid-deficient 4; bZIP: basic leucine zipper; PP2C: protein phosphatase 2 C; NCED: 9-cis-epoxycarotenoid dioxygenase), brassinosteroids (BZR1: brassinazole resistant 1; DLT: dwarf and low-tillering; D1: Dwarf 1; TUD1: taihu dwarf 1), salicylic acid (SIPK: salicylic acid-induced protein kinase; NPR1: nonexpressor of pathogenesis-related genes1), jasmonic acid (gamma-GCS: gamma-glutamylcysteine synthetase; GS: glutathione synthetase; JAZ: jasmonate ZIM-domain; OPR: 12-oxophytodienoic acid reductase 3; PCS: phytochelatin synthetase), nitric oxide (OsNIP: nodulin 26-like intrinsic; OsGSTL1: glutathione S-transferases; GRXs: glutaredoxins) strigolactone (OsGSH1:γ-glutamyl cysteine synthetase 1; OsABCC1: ATP-binding cassette (ABC) transporter; OsPCS1: phytochelatin synthase 1; OsHAC1;1: high arsenate content 1; OsPT: phosphate-transporters)

root growth. Moreover, Pacenza et al. (2021) reported an improved biosynthetic pathway of auxin via enhanced expression of biosynthetic genes along with diminished expression of genes like (AUX/IAA, GH3.3, NIT2, CYP71A13) (Fig. 15.2) responsible for auxin methylation, conjugation, and suppression of signalling pathways and ultimately lessened Cd noxiousness. Furthermore, selenium has been reported to ameliorate As toxicity in *Oryza sativa* through the improved expression of IAA31, IAA14, and SAUR genes, which are associated with the synthesis of auxin (Chauhan et al. 2020). A specific class of bacteria, which comprises a varied range of rhizobacteria/fungi, is well recognized to quicken the method of plant-assisted remediation, resulting in improved growth and enhanced tolerance of plants to heavy metal/metalloid stress. Likewise, when bacterial strain *Brevundimonas diminuta* was introduced in As(V) contaminated soil, it significantly abridged As buildup in the shoot particularly in the edible part of rice (Singh et al. 2021). In another report, exogenously introduced IAA synthesizing *Bacillus flexus* significantly decreased absorption of As by roots to the above-ground portions and its accretion in rice grains under As stress (Das et al. 2017). Consequently, AUX-producing as well as As-oxidizing rhizobacteria/fungi possess the ability to ameliorate As stress in paddies and act as soil-inoculants. However, the thorough comprehension of the crucial systems modifying the interaction between AUX equilibrium and HM stress is still missing and needs supplementary investigation.

15.2.2 Ethylene

Ethylene (ET) being a gaseous phytohormone rapidly diffuses from the site of its synthesis and is identified as a crucial hormone required in diverse plant metabolic processes such as flower ripening, germination, pollination, leaf abscission, epinasty stimulation, and gravitropism as well as responses to several stresses. Under HM stress circumstances, there is diminished growth of plants along with a quick surge in ET synthesis, suggesting a major contribution of this phytohormone in plant responses to HM toxicity (Bücker-Neto et al. 2017). The ethylene biosynthetic route is comparatively simple, involving only two dedicated enzymatic steps in which the first one is catalyzed by the enzyme ACC synthase (ACS), converting *S*-adenosyl-l-methionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC) and 5′-methylthioadenosine (MTA). Then the second step involves the conversion of ACC to ethylene, CO_2, and cyanide, under the influence of the enzyme ACC oxidase (ACO) (Ververidis and John 1991). The deadly side-product cyanide is quickly converted to β-cyanoalanine through a set of β-cyanoalanine synthases (Yip and Yang 1988). Since ACO and ACS are the only two enzymes devoted to ethylene synthesis, that's why the majority of the modulation of ethylene synthesis arises by altering the translation and protein fidelity of these dual enzymes belonging to multigene families (Booker and DeLong 2015). Moreover, metabolic control of ethylene synthesis is attained by ACC balancing, which includes biosynthesis of ACC, its transport and conjugation. It has been proposed that Cd could be the most phytotoxic inorganic ion able to excite ethylene synthesis by plants. Cadmium-persuaded upsurges in ethylene production were detected in *Hordeum vulgare* (Vassilev et al. 2004), *Triticum aestivum* (Khan et al. 2015). Chromium Cr (VI) toxicity leads to induction of oxidative stress and elevation in lipid peroxidation, which is identified as a major concern for the growth of seedlings in rice (Zeng et al. 2012). On the basis of transcriptomic profiles of rice seedling roots obtained after 1 and 3 h of application of Cr (VI), increased biosynthesis, and signalling of ethylene through elevated expression of genes (ACS2, ACS1, ACO5, ACO4, EIN4, AP2) (Fig. 15.2), vesicle trafficking and modulation of reactive oxygen species (ROS) levels were identified as a part of the ethylene-induced Cr tolerance pathway (Trinh et al. 2014).

Cd-induced expression of several ethylene response factors (ERF) genes in *Oryza sativa* directs the specificity of ERF proteins towards various genes which are produced as a consequence of different Cd levels (Thapa et al. 2012). It has been verified that the diminished expression of stress-related transcriptional factors (dehydration responsive element binding) DREB in ethylene pathway can play a chief role in directing stress-perceiving genes during Cd-stress in roots (Nakashima and Yamaguchi-Shinozaki 2006). This finding proposed that the decreased expression of DREBs reduced the influx of heavy metal-polluted water and permitted the conservation of cellular potential by overloading the metal ions into vesicles to avoid toxic effects. Likewise, (Cao et al. 2014) proposed that Cd tolerance in *H. vulgare* is linked to the higher potential of ethylene signalling via normal working of the cell wall and proteins related to the defense system. However, the exogenous supplementation of ethylene precursor ACC has been reported to negatively regulate the efflux of malate ions from the roots of wheat under Al stress. Malate ions form extracellular complexes with Al, explaining the mechanism behind increased Al tolerance in ethylene-insensitive genotypes (Tian et al. 2014). Therefore, the possible benefits of ethylene being able to lessen the growth of roots and shoots under heavy metal stress must be looked at while reviewing the results. Henceforth, the above-mentioned reports establish a link between ethylene and the plant's HM sensitivity along with the tolerance mechanisms induced by the hormone.

15.2.3 Cytokinins

Cytokinins (CKs) are a class of adenine-derived phytohormones, comprising different molecular structures, including cytokinin derivatives such as isopentenyl adenine (iP), (cZ) cis-zeatin and (tZ) trans-zeatin (Li et al. 2021). CK has well-identified roles at cellular levels like cell division and growth, chloroplast biogenesis, promotion of photosynthesis, improvement of sink strength, and development of vegetative and reproductive organs. Besides the multifunctional roles of CKs, it has been proposed that the variations in the content of hormones during environmental stress conditions must be playing an effective part in the course of adaptation of the plant to adverse conditions. However, different studies reported the adverse role of CKs in plants' acclimation to several stresses (Zwack and Rashotte 2015), proposing that the decreased contents of CK are required for the advances in plant tolerance to abiotic stress in certain cases. The biosynthetic pathway of CKs starts with the inclusion of a prenyl group which is a derivative of dimethylallyl diphosphate to ADP/ATP at N^6 position, and this reaction is conducted by an isopentenyl transferase (IPT) enzyme (Sakakibara 2006). The resultant iP ribotides are further transformed into *t*Z-type CKs through hydroxylation of the lateral chain of isoprenoid, and the reaction is catalyzed by the cytochrome P450 enzyme. However, the formation of *t*Z-type cytokinins has been reported to play a significant role via enhancing shoot expansions in *Arabidopsis* (Kiba et al. 2013). The active forms of CKs are derived from ribotides only through one step conducted by cytokinin nucleoside 5′-monophosphate phosphoribo-hydrolases of the LONELY GUY (LOG) family

(Kuroha et al. 2009). Moreover, (Werner et al. 2006) identified that the status of bioactive CKs could be modified through coupling to sugars (frequently to glucose) via permanent partition by cytokinin oxidases (CKXs). The signalling of CK is a multistep-phosphorelay pathway involving the transmission of stress signals via targeting genes such as AHK4, AHK1, AHK3, and AHK2 (Fig. 15.2) in plants (El-Showk et al. 2013).

CKs are regulatory molecules that have been reported to impart tolerance to heavy metals through diverse signalling pathways, and the defensive role of artificial CKs is ascribed to the presence of a kinetin group in its molecular (Hönig et al. 2018). Exogenously applied synthetic cytokinin thidiazuron and analog of natural cytokinin i.e. kinetin has been reported to impart significant resistance to Ni and Zn stress in maize seedlings through enhanced activity of ascorbate peroxidase (APO) enzyme (Lukatkin et al. 2007). In another report, exogenously supplemented thidiazuron significantly improved the growth patterns and decreased the lipid peroxidation rate in the seedlings of *Triticum* when subjected to Ni and Zn stress (Sazanova et al. 2012). In a recent report, the inoculation with *Bacillus toyonensis* strain Bt04 resulted in enhanced growth and root development in maize through increased synthesis of cytokinins under aluminium stress (Zerrouk et al. 2020).

One of the major mechanisms imparted by CKs under heavy metal stress environments is to decrease the amount of hormone to improve the overall efficiency of the plant to manage the stress (Kohli et al. 2013). It was discovered in a study exploring the consequences of endogenous CKs in *Arabidopsis thaliana* under arsenic stress that the diminished CK signalling and the CK-synthesizing mutant plants displayed augmented tolerance to arsenic (Mohan et al. 2016). Similarly, (Veselov et al. 2003) reported degradation in the level of CK in Cd-stressed wheat plants through the induced expression of CK catabolic enzyme i.e. CK oxidase. Hence, the precise functioning of CKs in HM stress regulation is, however, unclear and requires more clarification of different parameters at the genetic and molecular levels, especially in cereals.

15.2.4 Gibberellins

Gibberellins (GAs) are a group of tetracyclic diterpenoids and were initially isolated from the metabolic outcomes of fungi, *Gibberella fujikuroi*, in the rice plant (Santner and Estelle 2009). GAs play a pivotal role in seed germination, stem elongation, flowering, pollen maturation, leaf expansion, growth and development, dormancy, sex expression, senescence of fruit, and enzyme induction for hormonal balancing (Hyun et al. 2016). The outcomes of different studies validate that GAs are chiefly aimed at stress-brought changes in growth-linked developments in cereal crops.

However, most of them are not considered active hormones. Only a few groups of Gas, counting GA3, GA1, and GA4, function as bioactive particles in plants. GAs are generally synthesized by the methylerythritol phosphate (MEP) pathway in which (GGDP) trans-geranylgeranyl diphosphate is transformed into the biologically active form of GAs (Hedden and Thomas 2012). GGDP (20-carbons) (precursor for the synthesis of GAs) is going to be formed as a result of the condensation of isopentenyl pyrophosphate (IPP) in plastids. Further, they are modified in the endoplasmic reticulum and cytosol and are then converted into functionally active forms. The conversion of GGDP to GAs involves the participation of the following enzymes: cytochrome P450 monooxygenases, terpene synthases (TPSs), and 2-oxoglutarate-dependent dioxygenases (2ODDs). Furthermore, a group of genes regulating the biosynthesis of GAs is GA20ox (GA 20-oxidase), GA3ox (GA3-oxidase), and GA2ox (GA2-oxidase). Amongst them, GA2ox has been tested to be taking part in plant responses to abiotic stress (Colebrook et al. 2014). However, nuclear DELLA protein which is a transcriptional regular acts as a potent suppressor of GA-mediated responses and is characterized as the most important component activated in response to abiotic stress. DELLA limits the plant growth, whereas GA-fortified signal promotes the development by minimalizing DELLA-triggered progress constraints in growth (Sharan et al. 2017). Recently, two GA transporters (SWEET13/14 proteins and nitrate transporter 1/peptide transporter family) taking part in facilitating the distribution and extended transport of GA have been identified (Kanno et al. 2016).

GAs are vital phytohormones that have been well studied for their impact on physiological and anatomical parameters under stress conditions. Amri et al. (2016) reported that the exogenous supplementation of GA3 (0.5 μM) enhanced the activity of 4 hydrolytic enzymes (acid and alkaline phosphatase, α- and β-amylase) in Cd and Molybdenum (Mo) stressed Barley. Elevated activity of these enzymes increased the content of free sugars and amino acids, restoring the mobilization of starch and protein reserves to roots during germination. Moreover, enhanced concentrations of GAs have been reported in rice under As stress due to the upregulation of genes GA2ox3, GA2ox9 (Huang et al. 2012). Another study reported the impact of Cu stress on growth, root hormone balances, nutrient composition, and protein modifications in the roots of pre-evolving maize seedlings. Cu exposure caused oxidative impairment and changed root hormonal balance with a sharp decrease in the concentration of gibberellins, particularly at the tip of the root, primarily inhibiting root growth (Matayoshi et al. 2020). Furthermore, a current experiment on arsenic-stressed rice plants reported modulated expression of diverse signalling genes of GA such as GA20ox, GA2ox, chitin-inducible gibberellin-responsive (CIGR) and gibberellin insensitive dwarf1 L2 (GID1L2) (Fig. 15.2) (Di et al. 2021). It is quite evident that HM stress is affecting the biosynthesis and signalling of GA in plants. However, further studies are essential to find out a definite relationship between endogenic GA content and HM stress resistance in plants at the molecular and genetic levels.

15.2.5 Abscisic Acid (ABA)

ABA is a dynamic plant hormone that controls numerous growth phases in cereal crops and is mainly associated with plants' adaptations to abiotic stresses (Chen et al. 2020). The core components of biosynthesis, modulation, and downstream signalling response of ABA have been identified through various biochemical, molecular, and genetic methods mainly in *Arabidopsis* (Cai et al. 2017). ABA is a sesquiterpene-derived carotenoid having 15 carbon atoms which is produced in plastids. ABA is reported to be synthesized in plants as well as in some of the phytopathogenic fungi with the help of two different routes. In phytopathogenic fungi, ABA is synthesized via mevalonate pathways with intermediates having no more than 15 carbons, also known as the direct pathway (Takino et al. 2019). Plants follow the indirect pathway which is initiated by the cleavage of the C_{40} precursor (β-carotene) into zeaxanthin followed by the synthesis of cis-isomers of neoxanthin and violaxanthin. Then neoxanthin and violaxanthin both are oxidatively cleaved into xanthoxin (C-15), which is transferred from plastids to the cytoplasm and finally transformed into ABA.

The different steps of biosynthetic pathways are catalyzed by multiple enzymes including β-carotene hydroxylases, zeaxanthin epoxidase, abscisic aldehyde oxidases, 9-cis-epoxycarotenoid dioxygenase, short-chain alcohol reductases, and molybdenum cofactor sulfurase. Under stress conditions, the increase in de novo ABA biosynthesis through the strong expression of ABA biosynthetic genes OsNCED3 and OsNCED2 and also the upregulation of ABA signalling genes (ABA4 and NCED) have been reported, suggesting an involvement of this phytohormone in the induction of protective mechanisms against heavy metal toxicity. Three main pathways triggered by ABA in the detoxification of toxic metals and metalloids include inhibition of uptake, alterations in the transportation rate, and promotion of coupling with chelators. Numerous transcription factors imparting Al tolerance in rice have been characterized such as Al resistance transcription factor (ART1), abscisic acid stress and ripening 5 (ASR5), and WRKY22 (Arenhart et al. 2014). ART1 is a Cys2His2-type zinc finger transcription factor regulating more than 30 genes taking part in both internal and external decontamination of Al where the accumulation of heavy metal in roots is the most selective response to metal toxicity (Che et al. 2018). In another report, rice plants exposed to As stress resulted in the boosted biosynthetic and signalling pathways of ABA through the modulated expression of genes like NCED3, NCED2, PP2C4, ABA4, bZIP10, and PP2C5 (Fig. 15.2) (Huang et al. 2012).

Hsu and Kao (2003) established a clear constructive correlation between the endogenic ABA content and Cd tolerance when ABA was synthesized more significantly in the roots and shoots of Cd-resistant rice varieties than in the sensitive ones. Xylem loading is a restraining step for the accretion of metal ions in shoots, and the action is principally reliant on transpiration movement which is reported to be hindered by exogenous supplementation of ABA (Deng et al. 2021). ABA has an innate effect on root hydraulic conduction that supports the downhill passage of metals in the cortical tissues of roots (Olaetxea et al. 2015). Silicon has been reported to modulate the levels of ABA in plants under stress conditions. In a study, Kim et al. (2014) observed that Si enhanced the growth of rice (*Oryza sativa*) plants and abridged the poisonous effects of Cd/Cu through modulation of ABA phytohormones involved in response to stress. Hence, ABA is indisputably playing a major part in mitigating HM stress, and further investigations are still needed to elucidate the communication systems between ABA and HM stress.

15.2.6 Brassinosteroids

Brassinosteroids (BRs) are endogenous plant steroidal hormones and were first isolated from *Brassica napus* pollen. BRs are poly-hydroxylated steroids having a key role in a wide spectrum of plant growth progressions such as cell division, elongation, vascular differentiation, photomorphogenesis, etc. and also functioning as principal switches in activating the stress-mitigation responses to deadly environmental situations. BRs are derivatives of 5α-cholestane present in all parts of the plants with the highest concentration in the seeds and pollen grains. The biosynthesis of BR follows a triterpenoid pathway, where triterpene squalene is going to be cyclized into cycloartenol and the reactions are being catalyzed by specific enzymatic machinery. The biosynthetic pathway begins with the four successive hydroxylation steps reducing campesterol into campesterol, followed by two similar routes counting the initial C-6 and late C-6 oxidation pathways (Noguchi et al. 1999). In the early C-6 pathway, the hydroxylation of campestanol yields teasterone, which is further epimerized to yield typhasterol. Typhasterol is further hydroxylated to yield castasterone, which is finally transformed into brassinolide (active brassinosteroid) (Noguchi et al. 1999). Similarly, in the late C-6 pathway, hydroxylation of campestanol yields 6-deoxoteasterone followed by epimerization to yield 6-oxotyphasterol. Finally, 6-oxotyphasterol is hydroxylated to yield castasterone, which is further changed into brassinolide. During a signalling cascade, BRs bind to the receptors on the cell where the signal is perceived by surface receptors having leucine-rich repeat receptor kinases BRI1 (BRASSINOSTEROID INSENSITIVE1). BRI1 is going to bind as a coreceptor with BRI1 ASSOCIATED RECEPTOR KINASE1 (BAK1), which undergoes dephosphorylation-phosphorylation cascades and further regulates the expression of the intricate network of genes involved in biochemical and physiological processes under heavy metal stress (Belkhadir and Jaillais 2015). BRI1 is present on the plasma membrane stimulating the signalling chain reactions and upregulating the synthesis of transcription factors and ultimately enhancing the expression of BR genes (Nolan et al. 2020).

The exogenous application of BRs can indirectly or directly curb the harmful impacts of heavy metals through the deactivation of negative regulators of BR signalling at the molecular level, scavenging ROS generation and activating antioxidant defense enzymes superoxide dismutase, catalase, glutathione reductase, guaiacol peroxidase, glutathione reductase and glutathione-S-transferase (Divi and Krishna 2009). The active BRs, (EBL) 24-epibrassinolide and (HBL) 28-homobrassinolide, are components of plant-assisted remediation helping plants to eradicate noxious metalloid ions via reduced absorption of HMs by changing the permeability of the cell membrane and also by activating the production of stress-related proteins. The machinery behind amelioration of HMs' toxicity regulated by BRs includes (a) stimulation of H_2O_2 synthesis, (b) inhibition of reactive oxygen species production, (c) upregulating expression of MAPK, and (d) lessening toxicity by enhancing the content of potassium and sodium ions along with osmolytes (Rajewska et al. 2016).

Yusuf et al. (2011) reported that 0.01uM HBL proved to be effective in mitigating Ni stress in *Triticum aestivum* through upregulation of the antioxidant system. Few studies specified that NADPH oxidase significantly converted O^{2-} to H_2O_2 with the help of SOD in the plasma membrane cells, which subsequently enhanced H^{++} ATPase functioning (Jakubowska and Janicka 2017). Though the absorption of poisonous metalloids is damagingly affecting cell membranes through lipid peroxidation and protein oxidation, still, plant hormones like brassinosteroids boost antioxidative defense machinery, ameliorating this deadliness of HM stress along with restoring normal osmoregulation. 0.1 nM EBL has been reported to upregulate the expression of catalase (CAT), ascorbate peroxidase (APOX), and glutathione reductase (GR), thus providing metal tolerance capacity to rice seedlings under chromium stress (Sharma et al. 2017). However, different molecular experiments have acknowledged a wide range of crucial genes such as DLT, D1, and TUD1 (Fig. 15.2) playing a vital role in sustaining numerous architectural structures of rice which are controlled by BRs through stressful conditions (Zhang et al. 2014). Owing to their diverse functions, extensive research has been conducted to promote BR as essential plant growth regulators for modern agriculture. However, further experiments illuminating the expression of genes regulated by BR under HM stress must be conducted in order to detangle the intricate signalling network.

15.3 Molecular Phytohormones Under Heavy Metal Stress

15.3.1 Salicylic Acid

Salicylic acid (SA) is a multifunctional endogenous phenol derivative also known as ortho-hydroxybenzoic acid that serves as a key regulator of various physiological processes in plants such as photosynthesis, thermogenesis, flowering, defense responses to abiotic and biotic stress including systemic acquired resistance, and so on (Muthulakshmi and Lingakumar 2017). Chemically, SA is amongst a large group of phenolics found in both free and conjugated forms in plants. Conjugated forms are formed as a result of hydroxylation, glucosylation, and/or methylation of the aromatic ring (Maruri-López et al. 2019). The biosynthetic pathway of salicylic acid follows two routes: the phenylalanine route and the isochorismate route. The first pathway, phenylalanine route, begins in the cytosol with the transformation of phenylalanine (Phe) into trans-cinnamic (t-CA) acid under the influence of the enzyme phenylalanine ammonia-lyase (PAL). The oxidation of trans-cinnamic acid into benzoic acid is subsequently followed by the hydroxylation of the ring of benzoic acid, and the reaction being catalyzed by the enzyme benzoic-acid-2-hydroxylase (BA2H) ultimately yields SA. The existence of hydrogen peroxide (H_2O_2) is mandatory for the enzymatic conversion of benzoic acid into SA (Shine et al. 2016). The second route is known as the isochorismate (IC) pathway, which occurs in the chloroplast (Rekhter et al. 2019). Firstly, chorismate is changed into isochorismate by the enzyme isochorismate synthase (ICS). Subsequently, the enzyme isochorismate pyruvate lyase (IPL) catalyzes the conversion of isochorismate into salicylic acid. Recently conducted studies on *Arabidopsis thaliana* confirmed that approximately 90% of defense-related SA is produced from isochorismate, whereas only 10% is derived from the PAL pathway (Garcion et al. 2008).

SA is reported to stimulate stress-responsive genes, HSPs, chaperons, secondary metabolites, MAPK pathways and NPR1 (nonexpressor of pathogenesis-related1) (Fig. 15.2) (Jumali et al. 2011). NPR1 is vital for SA-facilitated transcriptional refunctioning in which it interacts with bZIP transcription factors (TFs) (An and Mou 2011). Exposure to Cd stress lessened chlorophyll contents, transpiration, and photosynthesis in rice. However, the supplementation of SA inverted these repressive effects by increasing chlorophyll synthesis, photosynthetic rate, and transpiration rate (Yotsova et al. 2018). Similarly, exogenous supplementation of SA was reported to inhibit the negative impacts of Cd toxicity on shoot height and biomass in maize (Gondor et al. 2016). Moreover, several manuscripts stated that SA can mitigate HM toxicity by affecting both their uptake and/or buildup in plant organs (Safari et al. 2019) as well as scavenging and/or decreasing the accumulation of reactive oxygen species and improving the antioxidant defense system (Wang et al. 2019), protecting the stability and integrity of membrane (Belkadhi et al. 2015), and interacting with other phytohormones (Tamás et al. 2015). Additionally, the ameliorative effects of SA lead to an upsurge of endogenous H_2S and NO accretions boosting glutathione renewal pathways including glutathione S-transferase, glutathione reductase, and actions of S-nitroso-glutathione reductase along with the glyoxalase system (Hediji et al. 2021). Exogenous application of SA improved physiological processes in wheat plants under lead stress by inhibiting Chl degradation and accumulation of malondialdehyde and further enhanced the activities of SOD, CAT, and POD along with the production of proline and total soluble sugars (Alamri et al. 2018). Increased concentration of SA was reported in the roots of wheat under Cd stress which was possibly due to the enhanced activity of the antioxidant and metal detoxification systems endorsing tolerance in wheat (Kovács et al. 2014). Similarly, the increase in SOD and APOX activity and the reduction in catalase activity were reported in maize when pre-treated with SA (Krantev et al. 2008). Exogenously provided SA, calcium, or magnesium mitigates Al toxicity in rice seedlings by controlling the uptake of Al, restoring the integrity of the root membrane, and regulating antioxidative enzyme functioning (Pandey et al. 2013). In another report, SA pretreatment repressed the translocation of Cu in maize seedlings and subsequently ameliorated oxidative stress by decreasing MnSODII activity accompanied by a decrease in H_2O_2 concentration (Moravcová et al. 2018). Moreover, Tajti et al. (2019) reported enhanced expression of the salicylic acid-induced protein kinase (SIPK) (Fig. 15.2) gene which has increased the endogenic concentrations of SA in *Triticum aestivum* under cadmium stress. Still, there is a gap in evidence regarding the exact role of alteration in the endogenic levels of SA in the mitigation of HM stress. Hence in the coming years, the thorough documentation of the molecular webs contributing to SA synthesis and signalling is a precondition to elucidating the mechanism of tolerance conveyed by SA against HM stress.

15.3.2 Nitric Oxide (NO)

NO is a multifunctional bioactive and extremely diffusible signalling phytohormone acting as a signal transducer in numerous physiological developmental processes of the plant, such as initiation of seed germination, reduction of seed dormancy, movement of stomata, floral regulation, functioning of the photosynthetic machinery, gravitropism, automated death of the cell, and providing resistance to numerous abiotic stresses (Fancy et al. 2017).

Approximately eight main reductive and oxidative pathways have been recognized in plants that are supposed to be followed up in NO biosynthesis. Reductive paths comprise nitrite reduction of (1) nitrate reductase (NR), (2) plasma membrane-bound nitrite:NO reductase, (3) cytochrome-c oxidase and/or reductase, (4) xanthine oxidoreductase (XOR), and (5) non-enzymatic reduction of nitrite under acidic situations, while oxidative paths comprise oxidation of (6) L-arginine by NOS-like enzyme, (7) hydroxylamine, and (8) polyamines (Asgher et al. 2017). However, the conversion of nitrate to nitrite by enzyme nitrate reductase (NR) followed by the synthesis of NO is catalyzed by NR on its own or through the electron transport chain in mitochondria and is considered the major reason behind NO production in crop plants in the absence of efficient NOS proteins (Gupta et al. 2011). NO controls several plant biological courses by amending proteins via post-translational modifications (PTMs) such as S-nitrosylation, nitrosylation, and nitration (Romero-Puertas and Sandalio 2016). NO-dependent signal transduction through S-nitrosylation of cysteine residues has emerged as a crucial mechanism behind the regulation of plant processes against oxidative stress, defense responses, and hormonal signalling (Freschi 2013). Furthermore, one more main PTM reliant on NO includes the binding of NO at the central position in metalloproteins, and the process is known as metal nitrosylation, leading to stimulation of cGMP and crucial midway components in numerous NO catalyzed processes (Pagnussat et al. 2002). However, increasing evidence indicates that the purpose of NO is to break the chain of antioxidant-arresting lipid peroxidative reactions to regulate plant redox balancing, which is a critical facet of abiotic stress tolerance (Wany and Gupta 2018).

In recent years, developing technics have confirmed that the exogenous application of NO might affect the build-up of metal ions to guard plants against HM stress. It is well recognized that NO can bring about the development of adventitious roots along with the accumulation of root biomass in rice seedlings treated with As, resulting in the dilution of metal ions content (Kushwaha et al. 2019). Likewise, (Singh et al. 2016) reported that external supplementation of NO decreased the content of As in root and shoot and controlled the metabolism of GSH to mitigate As stress in rice. Mostofa et al. (2015) reported diminished Cu accretion and oxidative injury caused by Cu in the presence of NO, subsequently resulting in the amelioration of Cu toxicity in rice. Moreover, a current study reported enhanced performance of antioxidant machinery in rice under As stress, through NO-induced tolerance mechanisms, mitigating the negative impacts of stress (Praveen and Gupta 2018). Another study stated that the exogenous application of NO augmented the in-situ levels of NO and simultaneously increased the activities of SOD, APX, CAT, and GR in a dose-dependent manner (Kaur et al. 2015). Similarly, (Rizwan et al. 2018) indicated that external supplementation of SNP modulated endogenous NO-mediated tolerance to Ni–stress in rice by limiting Ni accumulation, sustaining photosynthetic activity and decreasing oxidative damage through the improved antioxidant system in rice plants. A current study reported that the supply of melatonin in Pb-stressed maize could enhance the activity of antioxidant enzymes, in that way imparting tolerance to Pb toxicity, while cPTIO (which is an inhibitor of NO) can reverse the tolerance to Pb toxicity (Okant and Kaya 2019). This has proved that NO participated in melatonin-encouraged stimulation of antioxidant enzymes and the communication between melatonin and NO was beneficial for imparting the Pb resistance in maize. Moreover, (Singh et al. 2017) reported modulated transcriptional behaviour of stress-receptive genes such as glutaredoxins (GRXs), glutathione S-transferases (GSTs) and genes encoding (NIP-nodulin 26-like intrinsic aquaporin channels) (Fig. 15.2) as the main component of defense mechanisms imparted by NO in AS-stressed rice plants. Hence, these outcomes have significant implications for illuminating the changes at the molecular level imparted by NO to ameliorate HM stress-induced oxidative injury in cereal crops.

15.3.3 Jasmonates

Jasmonic acid (JA) is an oxylipin growth hormone meant for healthy growth of the plant and also regulates numerous generative processes like seed germination, elongation of root, pollination, fruit maturation, and senescence of plant and also acts as a stress modulator for abiotic stresses such as heat stress, drought, and salt and metal toxicity (Per et al. 2018). Jasmonates are byproducts of fatty acids, counting elementary composites like JA, methyl jasmonate (MeJA) and jasmonate iso-leucine conjugate (JA-Ile), whereas JA is identified as the best characterized and most abundant among them (Wang et al. 2020). Jasmonic acid, its biosynthetic pioneers and byproducts, mentioned as jasmonates (JAs), are vital molecules having a central core made of 3-oxo-2–20-cis-pentenyl-cyclopentane-1-acetic acid. Biosynthesis of JA primarily involves a consecutive lipid esterification path in chloroplast and peroxisomes, starting with chloroplastic galactolipids releasing α-linolenic acid (α-LeA). Enzyme lipoxygenase (LOX) carries out the oxygenation of α-LeA at the C-13 position, yielding hydroperoxy-9,11,15-octadecatrienoic acid (13–13-HPOT), which is further cyclized into cis-12-oxo-phytodienoic acid (OPDA), and the reaction being carried out by enzyme allene oxide synthase (Wasternack and Hause 2013). OPDA has lifted ATP-binding cassette transporter COMATOSE (CTS) from chloroplast to peroxisome followed by reduction to 12-oxophytoenoic acid under the influence of enzyme OPDA reductase and is further subjected to three successive β-oxidation cycles (Wasternack and Hause 2013). OPDA is acting as a pioneer of

LOX-facilitated biosynthesis of JA, which is broadly studied in tomato, *Arabidopsis* and tobacco (Yan et al. 2012).

It is supposed that there is a minimum of twelve metabolic routes transforming JA into inactive, moderately active and active compounds mainly via conjugation, carboxylation of amino acid, esterification, O-glycosylation, sulfation, hydroxylation, methylation, and decarboxylation laterally with the formation of 12-OH-JA derivatives in lactone (Ruan et al. 2019). JA-induced signalling includes the local perception of stress signals and transduction events followed by synthesis of JA and subsequent activation of a complex web of genes and proteins that are going to communicate with other hormones and ultimately lead to the activation of the defense system. JAs are reported to be vital in symbiotic arbuscular mycorrhiza interactions where their establishment in the roots of *Hordeum vulgare* results in the accretion of jasmonates and activates the plant defense system throughout the premature phases of development (Hause et al. 2002). In another report, up-regulation of different biosynthetic and signalling genes of JA has been found in rice under As stress (Huang et al. 2012). Exogenous supplementation of JA (10 μM) has been observed to ameliorate the negative impacts of Ni-treated plants through the amplified activity of antioxidant enzymes SOD, APX, CAT, GPX, and GR in *Zea mays* (Azeem 2018).

Besides the defensive functions of jasmonates, they have been very well characterized to efficaciously weaken the translation of metal ion transporter proteins and also aid as an intermediator to control phytochelatin synthesis (Sofy et al. 2020). Moreover, in a recent experiment, when the Pb-exposed rice plants were treated with (0.5 and 1 μM) MJ, it curbed the transcript levels of the heavy metal-transporting P1B ATPases (HMAs), ABCC1, PCS1, PCS2 (Fig. 15.2) genes and by this means limiting Pb in the roots and inhibiting its translocation to the above-ground parts of the plant (Salavati et al. 2021). Likewise, a current study points out the accumulation of JA in rice plants under As stress due to modulated transcript levels of genes (OPR; jasmonate ZIM-domain, JAZ, LOX; 12-oxophytodienoic acid reductase 3) taking part in JA signalling (Di et al. 2021). Therefore, the above-cited discoveries resolved the regulatory roles of jasmonates in HM stress management. However, supplementary investigation is mandatory to discover the unseen mechanisms contributing to JA facilitated HM stress tolerance.

15.4 Newly Discovered Phytohormones Under Heavy Metal Stress

15.4.1 Strigolactones

Strigolactones (SLs) as a class of newly identified phytohormones are derived from carotenoids, which were mainly recognized as signal molecules in the rhizosphere, participating in symbiotic interactions between plant roots and fungi (Marzec 2016). As a novel phytohormone, SLs are involved in adventitious root formation, regulation of architectural aspects of growth, senescence of leaf, reproductive maturity, and also being a major controller of a plant's reaction to several environmental stresses (Jia et al. 2018). SLs also function as a promoter of numerous ABA-dependent signalling pathways by monitoring the expression of ABA-receptive genes and transcription of stress-receptive factors participating in growth and stress-induced mechanisms of plants (Van Ha et al. 2014). SLs are sesquiterpene lactones having structural similarity to terpenoids, signifying that they are byproducts of carotenoids comprised of both natural compounds and artificial equivalents; 19 types of strigolactones have been acknowledged, counting strigol, orobanchol, alectrol, sorgolactone, strigyl acetate, and 5-deoxystrigol (Yoneyama et al. 2018). Current studies have provided some understanding regarding the biosynthetic pathway of SL. Carlactone (CL) is the main precursor of SLs which is derivative of all-trans β-carotene formed under the influence of an isomerase (D27) and two carotenoid cleavage dioxygenases (CCD7 and CCD8) and the reactions are taking place in plastids. Further, the resulted CL is transported to the cytoplasm where further steps of CL oxidation, closure of rings, and functionalization take place, ultimately forming SLs and SL-like compounds (Zhang et al. 2014). After that, ABC-type transporters carry out the translocation of SLs and their pioneers to shoots and the root zone (Prandi and Cardinale 2014). Generally, the mechanism imparted by SLs to encounter metal stress is bilateral, which is associated with the structure and architecture of the root system (Kapulnik et al. 2011). A former study on phosphorus (Pi) suggested that SLs can modulate root systems by regulating the growth of lateral roots with an appropriate concentration of Pi and equally obstructing the appearance of lateral roots with a high concentration of Pi. Therefore, inhibiting the absorption of HMs in the plant by reducing the density of root hairs is one of the tolerance mechanisms imparted by SLs under HM stress (Ruyter-Spira et al. 2011). Arsenic (V) is quite similar to Pi in terms of structure and effortlessly enters into the roots of the plant with the help of Pi transporters. Pi transporter1 family (Pht1; TC 2.A.1.9) with high-affinity transporters of Pi have been recognized, few amongst them are too involved in the transportation of As (V) in plants, consequently causing Pi deficiency in plants (Li et al. 2016). SLs are reported to critically regulate plant's responses to nutrient deficiencies through increased transcription of genes involved in the biosynthetic pathway of SLs such as D10, D17, and OsMAX1 in roots. Currently, (Mostofa et al. 2021) studied the relative contribution of SL in wild type (WT), d17, and d10 mutants of *Oryza sativa* subjected to As stress and observed enhanced transcriptional rates of genes responsible for the synthesis of glutathione and phytochelatins OsGSH1, OsGSH2, OsPCS1, and OsABCC1 (Fig. 15.2), which were comparatively advanced in WT roots and sustain highly active detoxification system than in the roots of SL mutants, whereas up-regulation of Pi and As transporter genes (OsPT2, OsPT8, OsHAC1, and OsPT4) was seen in mutant plants as compared to WTs, indicating that SLs were inhibiting the uptake of metal ions, suggesting their active role in HM stress mitigation. Exogenous supplementation of strigolactone GR24 suggestively alleviated Cd-induced stress in barley (*Hordeum vulgare*) through improved photosynthetic performance, stimulated AsA/GSH and activities of the AsA-GSH cycle, increased absorption of Zn, Mn, Cu, and Fe coupled with reduced uptake of Cd (Qiu et al. 2021). However, in vitro and in vivo experiments have also discovered that the alterations in the structure and signalling pathways of SLs suggestively influence their functions in modifying the adaptation of plants to environmental stresses (Islam et al. 2013). Consequently, the recognition of exogenous chemicals that can amend the functions of SLs is a vital strategy for studying the approach of this phytohormone while managing environmental stress.

15.5 Conclusion

Plant scientists are highly concerned about the antagonistic effects of HM stress on plants because of their evolving threats to safeguarding maintainable advancements in crop cultivation. Exogenous supplementation of these phytohormones has been efficaciously used to get along with the damaging effects of HM noxiousness in cereal crops. Besides strengthening the antioxidant defense machinery, these hormones also decrease the biosorption of several HMs, advance the photosynthetic and gaseous exchange traits, modulate the ionic homeostasis, and increase the expression of stress-responsive transcription factors and so on. As we go ahead, the primary task is to recognize the interactions between phytohormones signalling and HM's encouraging responses in plants. Although the complex network of crosstalk between several phytohormone signalling molecules is acknowledged roughly to an extent, so far, the reports decoding their whole monitoring web during HM stress are lacking. Furthermore, elucidation of the intricacies between HMs and phytohormones is going to be of supreme importance and will open doors in the future to combat the damaging effects of HMs for refining crop produce. In addition, the management of the phytohormonal level will be an interesting approach to studying their successive roles in particular tissues/organs at the relevant developmental period in plants. Since phytohormones are going to target several members of protein families working independently or cumulatively, the biotechnological modulation of a specific crucial protein family can play a significant part in enabling a plant to withstand antagonistic growth conditions.

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Cereals and Phytohormones Under Mineral Deficiency Stress

16

Mona F. A. Dawood and Arafat Abdel Hamed Abdel Latef

Abstract

Climate and atmospheric fluctuations have serious impacts on plants with respect to mineral availability. Nowadays, cultivated lands are at risk of mineral stress in terms of a shortage of essential macronutrients (P, K, N, S, Ca, and Mg) or micronutrients (Fe, Zn, Mn, Cu, B, Mo, Cl, and Ni). Nutrient deficiency has a complex interaction with plants, making it very difficult to predict how cereals will cope with these environments, especially under future climate changes. Thus, it is critically important to declare the strategies that cereals have evolved to adapt to or tolerate these obstacles. Most cereals have developed nutrient uptake mechanisms that are adapted to their native soils and are initiated in an attempt to withstand mineral stress. The cereals change their root architecture (lateral root developments, density, and growth), leaf morphogenesis (thickness, duration, coloration), and hence plant productivity, which is closely associated with the change of ionic homeostasis, hormonal balance, photosynthetic machinery, and respiration. This suggests that cereals adapt to nutritional stress through a common regulation pathway—one of the little studied responses to the behavior of phytohormone biosynthesis. This chapter provides a summary of the previous works concerning the influences of nutrient deficiency on biochemical responses and more details about the action of phytohormones during mineral deficiency. Thus, the present chapter will include trade-offs between physiological adaptations and phytohormonal changes developed by cereals against mineral nutrition deficiency stress as a way to elucidate the main tolerant criteria that

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could be imparted by breeders to withstand nutrient deficiency/toxicity conditions.

Keywords

Cereals · Macronutrients · Micronutrients · Mineral deficiency · Phytohormones

16.1 Introduction

Plant growth and development especially cereals are largely determined by nutrient availability; therefore to ensure preferable productivity of cereals, it becomes essential to understand the dynamics of nutrients uptake, transport, assimilation, and their biological interactions (Wawrzyńska and Sirko 2014). A huge amount of information has been recorded during the past two decades on morphological and physiological changes in cereals due to the availability of mineral nutrients (Krouk et al. 2011a, b; Gruber et al. 2013; Krouk and Kiba 2020; Kumar et al. 2021). Cereals are frequently exposed to nutrient imbalance, which harmfully impacts several metabolic pathways. But, cereals have developed various techniques to deal with mineral-deficient environments. Although large number of elements are naturally available in the soil, 17 elements are documented to be important for the suitable growth and development of cereals. Furthermore, beneficial elements, such as selenium (Se) and silicon (Si), are crucial for favorable growth, development and production and are also beneficial trace elements for human health (Zhou et al. 2020). A deficiency or excess of the mineral elements causes physiological and metabolic changes in plants and dramatically affects cereal growth (White and Brown 2010). However, nutrient availability is largely constrained by soil physicochemical properties (Kim et al. 2016); hence, cereals have evolved many mechanisms to cope with the changes, ranging from deficiency to excess (Maathuis 2009; Krouk et al. 2011a, b; Gruber et al. 2013).

In the last decades, the impact of nutrient deficiencies on cereal growth and production has become a major concern, and the adverse effects threaten food safety and quality (Neset and Cordell 2012; Shahzad et al. 2014). To meet the global demand for food and agricultural raw materials, farmers rely heavily on the use of fertilizers to improve crop yield. However, long-term use of fertilizer is associated with negative ecological impacts, such as soil compaction and acidification, water loss, and soil erosion. The problems associated with the long-term use of fertilizers can be reduced by the use of nutrient-efficient crop varieties and previously uncultivated lands that are nutrient-rich for crop production. Therefore, for sustainable agriculture and reduced use of fertilizer, breeders and molecular scientists should focus on developing mineral-efficient crop varieties (Bouain et al. 2019; Fan et al. 2021).

16.2 Mineral Nutrition in Plant Life

Plants need 17 essential nutrients for the completion of their life cycle. These nutrients are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), chlorine (Cl), and nickel (Ni). All these nutrients are known as essential nutrients. According to the law of essentiality, in the absence of any of these nutrients, plants cannot complete their life cycle, these elements are directly involved in the metabolism of the cereals, and the deficiency of an element can be corrected only by supplying the element in question (Fan et al. 2021). These nutrients have been divided into:

16.2.1 Non-Mineral Nutrients

The non-mineral nutrients are H, O, and carbon. These elements help in the formation of tissues. They help in the biosynthesis of lipids, carbohydrates, proteins, nucleic acids, and hormones. Hydrogen is an element that is associated with nitrogen fixation and photosynthesis; this is ascribed to their reducing capacity, being a nutrient assimilated from the water. Oxygen is utilized from the atmosphere or water and is used during the process of cell respiration, where the sugar that is produced by photosynthesis is transformed into energy. The plant captures carbon in the form of CO_2 from the atmosphere. It is a nutrient with the functions of ensuring the occurrence of physical, chemical, and biological cycles and ensuring the balance of energy reserves throughout the vegetative stage (da Silva Lobato et al. 2016).

16.2.2 Nutrients and Minerals

These are nutrients needed for the plants to complete their life cycle. They are categorized into macro- and micro-nutrients (da Silva Lobato et al. 2016).

16.2.2.1 Macronutrients

The macronutrients included N, P, K, Ca, Mg, and S. High quantities of these nutrients are needed for plants to develop, carry out their physiological activity, and play vital roles in the plant structure (da Silva Lobato et al. 2016). These nutrients are macronutrients because they are required in large quantities (1–150 g/kg of plant dry weight) by the plants (Marschner 1997).

16.2.2.2 Micronutrients

Microelements have a role in the upregulation of the activity of the cell organelles. These nutrients are absorbed and present in small contents in plant tissues and provide the nutritional exigency of the plant (da Silva Lobato et al. 2016). Fe, Zn, Mn, Cu, B, Mo, Cl, and Ni are needed by plants in very small quantities

(0.1–100 mg/kg of plant dry weight) and are thus known as minor or micronutrients (Marschner 1997).

Ionome is a term that expresses the mineral nutrient and trace-element composition of a living organism (Salt et al. 2008). Also, the term "functional ionome" has been described (White et al. 2017), and the functional ionome contains all the mineral elements, which are essential for the growth and development of living organisms (Fan et al. 2021). In addition to macro- and micronutrients, several workers have described three additional elements, namely, silicon (Si), cobalt (Co), and selenium (Se), as essential elements for optimal growth (Van Hoewyk et al. 2008; Tan et al. 2010).

16.3 Nutrient Deficiency

All the essential nutrients are required in a suitable amount. Deficiency or excess of these elements in the soil triggers several disorders or stresses in cereals. The plant stress caused by deficiency or toxicity of nutrients is known as nutritional stress. Plants generally and cereals specifically express this stress in the form of visible symptoms like chlorosis and stunted growth. The stress might extend to the entire plant cycle, resulting in a loss of yield if relief from stress is not restricted. Low availability of primary nutrients such as N and P is a global problem that is mostly provoked by using synthetic fertilizers. However, intensive agriculture practices, uncontrolled use of fertilizers, and lack of micronutrient application to the soil have led to global micronutrient deficiencies in the agricultural soil (Sillanpaa 1990; White and Zasoski 1999; Shukla et al. 2014). Analysis of 190 soil samples from 15 countries revealed that 49% of these soils were low in zinc and 31% low in boron (Sillanpaa 1990). All essential elements are associated with some metabolic activities in the plants (Arnon 1954). Major elements are the main building block elements, while micronutrients play an important role in enzymatic activities in several physiological processes. Metallic micronutrients (Zn, Cu, Fe, Mn, Ni, and Mo) are effective as components or as activators or inhibitors of enzymes in the plant metabolic process. The deficiency or toxicity of micronutrients affects associated physiological activity and thus disrupts the normal process, leading to plant disorders or stress. Generally, micronutrient deficiencies exert secondary influences on the growth of plants by changes in growth pattern, chemical composition, antioxidant defence capacity of cereals and a decrease in the resistance of plants to biotic and abiotic environmental stresses (Hajiboland 2011). Therefore, deficiency or toxicity of micronutrients can impede these vital physiological processes, leading to plant stress and poor yield. The micronutrient-related stress on cereals has been described below.

The cereals exhibit different physiological and biochemical manifestations to cope with such nutritional stress as alterations in root architecture, release of root exudates to the rhizosphere, rhizospheric acidification, symbiotic associations with microbes in the soil, antioxidant defense activation, mobilization of stored nutrient pools, and enhanced nutrient uptake for translocation to the shoot (Singh and Mann

2012; Theocharis 2014). The root endodermis' permeability is altered by nutrient stress, allowing the uptake of specific nutrient ions through the vasculature (Barberon et al. 2016). The physiological and molecular strategies by which cereals sense and tolerate deficiency of nutrients are important for the cultivation of crops with better nutrient use efficiency (Zhang et al. 2019). It is suggested that multiple regulatory pathways may contribute to coordinating this kind of acclimation (Isidra-Arellano et al. 2020), which differ based on the mineral exhibited deficiency. Phosphate stress mediates complicated signaling cascades, which activate a series of downstream responses often associated with a large spectrum of genes implicated in various metabolic pathways organized at primary and secondary metabolic levels (Ma and Chen 2021). The phosphate stress-induced signal transduction pathway is composed of various key players, namely, sugars, hormones, peptides, transcription factors, and miRNAs (Foo 2017).

Another important macronutrient, nitrogen is an important nutrient required for plant growth and development as it is a core constituent of a plant's nucleic acid, proteins, enzymes, cell wall, and pigment system (Krapp 2015). In this regard, nitrate deficiency allows the development of larger root systems with more extensive branching, whilst shoot growth is restricted under N deficiency and photosynthesis reduced due to the acceleration of leaf senescence (Scheible et al. 2004). Leaf sugars (e.g. starch), and secondary metabolites (anthocyanins, phenylpropanoids, and flavonoids) accumulate in response to N deficiency (Fritz et al. 2006). Transcriptome profiling and the combination of transcriptome and metabolite data studies have reported that nitrate deficiency triggers the expression of genes associated with amino acid catabolism, protein degradation, autophagy and ubiquitin-proteasome pathways, and genes encoding phenylpropanoid metabolism, while genes encoding photosynthetic proteins and biosynthetic pathways that require N-containing metabolites are downregulated in maize (Amiour et al. 2012). Under N deficiency, reactive oxygen species (ROS) has been denoted to exacerbate in specific regions of the root revealing its significance to N-deficiency responses (Nieves-Cordones et al. 2019).

Generally, Mg deficiency causes smaller roots, stunted shoots, and necrotic spots on leaves, due to abnormal physiological pathways like impaired C metabolism and decline of chlorophyll and carbon fixation (Guo et al. 2016). Mg deficiency downregulates the loading of sucrose into the phloem, causing an accumulation of carbon in the producing leaves (Marschner 2012). A decline in Mg-ATP concentration at the phloem-loading sites may be the major reason for the inhibition of sucrose transport from Mg-deficient source leaves (Cakmak and Kirkby 2008) and is analogous to sucrose accumulation in leaves under K and Zn but not P deficiency (Marschner 2012). Sucrose loading into phloem is catalyzed by an H^+/sucrose co-transporter, whose activity requires a proton gradient maintained by an H^+-ATPase located in the plasma membranes of the sieve tube cells (Cakmak and Kirkby 2008). Growing evidence indicates that Mg-ATP is a major complex of ATP in cells and is essential for the proper functioning of H^+-ATPase (Igamberdiev and Kleczkowski 2001). Mg^{2+} acts as an enzyme activator or cofactor in carbohydrate metabolism so that Mg deficiency inhibits these enzyme activities and further leads to carbon accumulation in source leaves, such as fructose-1, 6-bisphosphatase (FBPase), glutamate synthetase, UDP-D-, ADP-D-, GDPD-glucose pyrophosphorylase, and UDP-D glucuronic acid pyrophosphorylase (Hermans and Verbruggen 2005). Over-accumulation of carbides in leaves leads to feedback inhibition of the photosynthesis rate (Hermans et al. 2004) and reduces chlorophyll content (Hermans and Verbruggen 2005). Impairment of photosynthetic CO_2 fixation also leads to an accumulation of unused electrons in the chloroplast, resulting in ROS generation and photo-oxidative damage to chlorophyll and chloroplast membrane lipids. Thus, Mg deficiency symptoms, such as leaf chlorosis, are aggravated by high light intensity (Cakmak and Yazici 2010). This process is due to the decrement of the transfer of excitation energy (or electrons) from chlorophyll a of PSII to chlorphyll a of PSI in the chloroplast (Chen et al. 2009), or due to the low content of PSI (Ceppi et al. 2012). The electrons are transferred to protoporphyrin IX, probably in association with the light-dependent generation of ROS, resulting in leaf chlorosis following the over-accumulation of protoporphyrin IX in tissues, especially under Mg deficiency and high light intensity. In this manner, protoporphyrin IX is over-accumulated in cells. Mg deficiency also activates antioxidative defense enzymes in some plant species (Kumar Tewari et al. 2006; Hermans et al. 2010). The key antioxidant molecules (dehydroascorbate and oxidized glutathione) were markedly increased under Mg deficiency (Hermans et al. 2010). Generally, leaf chlorosis is observed first in older leaves in response to Mg deficiency and is interpreted as the re-translocation of Mg^{2+} from older to younger leaves (Marschner 2012). A decrease in transpiration occurs prior to sugar accumulation and chlorosis in rice under Mg deficiency conditions (Kobayashi et al. 2013). These results indicate that plant Mg deficiency-response systems are complex and that many signal transduction pathways are unknown. Besides, the impairment by Mg deficiency of carbon metabolism in source leaves, N metabolism is also damaged. For example, lower N was reported in longan leaves (Li et al. 2001) under Mg deficiency treatment, and some enzymes of N metabolism were inhibited in spinach by Mg deficiency, including nitrate reductase, glutamate synthase, glutamate dehydrogenase, urease, glutamic–pyruvic transaminase, and glutamic–oxaloacetic protease transaminase (Yin et al. 2009).

As a significant micronutrient, Fe deficiency in plants causes chlorosis of leaves due to damage to chlorophyll (Chl) biosynthesis (Yuan et al. 2007). Spiller et al. (1982) indicated that Fe deficiency causes the accumulation and excretion of intermediates in the tetrapyrrole biosynthetic pathway, particularly coproporphyrin. Under Fe stress, biochemical changes result in an increased ability to acquire Fe and include the induction of a plasma-membrane Fe(III)-reductase and Fe(II) transporter, an enhanced proton extrusion capacity, and the release of low-molecular-weight compounds such as carboxylates, flavins, and phenolic compounds (Abadía et al. 2002). Nutrient stress as Fe and/or Zn deficiency induces ROS formation where enhanced production of hydroxyl ($^{\bullet}OH$), superoxide (O_2^{-}) radicals, and hydrogen peroxide was resultant (Del Rio 2015). A normal metabolic functioning involves a balanced generation and quenching of ROS, thereby preventing damage to the lipid membranes. An increased accumulation of ROS generates an enzymatic ROS scavenging mechanism in plants (Dawood 2022; Mourad et al. 2021; Dawood et al. 2021; Dawood and Azooz 2020). However, severe exposure to stressful conditions like nutritional deficiencies causes enhanced ROS production, exceeding the quenching capacity of enzymatic and non-enzymatic ROS scavenging mechanisms (Del Rio 2015). As a part of the electron transport chain in chloroplasts and mitochondria, the cellular redox balance is negatively impacted during Fe deficiency in plants which eventually generates the ROS elevation. The iron deficiency caused a significant increase in ROS, namely, hydrogen peroxide and superoxide radicals in the leaves of maize plants (Sun et al. 2007). The role of ROS scavenging molecules, such as glutathione (GSH) and ascorbate (AsA), is crucial to improving Fe availability and maintaining cellular Fe homeostasis.

16.4 Cross-Talk Between Macro- and Micronutrients Under Mineral Nutrient Deficiency

Andresen et al. (2018) reviewed the presence of multiple cross-talks between macro- and micronutrients that have been uncovered in several approaches. A complete understanding of ionome homeostasis requires a thorough investigation of the dynamics of the nutrient networks in plants. Although the ionome homeostasis is very poorly understood, several recent studies have shown the diagram of the ionomic networks and multiple cross-talks of the ionome in plant species (Baxter 2009; Courbet et al. 2019). Nutrient deficiencies can modify the functional ionome of plant tissues (Maillard et al. 2016; Courbet et al. 2019). Fan et al. (2021) concluded that the ionomic analyses support the occurrence of complex cross-talks between mineral nutrients in plants, indicating that, under certain deprivations, nutrient cross-talks stimulate or reduce the accumulation of other mineral nutrients, which modifies the ionomic composition of plant tissues. Applying low Pi in a growth culture medium induced an increment of Zn, Fe, and S levels and a decline of copper and cobalt contents in the experimental plants (Baxter et al. 2008). Maillard et al. (2016) identified 18 different interactions under mineral nutrient deficiency at the uptake level. Particularly, Mo uptake was significantly increased in plants under S, Fe, Zn, Cu, Mn, or B deficiency. Several reports have focused on the effects of S deficiency on mineral nutrients in plants at the transcriptomic or metabolic levels of various plants (Ciaffi et al. 2013; Maillard et al. 2015, 2016; Forieri et al. 2017). When the plants are exposed to S deficiency, several positive and negative interactions between S and other mineral nutrients have been reported (Bokor et al. 2015; Maillard et al. 2016; Courbet et al. 2019; Zhou et al. 2020). Furthermore, concerning Si and Zn cross-talks, supplying maize plants with Si and/or Zn significantly decreased the concentration of Pi, K, Mg, Ca, Mn, Ni, and Co in the roots but increased the concentration of Se (Bokor et al. 2015). Conversely, the positive effects of Si and Fe interaction on the growth and production of plants have been reported (Gonzalo et al. 2013; Dragama et al. 2019). Many workers have shown that the interactions of nutrients are a common process in plants (Briat et al. 2010; Bouain et al. 2019; Fan et al. 2021; Ji et al. 2022). Therefore, the dynamics in the functional ionome of plants subjected to individual mineral deficiency indicate that the complexity and the diversity of interactions occur between single and other mineral nutrients in plants (Fan et al. 2021).

16.4.1 Interaction Between Pi, S, and Fe Nutrient Homeostasis in Cereals

Rouached et al. (2011) reported an increase in root SO_4^{2-} concentration and a decrease in shoot SO_4^{2-} level during Pi deficiency, indicative of a complex process in the co-regulation of Pi and SO_4^{2-}- homeostasis in plants. Acquisition of S, K, and Fe by roots is of crucial importance for plant growth and yield, and some studies have revealed that the uptake systems for S and Fe nutrients are coordinated in barley plants (Astolfi et al. 2010). Moreover, Forieri et al. (2017) demonstrated that the plant is differentially co-regulated upon long-term Fe, S, and K deficiency through the systematic analyses of metabolism and the transcriptome in roots. The authors found the specific co-regulation between the S and Fe metabolic pathways in roots upon S or Fe deficiency. Interestingly, Fe deficiency regulated a distinct subset of the S assimilation genes that were not controlled by S deficiency itself, suggesting the presence of two independent signaling pathways in this network. In particular, the cross-talk between S and Fe pathways in roots had an opposing regulation component that was upregulated during S deficiency and downregulated during Fe deficiency or *vice versa* (Forieri et al. 2017), demonstrating the presence of specific signaling cascades for the cross-regulation of the S and Fe routes. On the other hand, fewer S- or Fe-deficiency-responsive genes were co-regulated in response to the K deficiency, while the genes involved in the S and Fe assimilation pathways were almost unaffected by low K application (Forieri et al. 2017). Therefore, the response to K deficiency shown did not participate in the cross-talk between S and Fe nutrients. In addition, a significant decrease in total sulfate in roots in response to K deficiency may be explained by the downregulation of important key components of the sulfate assimilation pathway upon K deficiency, providing evidence for the specificity of the K and S cross-talk, whereas the K-deficiency response resulted in a strong increase in the content of reduced S-containing metabolites (Forieri et al. 2017), demonstrating a shift of the oxidized sulfate to the reduced state. This can explain the unaltered total S concentration in roots during K deficiency.

16.4.2 Interaction Between N and Pi Nutrient Homeostasis in Cereals

N and P are two essential macronutrients necessary for plant growth and productivity, and a deficiency in either of the two nutrients may negatively affect plant growth and yield. The earlier reports revealed a mutual interaction between N and P nutrition in plants under diverse ecosystems. Reports have declared that plants possess highly developed mechanisms for maintaining Pi and N homeostasis due to Pi- and N-deficiency signaling (Medici et al. 2019). It was reported that interactions between

N and P signaling in plants were mediated by nitrogen limitation adaptation (NLA), a RING-type E3 ubiquitin ligase, which is involved in N-dependent P accumulation in shoots by promoting the degradation of PHT1 proteins with the help of PHO2 (Park et al. 2014). Medici et al. (2019) reported that N signaling modulates phosphate-deficiency response (PSR) in rice (*Oryza sativa*) through three molecular integrators (PHR1, PHO2, and NRT1.1).

16.4.3 Interaction Between N and Zn Nutrient Homeostasis in Cereals

Apart from N and P, Zn is one of the most yield-limiting nutrients in crop species, and N is a critical player in Zn uptake and translocation in wheat plants (Erenoglu et al. 2011). Reports on N-Zn cross-talk have confirmed that N-application improves Zn uptake and homeostasis in rice and wheat plants under Zn deficiency (Kutman et al. 2011; Ali et al. 2014) and that N and Zn applications increase grain crude protein as well as N and Zn contents (Nie et al. 2018). Cakmak and Marschner (1990) reported that low Zn supply reduced the nitrate uptake capacity of buckwheat. Ji et al. (2022) showed that Zn and N application increased the translocation of N and Zn, respectively, from roots, to stems, to the leaves, enhancing the brown rice yield. The transcriptomic data revealed that the expression of numerous N transports and homeostasis-related genes was upregulated in the shoots during Zn deficiency (Wang et al. 2018).

16.4.4 Cross-Talk between Pi, Zn, and Fe Homeostasis in Cereals

Pi deficiency causes Zn over-accumulation in the shoots of plants, and *vice versa* (Bouain et al. 2014; Ova et al. 2015), referring to the antagonistic impact of Pi and Zn nutrition in plants. Moreover, some records revealed similar physiological cross-talk between Pi and Fe (Zheng et al. 2009) and between Fe and Zn (Haydon et al. 2012). On the other hand, some studies have examined the complex tripartite interactions between Pi, Zn, and Fe (Briat et al. 2010; Saenchai et al. 2016).

16.4.5 Pi Availability Affects Zn Uptake in Cereals

In wheat and maize, Pi and Zn have been shown to have an antagonistic reaction, as an increase in Zn concentration results in a decrease in Pi concentration, and *vice versa* (Robson and Pitman 1983; Verma and Minhas 1987). Studies showed a negative correlation between Pi and Zn concentration. Although this interaction is known as Pi-induced zinc deficiency, the relationship is complex (Marschner 2012). Although higher levels of Pi increase grain yield in soil-grown plants, the Zn content of shoots decreases with increasing concentrations of Pi. However, if the available Zn is low, this effect can exacerbate Zn deficiency, as low Pi concentrations will initiate Zn uptake. A high level of Pi was associated with a lower Zn concentration in wheat tissue (Thompson 1990; Zhu et al. 2001; Zhang et al. 2012). High Zn content did not affect wheat yield under a low Pi environment, indicating that Pi was the yield-limiting nutrient of wheat (Ova et al. 2015). In addition, Zn deficiency and high Pi content cause Pi toxicity in plants. Pi-Zn interaction has also been identified in several biological systems (Marschner 2012; Kisko et al. 2018). In *Zea mays*, high levels of Pi can immobilize Zn in roots and nodes by increasing the Zn-binding properties of the cell wall (Bouain et al. 2014). A mild Zn deficiency in Pi-deficient plants can increase the abundance of high-affinity Pi transporters without accumulating excess phosphorus in barely (Huang et al. 2000).

16.4.6 Zn Availability Affects Pi Uptake in Cereals

When grown in Zn-deficient soil, plants exhibit an enhancing Pi-uptake capacity. Studies have shown the higher Pi concentrations in the shoots of both dicotyledon and monocotyledon plant species in response to Zn deficiency (Welch et al. 1982; Cakmak and Marschner 1986; Webb and Loneragan 1988; Welch and Norvell 1993). Moderate Pi levels increased the dry weight of Zn-deficient plants; however, at high-Pi levels, this effect was reversed, resulting in a decrease in shoot biomass. Conversely, the biomass yield of wheat plants was higher under moderate and high Zn concentrations (Ova et al. 2015). The effects of Zn deficiency as reported by Kisko et al. (2018) are exacerbated by the stimulation of shoot content of Pi. In conformity, others also reported that Zn deficiency enhances the root uptake of Pi in cereal plants (Cakmak and Marschner 1986; Huang et al. 2000). On the other hand, a high level of Zn decreases the rice-yield production and triggers P starvation by inhibiting root-to-shoot translocation and distribution of P into leaves by downregulating the Pi transporter genes *OsPT2* and *OsPT8* in shoots of rice plants (Ding et al. 2021). Unlikely, P supply decreased the Zn contents of rice plants, inhibiting the expression levels of the ZIP family Zn transport genes *OsZIPs* in roots (Ding et al. 2021).

16.4.7 Pi Availability Affects Fe Uptake and Homeostasis in Cereals

Another study denoted that Pi deficiency or excess can impact Fe homeostasis of cereals (Liu et al. 2000; Zheng et al. 2009). Fe can interact with phosphorus in the soil or growth medium, root surface, and in systems of cereals (Zheng et al. 2009; Bournier et al. 2013). Higher concentrations of Fe have been observed in Pi-deficient plants, and this is attributed to the activities of Fe-responsive genes in response to Pi deficiency (Zheng et al. 2009); however, this phenomenon was not observed in high Pi medium (Hirsch et al. 2006). The absence of Fe in the Pi-deficient medium promotes plant growth (Ward et al. 2008). Studies by Zheng et al. (2009) and Chaiwong et al. (2018) depicted that a lack of Pi enhanced the Fe content of rice seedlings' shoots; however, the root content of Fe was not affected, revealing an antagonistic effect between Pi and Fe. Thus, adjusting Pi homeostasis has a significant effect on the availability of Fe (Bournier et al. 2013). Fe was present only in the vacuoles under high-Pi conditions, whereas several large grains of starch typical of Pi-starved plants were observed in most of the chloroplasts under low-Pi conditions (Hirsch et al. 2006).

16.4.8 Fe Availability Affects Pi Uptake and Homeostasis in Cereals

When both iron and phosphorus are absorbed by plants, the retention of Pi in roots increases and the transfer of Pi to the ground decreases in a concentration-dependent manner. Fe enhanced Pi retention in the roots and decreased Pi translocation to the shoots (Cumbus et al. 1977; Mathan and Amberger 1977); but Fe deficiency causes overaccumulation of Pi in the roots and shoots. Similarly, Pi and Fe interrelated in an antagonistic way to regulate the growth of rice shoots (Zheng et al. 2009). The experimental data on Pi- and Fe-treated seedlings revealed that the availability of Fe affected the response of lateral roots to Pi deficiency of wheat.

16.4.9 Zn Availability Affects Fe Uptake and Homeostasis in Cereals

Zinc and iron deficiency reduces plant growth and affects grain yield and quality (Casterline et al. 1997). The antagonistic relationship between Fe and Zn in plants, and between Zn or Fe deficiency and Pi concentration has been examined by several workers (Jain et al. 2013; Zargar et al. 2015). Lešková et al. (2017) found that the excess of Zn exposure mimics Fe-deficiency-induced chlorosis in plant shoots, and analysis of Fe-related morphological, physiological, and regulatory responses in plants subjected to excess Zn reveals that the enhanced Zn uptake closely mimics Fe deficiency, resulting in low-chlorophyll contents but high-ferric-chelate reductase activity. In addition, Lešková et al. (2017) stated that these responses did not result from the high-Zn-reduced Fe uptake at the level of transport, whereas Zn simulated the transcriptional response of Fe-regulated key genes. This finding indicates that excess Zn disturbs Fe homeostasis at the level of Fe sensing.

16.4.10 Fe Availability Affects Zn Uptake and Homeostasis in Cereals

Kobayashi et al. (2012) reported that Fe deficiency accelerates excess uptake and accumulation of Mn and Zn in rice plants. The growth of *Zea mays* under both Fe and Zn deficiency was significantly higher than that under only Fe deficiency (Kanai et al. 2009). Fe deficiency has been triggered by Zn toxicity, while plant symptoms under excess Zn resemble symptoms of Fe-deficient plants. However, Zn deficiency slightly promotes early root growth (Bouain et al. 2018). On the other hand, when grown in excess Zn medium, the inhibition of growth was sufficiently recovered by

Fe addition (Zargar et al. 2015), indicating that the appropriate application of Fe can significantly alleviate the effects of Zn toxicity in plants when grown in Zn-contaminated soil. Moreover, Fe-mediated plant Zn tolerance may be sustained by the fine-tuned Zn homeostasis mechanism, which prevents high Zn uptake through Fe-regulated metal transporters associated with Zn tolerance. This suggests a cross-talk between excess Zn and Fe deficiency in plants.

The general biochemical responses of some mineral nutrients have been demonstrated previously, and more details about the phytohormones in response to nutrient deficiency will be illustrated in the following section.

16.5 Mineral Deficiency Affects Hormonal Homeostasis and the Role of Exogenous Phytohormones

The nutrient status influences its metabolism and growth and can affect the synthesis of the building block metabolites and the distribution of phytohormones. This interdependence is because nutrient deficiencies affect the concentrations of specific hormones capable of directing the translocation and accumulation of nutrients (Kuiper 1988). Suboptimal nutrient supply is a key factor regulating plant growth and development, and in most cases, this includes alterations in plant hormone (PH) homeostasis. Fluctuating concentrations of certain PHs in roots or xylem saps have even been proposed to monitor the nutrient status of the roots or to act as long-distance signals for the shoot, respectively (Sakakibara 2006). In general, changes in root or shoot concentrations of growth-stimulating or growth-retarding PHs have been observed under several nutrient deficiencies including those of nitrogen (N), phosphorus (P), potassium (K), and sulfur (S) (Sultan 2000; Rubio et al. 2009; Wolters and Jurgens 2009; Koprivova and Kopriva 2016). For instance, reduced shoot biomass formation under S or K deficiency coincided with enhanced abscisic acid (ABA) and salicylic acid (SA) concentrations in shoots (Forieri et al. 2017). On the one hand, shoot biomass under P deprivation coincided with a decrease in growth-stimulating CKs, which in turn is a prerequisite for the upregulation of phosphate transporters in roots and subsequent P accumulation in shoots (Rouached et al. 2010). On the other hand, P deficiency also affected genes involved in gibberellin (GA) biosynthesis and decreased GA concentrations in seedlings, suppressing root growth (Jiang et al. 2007; Rubio et al. 2009; Rouached et al. 2010). Likewise, Fe deficiency suppressed GA biosynthesis in roots and subsequent elongation of the primary root (Wild et al. 2016). Thus, there is ample evidence for nutrient deficiencies determining growth responses via altered PH homeostasis. However, in most cases, it has remained unclear to what extent nutrient deficiencies affect the synthesis, conjugation, or degradation of physiologically active PH species. In contrast to concentration changes of single PHs regulating plant growth under suboptimal nutrient supply, changes of plant hormonal networks or regulatory adjustments among different PH classes have rarely been documented in rice (Sun et al. 2014). To date, most of the current knowledge therein is built on the transcriptional responses of genes involved in PH biosynthesis or signalling, or on reverse genetic approaches describing conditional nutrient-dependent phenotypes of mutants or transgenic lines with altered expression of PH-related genes (Mouchel et al. 2006; Nemhauser et al. 2006; Wolters and Jurgens 2009; Davies 2010; El-Showk et al. 2013; Ristova et al. 2016). Alternatively, other studies have employed hormonal reporter genes to monitor tissue- and cell-type-specific responses to nutrient treatments (Miura et al. 2011).

PH biosynthesis, activation, or degradation shape PH patterns under certain nutrient deficiencies. Quantitative analysis of different PH species will help in addressing the question of how plants adapt their growth to specific nutrient deficiencies or whether changes in PH patterns are just the consequence of suppressed growth and a weaker sink activity. Metabolic pathways leading to an increase in active PH species or mediating their degradation remain poorly understood. This is even the case for the most intensively studied PH species, indole-3-acetic acid (IAA), for which multiple biosynthesis pathways exist and whose relevance is still unclear (Di et al. 2016). Reasons for the lack of analytical data on changes in different PH species under nutrient disorders are diverse: (1) One is the challenging analysis by chromatographic separation techniques coupled with highly sensitive mass spectrometry because PHs occur in plant tissues at very low concentrations (1–500 ng g^{-1} DW) and plant material is often limited (Davies 2010). (2) The complexity of PH analysis remains high due to a large number of different molecular species within one biosynthetic pathway (Davies 2010) and the existence of multiple metabolic routes leading to activation, derivatization, or inactivation of PHs (Di et al. 2016). (3) Some PH individuals show a particular instability during extraction and detection; for example, indole-pyruvic acid (IPyA), an important precursor for IAA biosynthesis, requires different methods for extraction and analysis compared to IAA. (4) Extraction and purification methods, matrix effects or co-eluting substances, liquid eluents, and the target analytes themselves affect detectability, requiring continuous adjustment of analytical approaches (Gosetti et al. 2010). These practical and analytical challenges increase the need for using isotopically labelled standards to ensure reliable quantitative analysis; however, isotope-labelled standards are expensive or often not available, posing additional methodological obstacles for PH metabolite analysis (Bruheim et al. 2013). Thus, methodological restrictions in particular have hindered PH individuals from being a part of routine metabolic determinations. With respect to the current gap in understanding PH responses, cross-talk and homeostatic effects under nutrient deficiency, the present chapter aims to investigate hormonal changes in response to mineral deficiency.

It has been reported that auxin and ethylene participate in the regulation of primary root elongation and lateral root formation triggered by several nutrient deficiencies (Chérel et al. 2014). Ethylene can activate auxin production and transport both rootward and shootward, and then change root development (Street et al. 2015). Primary root elongation is decreased by the synergistic effects of auxin and ethylene, while lateral root production is activated by auxin accumulation but hindered by ethylene (Miura et al. 2011; Muday et al. 2012; García et al. 2015).

Strigolactones (SL) and their derivatives have been identified as novel phytohormones capable of regulating root development. Significant increases in SL level in roots in response to P deficiency have been reported in many plant species, including rice (Umehara et al. 2008) and sorghum (Yoneyama et al. 2007). In rice, the SL biosynthesis genes *D10*, *D17*, and *D27* are upregulated in response to P deficiency, while the expression of SL signaling pathway components *D3* and *D14* is inhibited by Pi starvation (Sun et al. 2014). Hence, the production of SLs is promoted. In addition, the length of the seminal root is enhanced and lateral root density is decreased upon using SL-analogue GR24 in WT and the SL synthesis-defective mutants *d10* and *d*27, but not in the SL-insensitive mutant *d3* (Sun et al. 2014). This implies that *D3* is crucial for the alteration of root growth in SL signaling pathway-mediated responses to Pi starvation. Additionally, SLs have been recently found to participate in the regulation of primary and lateral root development of rice triggered by P deficiency mainly via interactions with auxin (Sun et al. 2014).

Phytohormone signaling under P starvation is one of the main pathways which modulate plant response to abiotic stress through cross-talk with other stress signaling pathways (Baek et al. 2017). Plant hormones play a vital role in linking gene transcription to P starvation response mechanisms. Auxins (AUXs) (Jiang et al. 2017), cytokinins (CKs) (Franco-Zorrilla et al. 2002; Wang et al. 2006; Shen et al. 2014), gibberellin (GAs) (Jiang et al. 2007), ethylene (ET) (Song and Liu 2015), abscisic acid (ABA) (Vysotskaya et al. 2016; Silva-Navas et al. 2019), and strigolactones (SLs) (Czarnecki et al. 2013, Ha and Tran 2014, Torres-Vera et al. 2014) are the main hormones which regulate the P starvation response. Auxin is one of the most important phytohormones involved in root development, with effects on primary roots, lateral roots, and root hairs in response to Pi starvation (Grieneisen et al. 2007). The arrest of primary root elongation and the promotion of root hairs are thought to be independent of auxin signaling, while auxin is regarded as a crucial requirement for facilitating the formation of lateral root primordial (Himanen et al. 2002). This is supported by the activation of lateral root formation with exogenous use of auxin (Blakely et al. 1988) and inhibition of lateral root formation by auxin transport inhibitors (Reed et al. 1998). Also, in response to P deficiency, ethylene plays crucial roles in the inhibition of primary root growth and promotion of lateral root elongation (Borch et al. 1999; Ma et al. 2003). Higher ethylene production in roots has been detected in P-deficient stressed plants (Borch et al. 1999; Kim et al. 2008; Li et al. 2009). It has also been reported that not only does Pi starvation increase ethylene synthesis (Borch et al. 1999; Lynch and Brown 2001; Li et al. 2009), but also it enhances ethylene responses in roots. This suggests the involvement of endogenous phytohormones (auxins and cytokinins), which may act in an antagonistic manner in the P-starvation response. Lamont (2003) stated that root-cluster production is controlled by the interplay between external and internal nutrient levels and modulated by auxin and other hormones to which the process is particularly sensitive.

Certain studies involving specific hormonal precursors and functional inhibitors suggest that the regulation of Fe deficiency stress responses might be related to variations in the concentration of certain hormones in the roots (Rubio et al. 2009).

Studies revealed that auxins participate in the regulation of Fe deficiency stress (Landsberg 1981a, b, 1984; Römheld and Marschner 1986) and others confirmed the importance of ethylene in such regulation (Lucena et al. 2006; Romera and Alcántara 2004; Romera et al. 2006; Waters et al. 2007). Other coworkers described the role of nitric oxide (NO) in the regulation of Fe homeostasis in the shoot and in the expression of Fe stress responses in the roots (Murgia et al. 2002; Graziano et al. 2002; Graziano and Lamattina 2007). Ethylene production is elevated by NO in roots, and NO and ethylene together act by aiding the transcription of genes responsible for Fe acquisition (Garcia et al. 2011). Another hormone with auxin-like activity is melatonin (N-acetyl-5-methoxytryptamine) (Dawood 2022), which modulates the gene expression of a number of receptors and hormone signalling pathways to impart growth-promoting attributes in plants (Tiwari et al. 2020). Melatonin acts by elevating the remobilization of Fe, bound to pectin and hemicellulosic components of the cell wall, through polyamine-mediated NO accumulation (Zhou et al. 2016). Abscisic acid (ABA) alleviates Fe deficiency-induced chlorosis by reducing the root apoplastic Fe and elevating the level of shoot Fe content, which is suggestive of improved reutilization and transport of Fe from root to shoot under Fe deficiency (Lei et al. 2014). Gibberellins (GAs) cause a reduction in Fe transport and translocation from root to shoots, thereby negatively modulating Fe utilization in rice seedlings (Wang et al. 2017). Furthermore, cytokinins (CTK), jasmonic acid (JA), and brassinosteroids (BRs) inhibit the expression of genes regulating Fe acquisition, namely, IRT, FRO2, and FIT (Hindt and Guerinot 2012; Maurer et al. 2011). The Fe deficiency is also reported to be regulated by ethylene and NO, which is associated with ROS-mediated signalling (Xia et al. 2015). A number of hormones act through intricate signalling pathways to modulate the gene expression and root system architecture under Fe deficiency. Each hormone has specific roles in the plant system and perception of Fe deficiency induces a cross-talk mechanism whereby they regulate the alterations mediating the plant's survival during Fe-limited conditions. Auxin, ethylene, and nitric oxide (NO) have been suggested as positive regulators of Fe acquisition in wheat (Garnica et al. 2018), while cytokinins and jasmonates are found to be negative regulators (Hindt and Guerinot 2012). Increased auxin synthesis during Fe deficiency is linked to regulating lateral root growth by affecting the AUX-1 transporter in strategy I plants (Giehl et al. 2012), while the strategy II plants are suggested to involve an auxin response factor like OsARF12 in rice (Qi et al. 2011). Ethylene, in response to Fe deficiency, is reported to work by influencing the interaction of ETHYLENE INSENSITIVE3 and ETHYLENE INSENSITIVE3-LIKE1 (EIN3/EIL1) directly with FIT, wherein they are reported to aid Fe acquisition by regulating FIT stabilization (Lingam et al. 2011). NO is a signalling molecule mediating reversion of chlorotic effects in maize (Graziano and Lamattina 2005). A model suggestive of the concerted roles of positive regulators entails that Fe deficiency induces elevated auxin levels that act upstream, increasing NO levels which act to upregulate the genes responsible for higher Fe acquisition.

Plants respond to Zn deficiency by eliciting a signalling cascade that traverses between roots and shoots to maintain nutrient homeostasis in maize (Kabir et al.

2017). Hormonal signalling mediates the mineral needs of plants during Zn deficit status. Indole-3-acetic acid, the major auxin in plants, plays a critical role in plant development and the Zn status greatly influences the auxin-mediated responses while auxin signalling triggers Zn acquisition efficiency in plants. The Zn transporter genes in rice including OsIRT1, OsZIP4, and OsZIP1 were expressed upon exposure to auxin inhibitor in roots under Zn deficiency. while the absence of auxin inhibitor imparts zinc efficiency attributes in rice (Begum et al. 2016). Auxin signalling is, therefore, crucial for Zn- efficiency in plants under Zn-limited environments. The level of gibberellic acid in *Zea mays* L. was also recorded as low in Zn-deficient plants with variable responses shown by GA1 and GA20. The concentration of GA20, a precursor of GA1, showed a lesser reduction, while GA1 recorded 2.6–6.3-folds lower levels in Zn-deficient plants. Thus, Zn is suggested to affect the conversion of GA20 to GA1 by interfering with transcription or translation steps (Sekimoto et al. 1997). A weaker ethylene response due to slower activation of senescence, since Zn is a component of the receptor for ethylene response and its deficiency may reduce the plant's sensitivity to ethylene (Navarro-Leon et al. 2016).

The classical plant hormone, ethylene is considered a potent hormone that regulates various physiological and morphological responses in plants by interacting with other signaling molecules (Fiebig and Dodd 2015; Khan et al. 2015a, b). Ethylene plays an important regulatory role in plant responses to mineral nutrient availability, such as nitrogen (Iqbal et al. 2015), phosphorous (Li et al. 2009), potassium (K; Jung et al. 2009), calcium (Ca; Xu et al. 2010), magnesium, manganese (Dorling et al. 2011), copper (Arteca and Arteca 2007), and zinc (Khan and Khan 2014), and upregulates plant responses under both optimal and stressful conditions (Iqbal et al. 2013).

Numerous studies have demonstrated that ethylene is involved in root developmental responses to nutrient deficiency, including phosphorus starvation and iron restriction. The involvement of ethylene in potassium, sulfur, and boron deficiency reactions has been confirmed, and it has also been proposed to be associated with magnesium starvation (Hermans et al. 2010). The possible contribution of ethylene to N-related physiological responses could be linked to the susceptibility of expression of NRT1.1 and NRT2.1 (the NO_3^- transporters) to ethylene, and maize is more sensitive to ethylene under low N conditions (Schmelz et al. 2003).

Ethylene biosynthesis and plant responses vary with the availability of mineral nutrients (Iqbal et al. 2013). The role of ethylene in responding to N status in plants has been identified (Fiebig and Dodd 2015; Iqbal et al. 2015). The availability of N concentrations modifies the effect of ethylene and plant responses, like other mineral nutrients such as phosphate (Li et al. 2009), sulfate (Zuchi et al. 2009), potassium (Shin and Schachtman 2004), iron (Romera and Alcantara 1994). Plants under low N conditions accelerate their development and usually show an early transition to the reproductive stage, reaching the earlier senescence stage where ethylene is coined as a senescence hormone.

Ethylene is synthesized by two enzymes encoded by small gene families: 1 aminocyclopropane 1 carboxylic acid (ACC) synthase (ACS) and ACC oxidase (ACO). The reaction is first catalyzed by ACS, which converts S-adenosyl-L-methionine (SAM) to ACC, and then ACC oxidase catalyzes the conversion of ACC to ethylene with the release of CO_2 and cyanide. ACS is the rate-limiting step in ethylene biosynthesis and controls the main step in stress-induced ethylene regulation (Tsuchisaka et al. 2009), whereas ACO activity is constitutively present in most vegetative tissues. The ethylene biosynthetic pathway is relatively simple, but its production is strictly regulated at various N levels. In addition to transcriptional regulation (Tsuchisaka and Theologis 2004), post-translational regulation is pivotal for developmental and stress-induced ethylene production (Lyzenga et al. 2012). In the case of nitrate starvation, 1-aminocyclopropane 1 carboxylic acid ACC synthase ACS7 and a putative ACO (and ACS10) were strongly repressed in seedlings, but both were induced in rosette samples treated with low and high N levels, whereas ACC synthases ACS8 and ACS4 and ACC oxidases ACO1, ACO5, and ACO2 were negatively regulated under both conditions. However, ETO1 (OVERPRODUCER1), SAM1, EOL1-like (ETO-like) and other putative ACO were induced in response to N deprivation and low/high N conditions. Thus, the multi-gene ACS and ACO families are both temporally and spatially differentially expressed under low N environmental conditions, as has previously been shown in the case of stresses such as Pi-deprivation (Kim et al. 2008), and depend on the species, tissue, and developmental stage of plants (Trivellini et al. 2011). Large-scale transcriptome analysis has detected an ACO6 homolog involved in ethylene synthesis during the early response of seedlings to N deficiency (Zhao et al. 2015), and the induction of an ACO4 homolog and an ACO-like transcript has been observed in response to N starvation in studies of chronic low N conditions. Khan et al. (2015a, b) reported that the expression of ACS2, ACS6, and ACS7, and ACO2, ACO3, and ACO4 was increased during the senescence of wheat plants, but only ACS6 was first induced after 4 days of N deficiency and then reduced 3 h after N resupply. ACO2 and ACO4 transcript levels were also increased by N deprivation and then alienated in wheat after 3 days of N resupply, once again highlighting the complexity of ACS and ACO regulation by various stress signals. Khan et al. (2015a, b) showed that ETO1 and EOL1 are slightly expressed under low N treatment. Khan et al. (2015a, b) stated that ethylene-responsive genes typically involved in hypoxia are potential connectors in the gene/metabolite/hormone-related network of response to N starvation, but further studies are necessary for verifying their possible involvement in the N assimilation and signaling mechanisms.

The presence of N in available sources affects ethylene production and photosynthesis, stomatal conductance, and plant growth. Iqbal et al. (2015) have reported that N availability regulates ethylene formation, which regulates plant N content and nitrate reductase (NR) activity. Nitrogen deficiency leads to strong synergistic interactions between volicitin and ethylene, indicated by the induction of volatile sesquiterpene and indole emissions. Whereas volicitin-induced volatiles are greatly reduced in plants with medium N levels, there are virtually no interactions with ethylene. The altered volicitin–ethylene interaction due to changes in the magnitude of induced volatile emissions observed in plants with low and medium levels of N availability is consistent with the known increase in ethylene sensitivity that occurs during N deficiency (Schmelz et al. 2003). N deprivation enhances the sensitivity of ethylene-responsive cells in the root cortex, thus leading to cell lysis and aerenchyma production, and using ethylene further enhances aerenchyma formation in N-starved roots (He et al. 1992). N starvation increases the number or affinity of root receptors, thus allowing roots to respond to lower concentrations of ethylene than those found in unstressed maize roots (Saiz-Fernández et al. 2015). Ethylene regulated fully developed and expanding leaves by decreasing their leaf area when ethylene increased in developing tissues (He et al. 2009).

N deficiency triggers root sensitivity to ethylene and follows aerenchyma production in maize seedlings (He et al. 1992), although ethylene production is reduced (Drew et al. 1989). N deficiency also increases ethylene evolution in leaves as a consequence of stress (Legé et al. 1997). N starvation or deficiency also induces leaf senescence (particularly leaf yellowing), promotes the re-mobilization of nutrients from leaves to storage organs, and increases tissue sensitivity to ethylene. Many plants react to N starvation by activating the phenylpropanoid pathway and accumulating anthocyanins (Lea et al. 2007). In particular, low N levels in soils or growing media activate phenylalanine ammonia lyase (PAL), the key enzyme of phenylpropanoid compounds. Moreover, N availability affects fruit development and quality. In particular, low nitrogen content delays ripening, and fruits are poor in sugars, affecting negatively the overall quality. Plants harvested from the soil with deficient (0 or 50 kg ha^{-1}) or excess N (165 kg ha^{-1}) levels have the same rate of ethylene biosynthesis. Mi et al. (2008) reported that, under low N conditions, the auxin, cytokinins (CK), and nitric oxide (NO) are implicated in regulating root elongation: an abundant N supply promotes CK but reduces auxin and NO levels in the roots of maize. In addition, the application of CK enhances ethylene production (Stenlid 1982; Bertell et al. 1990). Nitrate-induced inhibition of root elongation in maize is significantly reversed by treating the roots with a NO donor (SNP) and IAA (Zhao et al. 2007). In the presence of high nitrate levels, endogenous levels of NO in the root apices of maize seedlings are much lower than those in apices grown in the presence of low nitrate levels. The inhibition of NO synthesis reduces root elongation in maize plants grown in a low-nitrate medium (Mi et al. 2008).

It has been reported that N application causes CK production in detached leaves (Salama and Wareing 1979). The nitrate transporter NRT1.1 modulates AtIPT3 expression as a response to nitrate (Ho et al. 2009). Kiba et al. (2011) reported that CK represses the nitrate transporter gene and nitrate uptake regardless of plant N status. However, CK regulates the expression of N uptake- and assimilation-related genes, as well as root architecture (Rubio et al. 2009; Krouk et al. 2011a, b). CK may act as a long-distance "root-to-shoot" signal associated with NO_3^- supply (Sakakibara 2006). In addition, Ruffel et al. (2011) found that CK is important for the root-shoot-root signaling mechanism which conveys the NO_3^- status of the plant, thus enabling a compensatory increase in lateral root growth in NO_3^--rich places of the root foraging for N resources in a heterogeneous N condition.

Sun et al. (2015) denoted that the NR produces NO in *Oryza sativa*, which enhances N acquisition capacity by increasing the initiation of lateral roots and the uptake of inorganic N, a strategy that allows the plants to adapt to a fluctuating nitrate supply and increase NUE. Liu et al. (2010) found that ethylene triggers

NO. In this respect, N availability affects ethylene biosynthesis and signaling, which further increases N uptake and transport to enhance plant growth. Ethylene induces N absorption on root architecture and affects N transport-related genes. The action of ethylene on N uptake or root growth is linked to other phytohormones as low nitrate contents induce CK, auxin, ABA, and NO. CK enhances ethylene biosynthesis, which acts in combination with auxin to secure root growth and the production of the lateral root. These hormones are affected by N and affect root growth, as their cross-talk enables them to get N during the conditions of limited supply. Inhibiting these phytohormones under the condition of limited N availability could provide insights into their mechanism of action, and enable the use of ethylene as a means of increasing plant NUE, avoiding N wastage, and preventing environmental pollution.

In conclusion, cereals have induced multiple strategies to grow on diverse soil types. These adaptations are associated with many alterations in root/shoot growth, biochemical changes, antioxidants, and reactive oxygen species and modulated by variation in phytohormone accumulation and distribution. These alterations at the level of phytohormones could be upregulated or downregulated based on the deficit nutrient.

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Cereals and Phytohormones Under UV Stress

17

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Abstract

The global population is growing at a rapid pace that is directly proportional to increasing food demand. Besides productivity is likely to stay steady and perhaps even decline due to climate change and various other abiotic factors including UV. This stress is significantly enhanced by environmental contamination such as halogenated hydrocarbons. Since plants are regarded as sessile organisms, they are unable to escape exposure to potentially stressful environmental conditions. Mild stress conditions can result in active acclimation responses, whereas according to research more severe stress conditions can result in metabolic abnormalities. Changes in the amount and ratio of phytohormones produced by plants are among the initial responses of plants to environmental stressors. Sunlight is a key characteristic of photosynthesis that allows crops to fine-tune their morphological traits, growth, and metabolic processes. A part of solar radiation known as ultraviolet light has a substantial influence on the development and metabolism of plants. The buildup of antioxidants and secondary

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metabolites in plants is a frequent acclimatization response to a variety of environmental stresses in the environment. When it comes to metabolites, UV light has a significant impact on the levels of a diverse spectrum of substances such as phenolic, terpenoid, and alkaloid compounds. In this chapter, we illustrated the levels of several of these phytohormones' responses because of ultraviolet radiation.

Keywords

Phytohormone · Cereals · Biostimulants · Metabolites · Ultraviolet rays

17.1 Introduction

The population of the earth is growing at a rapid pace with an estimated 9.1 billion individuals by the end of 2050, yet the output of agriculture production is not sustainable for the grown population. It is highly complicated to raise productivity since the cultivation area is likely to stay steady and perhaps even decline as non-farming activities put more demand on soil and other resources (Schröder et al. 2018). Considering climate warming on the horizon, abiotic factors are seen as a key stumbling block to agricultural output. According to various assessments, abiotic stresses are responsible for around 70% of the overall agricultural production reductions, either actively or passively (Ali et al. 2021; Fakhar et al. 2020; Khatoon et al. 2020). Abiotic stress can cause structural, metabolic, hormonal, and genetic modifications and negatively affect the development and production of plants. Salinity and extreme temperatures that result in drought (Ortas et al. 2021) and UV radiation are indeed the principal factors of reduction of yield or crop failure throughout the world, posing danger to food and nutrition stability. The introduction of species that tolerate stress effectively can be a viable solution to these issues. For agricultural plant functional genomics, all traditional reproductive strategies have widely been used, namely, screening, polyploidy, hybridization, and mutations. Discovery of innovative methods and their applications along with current standard and modern breeding technologies seem critical achieving of today.

Today's world wants significantly to boost productivity with scarce supplies such as fertilizers and water. The understanding of various systems that are formed and performed by plants to cope against abiotic stresses to maintain growth and even for survival during extreme conditions has a significant influence. Phytohormones such as auxins, ethylene (ET), gibberellins, and cytokinin (CK), as well as their novel counterparts such as brassinosteroids, strigolactones, and jasmonates, have recently been shown to be important metabolic engineering targets for inducing abiotic stress resistance in plants (Raza et al. 2019). Abiotic stresses meeting the challenges of a changing world heat, drought, salt, freezing, chilling, viruses, ozone, and ultraviolet radiation are a few of the environmental conditions that have a significant impact on crop growth.

Anthropogenic and environmental factors including temperature such as freezing, chilling, drought, salinity viruses, ozone, and UV radiations all have a significant impact on plant growth and agronomic yield (Amin et al. 2021; Egamberdieva et al. 2017; Gurmani et al. 2021). Plant associated with adverse health effects could be regulated substantially through reproductive phases of plant biotic and abiotic stress. Different genotypes of different species influence the susceptibility to various stresses markedly. Regrettably, the processes through which plants maintain production in the presence of abiotic stressors are still incompletely defined. Light is an essential element for photosynthesis that also contributes to collecting data about the atmosphere, weather conditions, and length of day/night, allowing crops to tweak their morphological characteristics, growth, and metabolic activities. Light energy is absorbed via photoreceptors inside spectral bands, allowing crops to interpret qualitative and quantitative data. Technological advances are indeed being invented to improve complex physiological and genetic responses executed by plants to increase survival rate and minimize loss under various stresses. The solar spectrum comprises UV radiation. The radiation ranges from UVB (280–315 nm) and UVA (315–400 nm) are least harmful to flora and other life forms and are not quite as efficiently intercepted, whereas the ozone layer absorbs the majority of UVB and whole UVC rays that measured less than 280 nm. Unfortunately, owing to the ozone layer's degradation, intense solar UV radiation often hits the crust. As a result, plants and other life forms' prolonged exposure particularly to UVB, has risen (Sharma et al. 2020).

UV rays cause structural modifications within biomolecules like lipids, carbohydrates, DNA, RNA, and proteins. It is depicted as high levels of UV exposure can affect physiological and metabolic activities in plant cells, including suppression of photosynthesis, reduction in nitrogen absorption, biomass degradation, and suppressed cell growth and division or even plant growth arrest. Plant resistance to UVB is affected by atmospheric temperature and humidity, plant species' geographical area, as well as vegetation at locations with chronic exposure, which is highly immune to ultraviolet rays versus those that get intermediate ultraviolet light. Several writers argue whether UV radiation seems to have little or no discernible impact on crops but rather that it also might induce beneficial contributions like the expansion in chlorophyll and mineral concentrations (Egamberdieva et al. 2017). Nonetheless, it is widely held that perhaps the influence of ultraviolet radiations on vegetation is dependent on UV light intensity and length of contact (Vanhaelewyn et al. 2016).

17.2 Ultraviolet (UV) Stress

The depletion in the stratospheric ozone layer primarily due to the consequence of human-induced activities that significantly enhanced environmental contamination such as halogenate hydrocarbons has become a major topic of attention over the latest generations. The deterioration of the ozone layer might result in a massive rise in UVB (290–320 nm) radiation that reaches the earth's crust (Fig. 17.1).

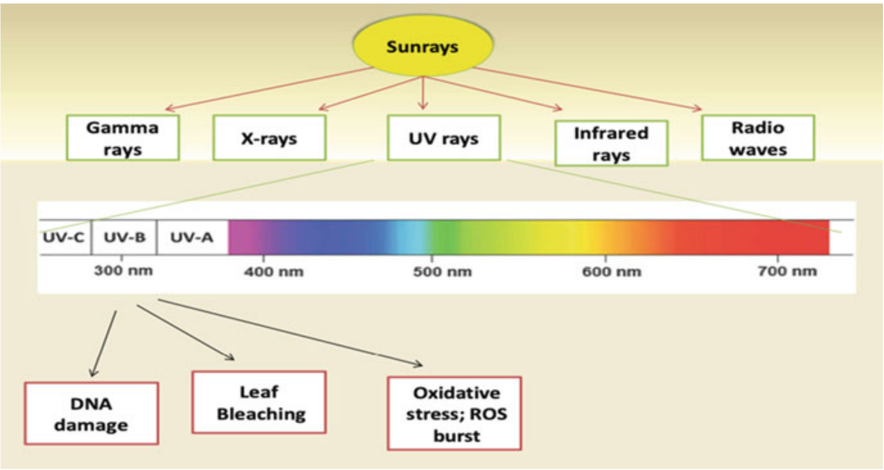

Fig. 17.1 The UVB stress accounts for the majority of photoexcited injuries in plants. Adapted from (Banerjee and Roychoudhury 2016)

The impact of UVB exposure enhances the thickness of leaf, epidermal reflectance, lignin levels and the buildup of the UV-absorbing compounds notably flavonoids. Poor growth and decreased chlorophyll content seem to be common side effects of these adjustments. Caputo et al. (2006) reported that the effects of natural UVB on plant quality appear to be mediated by activation of signaling circuits which is related to jasmonic acid's functional role. Ultraviolet light has reportedly shown linked with the browning of leaf and the degradation of cellular membrane-sensitive sites like photosystem II (PSII) reaction center, acceptor and the donor sites, and the light-harvesting complex (LHC) has been identified because of multiple incomplete processes of the mitochondrial electron transport chain. Investigations revealed that whenever the water-splitting complexes and P680 on the oxidizing end of photosystem II were exposed to ultraviolet radiation, their operational coherence between them was disrupted (Agrawal 2019). It is known that UVB radiation swiftly destroys the chloroplast protein D1 (QB) (Cai et al. 2016). The agglomeration of Mn of water redox is the more vulnerable member of the electron transport system, and UVB light uptake by the protein network or other oxidative molecules can destabilize the cluster of Mn and render photosynthesis activities. Plants grown under observation in conservatories perform distinctively and shown low PAR than those growing in regular lighting.

The acids that include an aromatic ring or aromatic amino acids, namely, tyrosine, phenylalanine, tryptophan, histidine, cysteine, and cystine, usually capture more UVB radiations and therefore set themselves as primary UVB rays' victim. Even though cysteine is a weak UVB absorbent, it may suffer photolysis by the strong quantization rate, resulting in the breaking of covalent disulfide structures into hazardous sulfhydryl radicals. Consequently, the whole protein's structure disrupts, resulting in the development of aggregates. The example of disruption includes protein components of PS (I and II), ATPase, ribulose 1, 5-bisphosphate (Rubisco), and violaxanthin de-epoxidase (or violaxanthin). Unsaturated fatty acids (FAs), phospholipids, and glycolipids that are usually found abundant in cells are also degraded by UVB radiation in the existence of oxygen in plant cellular membrane (Schmidt et al. 2016). UV radiation has the potential to cause damage to DNA molecules by causing the formation of pyrimidine (6–4) pyrimidinone dimers (6–4 PPs) along with cyclobutene pyrimidine dimers (CPDs). As a precursor for the synthesis of such amides, polymerases become unable to reach certain substantial areas, causing transcription, multiplication, and ultimately death of cells (Gillet et al. 2021). After contact of plant cells with UV gamma radiation polygalacturonase and pectin, methylesterase activities are enhanced because of the dissolution of the pectin. Low light density is roughly about 40–50% of the normal intensity of light. Consequently, it is around 40–60% lower than that of the intensity of light over the summer months (Lu et al. 2016).

During low light intensity, the growth curve and production of two rice cultivars (indica) from Kharif and three from Rabi season were evaluated. The buildup of dry matter is influenced by plant development in the shadow at all phases. From primal commencement onwards, those impacts remained crucial. The emergence of the panicles seemed to be a product of the luminosity inside the zone of 26–9 °C of average peak temperatures. Reduced illumination level was shown to represent a key barrier to increased production throughout the rainy season, with lower returns around 3.2–4.4 tones ha^{-1} in rice genotypes that achieved 8–10 tones ha^{-1} with strong exposure. Hence, reduced light environments appear as stress producers, due to the lack of energetic photons to feed photosystems and control photosynthesis. Inadequate photosynthesis enables autotrophic vegetation to produce limited energy, resulting in either unusually delayed growth rates or decreased output. Rice cultivars incubated by using 5-aminolevulinic acid (ALA) inside the dark and independently subjected to reduced illumination showed comparable oxidative damage characteristics under drought, which was attributed to the production of singlet oxygen (dioxygen) in the seedlings including equally drought stress after incubation with ALA. Exposure of rice seedlings to ALA led to a significant buildup of protochlorophyllide that photodynamically produced singlet oxygen (dioxygen) amid the lower light concentration.

When crops are subjected to excessively higher intensity light, acute photoinactivation and dermatophytosis of the photosynthesis system along with the deterioration of photosynthetic enzymes and proteins have already been reported. The greatest downside consequences of intense luminosity include the breakdown of Rubisco's large subunit, PSII D1 proteins, and reduced concentrations of PSI polypeptides such as *PsaA*, *PsaB*, and *PsaC* (Banerjee and Roychoudhury 2016). The amenable paths linked to UVB influenced reactions in crops, even though the stress produced by the light is primarily centered on UVB-mediated stress. The significant UVB antibody is UVR8, a seven-bladed propeller protein that was initially defined in *Arabidopsis* mutant strains that demonstrated hypersensitivity to UVB radiations. As per findings from UVR8 transcriptional research, UVR8 is indeed a master controller of several genes engaged in UV injury healing. UVB

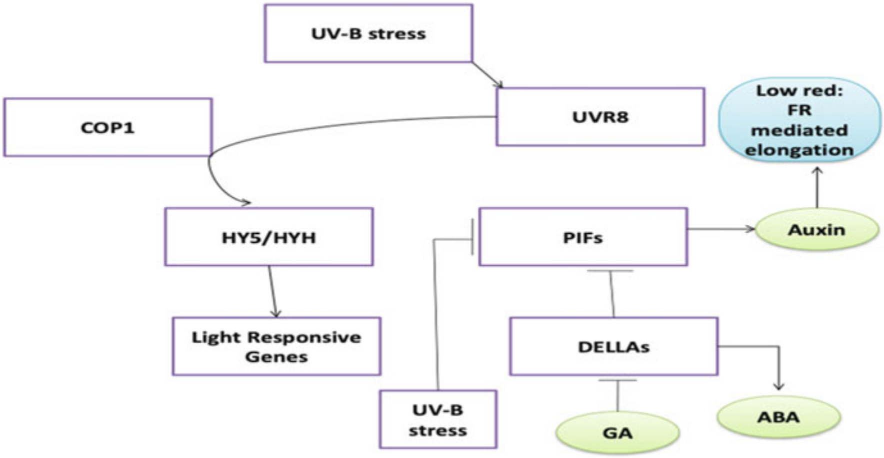

Fig. 17.2 COPI is defined as a retained RING finger E(3) ubiquitin ligase that plays an important role in plants' cell growth, plant cell survival, and metabolism in mammals (Banerjee and Roychoudhury 2016)

radiation stimulates UVR8 circulation inside the cells, focusing it primarily on the nucleus.

The biological significance of UVR8 is still unknown; however the protein can act as a transcription variable that interacts with elongated hypocotyl 5's promoter domain (HY5). HY5 would be a *bZIP* transcription factor that regulates photomorphogenesis across a broad spectral range involved in the vertical or horizontal regulation of light-responsive genes. Since hy5 alleles are sensitive to UV-B, HY5 is a favorable mediator in UVB-induced signaling. Cop1 and UVR8 are the new alleles, which were identified by (Favory et al. 2009), who highlighted the relevance of UVR8's structural contact with COPI, an E3 ubiquitin ligase (Heilmann et al. 2016) (Fig. 17.2).

17.3 Responses of Phytohormones Under UV Stress

Although it is unsurprising that hormones significantly contribute to UVB-induced stress signaling, the research on this specific issue continues to remain limited and enigmatic, although several promising results show how hormones may reduce severe ultraviolet radiation stress via modulating anti-inflammatory molecules. Auxins regulate all growth processes of the plant including root, leaf, and shoot growth, cellular elongation, and division as well as photo- and gravitropic progress. These constitute primarily biosynthetically generated by amino acid tryptophan and are recognized via two kinds of proteins, firstly membrane-associated auxin-binding protein (ABP)1 and secondly TIR1/auxin signaling F-box (AFB) receptors' UVB-induced alterations in the auxin-related expression of genes in saplings and mature foliage (Ku et al. 2018). Auxin participation in UVB-mediated metamorphosis may take place at several stages. Photooxidative injury, biosynthesis conjugation, or breakdown can all impact auxin equilibrium. Photodegradation of indole acetic acid (IAA) decreases its amount and potency. It would have an immediate impact on cell biology and unable plant cells to digest or use IAA as a result (Souza et al. 2017). The number of plant growth promoting rhizobacteria (PGPR) that can produce IAA can be used (Rafique et al. 2019).

17.4 Phytohormones: Fundamental Entities of Plant Defense to Cope Abiotic Stresses

Plant hormones are defined as biological substances that regulate plant/seed germination and growth, fruit development, and seed production. As a result, when plants come under stressed conditions, these biological compounds elicit behavioral reactions. Through stimulation to the expression of genes, phytohormones regulate complicated signaling networks. Indole-3-acetic acid (IAA), in cytokinin (CK), abscisic acid (ABA), ethylene (ET), gibberellic acid (GA), brassinosteroids (BR), jasmonic acid (JA), salicylic acid (SA), and strigolactone (SL) are some of these hormones (Sharma et al. 2020).

17.5 UV and Auxin

Auxin modulation is related to transcriptional elements involved in UVB signaling. HY5 is a transcriptional mediator involved in auxin signaling and auxin trafficking according to genetic sequencing of HY5-targeted genes. Auxins are responsible for cellular growth and division, leaf formation, shoot/root growth, and photo- and gravitropic development. These constitute primarily biosynthetically generated by amino acid tryptophan and are recognized via two kinds of proteins, firstly membrane-associated ABP1 and TIR1/AFB receptors. The AFB is involved mostly in the breakdown of AUX/IAA receptors that are ARF regulators. Consequently, auxin behavior is regulated passively by auxin. UVB-subjected seedlings have a pygmy morphology, having tiny dense foliage on little branchlets, leaf twisting, little flowering, with a higher root and shoot ratio. Such UVB-produced morphological alterations indicate auxin-regulated mechanisms, implying as auxins are engaged in UVB-controlled adaptation activities with medium UVB concentrations as well as the stress reaction caused by severe UVB levels. Auxin engagement in UVB-produced metamorphosis may take place through several stages. Photooxidative degradation, biosynthesis, conjugation, or even destruction could all impact auxin stability.

The photoreceptor of the UV-B resistance 8 (UVR8) intercedes various ultraviolet B reactions in crops; however, the potential of UVB resistance 8 (UVR8) in managing the growth of root is still not examined recently. We demonstrate here how UVB radiation inhibits *Arabidopsis* secondary root growth in a UVR8-dependent manner. Monomeric UVB resistance 8 (UVR8) hinders auxin reactions inside tissue-autonomous way and consequently manages secondary root development. Across the genome quality articulation investigation showed that auxin, what's more, UVB illumination, unfairly controls auxin-managed quality articulation. Researchers further demonstrate that UVR8 communicates with MYB73/MYB77 (MYB domain protein 73/77) in a UVB relying on manner. UVB resistance 8 (UVR) hinders the improvement of the lateral root through the guideline of MYB73/MYB77.UVR8 gets activated via UVB radiation that restricts the DNA-restricting activities of MYB73/MYB77, as well as the preservation of respective objectives of auxin-responsive characteristics. According to our findings, ultraviolet B light and UVB resistance 8 (UVR) are required for both plant morphology and root development. UVB resistance 8 (UVR) and MYB73/MYB77 form a major UVB subordinate interaction that integrates light and auxin warning, plus handles additional UVR8 reporting functions in plants (Wan et al. 2018).

Ultraviolet B radiation-initiated root twisting has been accounted for; notwithstanding, the hidden instruments generally stay muddled. Those plants exposed to UVB develop a dwarf phenotype, which includes small, thick leaves with short petioles; leaf curling; a short inflorescence; and an increased root/shoot ratio, among other characteristics. UVB-induced changes in plant morphology allude to the involvement of auxins in specific auxin-regulated processes, implying that auxins are engaged in UVB-induced acclimation processes under moderate UVB doses as well as the stress response generated by high UVB doses (Vanhaelewyn et al. 2016).

17.6 UV and Jasmonic Acid

Jasmonic acid (JA) is a notably recognized hormone that act as protection against herbivores as well as injury reaction. Ultraviolet B has already been found to enhance the synthesis of JA at significant concentrations. For instance, following UVB exposure, JA been found to function as a facilitator in stress responses by inducing superoxide dismutase (SOD) and peroxidase (POD) functions in *Hordeum vulgare* (Quan et al. 2018). Exogenous JA was lately demonstrated to decrease catalase (CAT) action and anthocyanin accumulation in wheat (*Triticum aestivum* L) plants under UVB treatment while increasing SOD and POD capabilities. In contrast to plants administered simply by methyl jasmonate (MeJA), the efficiency of photosynthesis in plants pretreated with methyl jasmonate (MeJA) increased marginally following UVB irradiation. Simultaneous UVB and methyl jasmonate (MeJA) reduced carbon dioxide (CO_2) fixation in barley plants, but methyl jasmonate (MeJA) illustrated a greater impact. Instead of acting as just an osmotic compensation facilitator, methyl jasmonate (MeJA) induced proline buildup in barley plants which is an element of the antioxidative resistance mechanism. The rise in methyl jasmonate (MeJA) concentration coincides with the onset of stress, and via stomatal conductance, the seedlings were able to adapt to atmospheric variations, osmotic adaptation, production of stress proteins, reduced ionic buildup, and an elevated amount of internal proline. While barley plants were exposed to methyl jasmonate (MeJA), antioxidant enzymatic functions, for example, SOD, CAT, and POD, which are engaged in efficient hydrogen peroxide (H_2O_2) sequestration mechanisms, increased (Yu et al. 2018). In a study when wheat was treated with methyl jasmonate (MeJA) and subjected to UV radiation, increased antioxidant enzyme activity, proline and anthocyanin accumulation, chlorophyll a and b content, maximum potential and effective quantum yields, as well as the rate of electron transport were observed. Similarly exogenous JA lowered cat activity and anthocyanin concentration in wheat seedlings when exposed to UVB but increased SOD and POD activities in the same plants, demonstrating that JA works as a mediator in plant defense (Souza et al. 2017).

17.7 UV and Brassinosteroid

Brassinosteroids (BR) are known as plant-specific androgenic steroid hormones that have potent development effects, and therefore, they are usually involved in almost every plant growth stage. Along with white light, the BR antithetically controls the evolutionary transformation from debility in night to photomorphogenesis during day times. In a nutshell, BR signaling works through using underlying methodology: brassinosteroid insensitive 1 binds to BR (BRI1), which causes the intracellular kinase domain to be activated, triggering a descending signaling cascade which ultimately results in beneficial synchronization of the BR reactions through nuclear navigation and dephosphorylation of two different transcriptional regulators, namely, brassinazole resistant1 (BZR1) and brassinosteroid insensitive1-ethyl methanesulfonate-suppressor (BES1). DWARF1 (DWF1), brassinosteroid insensitive 1 suppressor 1 (BRS1), and BES-interacting MYC-like protein (BIM1) are all regulated by ultraviolet B, indicating that ultraviolet B actions are dependent on BR signaling.

Seedlings can be stressed by ultraviolet B radiation, although it’s unclear why they combine their development and ultraviolet B stress reactions. According to a new study, BR signaling reduces UVB stress in plants through regulating flavanol production. BRI1-EMS-SUPPRESSOR 1 (BES1) is also shown to influence the balance between plant development and ultraviolet B defensive reactions. MYB11, MYB12, and MYB111, transcriptional genes that promote flavanol production, are repressed by a dominant transcriptional regulator implicated in BR signaling. Branching enzymes (BES1) links immediately to the enhancers of such myeloblastosis.

The MYBs in a BR-enhanced way, repressing their activity and therefore lowering flavanol synthesis. On the other hand, broadband ultraviolet B suppresses branching enzymes (BES1) activity to increase flavanol synthesis. Such results indicate how branching enzymes (BES1) triggered by BR stimulate expansion while inhibiting flavonoid production. Ultraviolet B stress reduces branching enzymes (BES1) transcription to spend resources upon flavonoid biosynthesis and ultraviolet B stress reactions, thus, enabling seedlings to transition from development to ultraviolet B stress reactions more quickly (Liang et al. 2020).

The species and cultivars can differ significantly in their response to ultraviolet radiation, and as with other environmental signals, a thorough understanding of genotypic sensitivity to ultraviolet radiation is essential for achieving increased crop resilience in the field. The selection of cultivars that orient in a manner that may allow for the prediction-based exploitation of beneficial UV-mediated outcomes is arguably a key determinant of UV response. In more general terms, genotypic variation is bound to result in variation in plant architecture, which may expose plants to more or less UVB depending on the genotype present. For example, there are several significant cases in which a higher photosynthetic rate has been seen in a variety of research focused on monocotyledonous species, such as wheat, barley, and rice. Further research into the regulating effects of ultraviolet radiation on architectural development would be a wise investment of time and resources. Further research in regulating effects of UV radiation on architectural development can be a wise investment. For example, rice grain yields have been connected with changes in leaf angle and dwarf habit caused by loss of function of the brassinosteroid insensitive1 orthologue OsBRI1 (Wargent and Jordan 2013). Interestingly, there are already early indications that brassinosteroid activity may contribute to the UVB growth response, which is a promising development (Hectors et al. 2007).

17.8 Gibberellins

Gibberellic acid (GA) constitutes hormones that stimulate seed germination and then flowering; according to the scope of the present study, they also act as favorable promoters of expanded growth, but their signaling is highly based on the degradation of key DELLA proteins, which inhibits development (Xie et al. 2016). The spectrophotometric properties of GA may be somewhat altered by ultraviolet B, although this does not affect their development abilities. Ultraviolet B management of GA routes is likely genetically regulated, and connections among ultraviolet B signaling elements and GA signaling corroborate with this. Ultraviolet B tends to have a general detrimental influence on GA concentrations since ultraviolet B decreases GA concentration in rice. Complex interactions among multiple hormones manage a plant’s overall growth and development which is critical at various phases of development. Plant mortality, propagation, and seedling growth in an adverse environment are all important parts of plant growth. GA and ABA are major phytohormones that regulate the linked physiological processes. Seed germination and growth, root propagation, leaf area determination, floral origination and growth, mating, and fruit growth are among the processes in which GAs play a role. For healthy plant growth and development, ABA is necessary, despite its relationship with abiotic stressors. It regulates many downstream ABA-dependent stress responses in response to various abiotic stressors. Plants maintain a steady equilibrium of GA and ABA levels at various tissues and organs throughout the embryonic process, even in unfavorable environmental or physiological situations. In this paper, we will look at how GA and ABA regulate distinct plant growth phases, with an emphasis on abiotic stresses and root development. The potential for GAs and ABA to interact activities from the pathways would be investigated, along with an emphasis on downstream stress signaling factors, kinases, and transcription factors (TFs). It will be demonstrated how important numerous critical ABA and GA signaling intermediates are. Such research will also aid in the development of future crop improvement methods by providing a firm foundation (Vishal and Kumar 2018).

Since the plant hormones, ABA and GA, play an important role in a variety of growth phases, including seed protection and sprouting, root growth, and blooming cycle regulation, in an antagonistic manner, finding the right balance between the two is critical for the growth of plants. Although, the exact mechanisms governing ABA–GA opposition have remained unclear for more than a 50 after their introduction. ABI4 in *Arabidopsis* and OsAP2-39 in rice are twin APETALA 2 (AP2)-domain-containing transcriptional (ATFs) that tend to contribute significantly to ABA and GA antagonism, according to new data. These twin signaling pathways regulate the expression sequence of GA and ABA biosynthesis or inactivation genes, therefore mediating ABA and GA concentrations (Shu et al. 2018).

17.9 Abscisic Acid

A variety of researches on ABA and ultraviolet B interconnections are published. Ultraviolet B radiations have a detrimental impact on ABA even at limited uptake. ABA seems to rise in response to stress and have an antioxidative function under this situation since ABA biosynthesis variants seem to be more susceptible to UVB in terms of foliar damage (Vishwakarma et al. 2017). It is still unknown yet if the former finding results in even lower ABA or represents a return suppression mechanism designed to counteract an ABA surplus. During the second research, it was discovered when ultraviolet B bombarded *Zea mays* leaves, depicted 100% rise in ABA content (Tossi et al. 2009). The plant hormones ABA govern plants growth and development, stress reactivity, stomatal sealing, senescence of leaf, osmotic management, accumulation of cuticular wax, seed germination, bud dormancy, and growth arrest. Through transcriptional and posttranscriptional pathways to abiotic and biotic changes in the environment are regulated by ABA. The ABA biosynthesis and several of its signaling pathways have been well studied during the last 20 years (Chen et al. 2020).

Under water-stressed conditions, the ABA is critical for regulating stomatal movement. In the last decade, research has considerably enhanced our understanding of the mechanisms at the molecular level governing ABA-mediated stomatal closure, thanks to the discovery of ABA receptors and signaling core, which includes protein phosphatases (PP2C), PYL/PYR/RCAR, ABA receptors, and serine/threonine kinases (SnRK2) protein kinases. With the help of recent studies understanding the ABA signal transduction governing systems, as well as the physiological consequences of basic ABA signaling in CO_2 and evaporative pressure imbalance, stomatal homeostasis becomes easier. In addition, recent progress in identifying the interconnections between ABA and supplementary stomatal signaling route is discussed in the literature (Hsu et al. 2021).

In a study Vanhaelewyn et al. explained the accumulation of more ABA in rice upon moderate to high UVB levels. In this case, ABA appears to increase upon stress and cause a photoprotective effect as ABA biosynthesis mutants are more sensitive to UVB with respect to leaf injury (Vanhaelewyn et al. 2016). Phytohormones control numerous characteristics of plant growth, development, and tolerance to biotic and abiotic stress. Phytohormones have been extensively investigated concentrating on the modes of behavior and the systems that they control. The latest study, on the other hand, now shifted its attention toward a further difficult issue on how various plant hormones combine to control growth and development. The phytohormones ABA and auxin are the topics of this chapter. We will start with a quick rundown of each hormone individually. Then, whenever possible, in-depth investigations of ABA and auxin interactions focus on the connections that arise in tissues and how those develop. Finally, we conclude with a brief overview of the field's future possibilities (Emenecker and Strader 2020).

17.10 Ethylene

Ethylene is defined as a gaseous hormone that plays an important role in morphological and stress signaling activities. The interplay of ethylene and ultraviolet B signaling has received little attention in recent decays. The lack of ethylene insensitive 2 (EIN2), a major constituent and beneficial controller of ethylene signaling, has been found to result in increased resistance against ultraviolet B radiation via increasing flavonoid concentrations. Ultraviolet B-mediated ethylene is thought to also be generated through pectin inside the leaflets. In a second similar study, this was discovered that high photosynthetic photon flux density (PPFD) and a significant far-red (FR) lighting proportion enhanced phytochrome B-1 (PhyB-1)-induced ethylene synthesis in sorghum. Elevated ethylene generation facilitated shadow prevention through decreasing lamina and leaf sheath lengthening, while overall stem length was hampered. Finlayson et al. (2007) additionally found that phytochrome-A (PhyA) might help light-grown sorghum seedlings transduce shade signals via activating ethylene-induced reactions. Ethylene regulates germination rate, root development, flowering maturation, fruit ripening, and aging and responds to biotic and abiotic stresses. As a result, it has a significant influence on climatic responses which affect a plant's flexibility to cope and proliferate. The molecular processes that control ethylene synthesis and action have made significant progress in recent years. Several novel genes for ethylene synthesis, signaling, and reaction networks have been identified because of this study. The regulatory intricacy of ethylene is in stark contrast to its molecular simplicity. This one is demonstrated by the ample supply of genes that encode the vital ethylene biosynthesis enzymes 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and oxidase, along with numerous ethylene synapses as well as signal transduction constituents.

The sophistication of the supervisory process involves signaling transmissions and regulation of protein and mRNA interpretation and retention (Gao et al. 2020).

The first gaseous phytohormone discovered was ethylene. It is known as the highest fundamental olefin gas that is produced through plants to control their growth and stress behaviors via an erudite signaling pathway. The triple reaction is one of the first documented responses to ethylene. When dicotyledons grow in the shade, decreased hypocotyl and root development and expanded hypocotyl thickness and apical hook, these all seem to be indications of this reaction. The above method worked well enough for genetic assays, enabling researchers to identify several elements of the ethylene signaling system. The endoplasmic reticulum (ER) layer contains a series of ethylene sensors including ethylene-insensitive 2 (EIN2), constitutive triple response 1 (CTR1), an ER-inhibitory transmembrane protein with unclear biological function, a protein kinase along with different transposable elements, namely, EIN3-like (EIL), ethylene response factors (ERFs), and EIN3. According to our findings, homologous receptors communicate to CTR1 that suppress EIN2 and suppress downstream signaling in the deficiency of ethylene. Ethylene acts as an inverted agonist by inhibiting its receptors, decreasing CTR1 functioning, and releasing EIN2 inhibition. Most ethylene responses are triggered by EIN2 altering transcription and translation. Alternative mechanisms also affect ethylene responses, even though this is the most common signaling pathway (Binder 2020).

A study by Wang et al. showed that UVB radiation at various, mainly high, intensities stimulates ethylene production in many plant species including maize (Wang et al. 2006).

17.11 Salicylic Acid

Salicylic acid (SA), a biotroph protective hormone, has also reportedly been linked to reactive oxygen species (ROS) on several occasions. UV radiation may trigger the formation of ROS; therefore it’s no coincidence that this is linked to SA. When seedlings are exposed to ultraviolet B, a rise in SA has been reported several times. Ultraviolet B causes the buildup of SA in the leaves and roots of wheat and barley. Ultraviolet B stimulated considerable SA and avoided fading in wheat when combined with the osmolyte polyethylene glycol (Vanhaelewyn et al. 2016). Salicylate-induced ROS diminishes metabolism, increases persistence, and decreases membrane potential. To reestablish such results, cells can be grown in the context of a ROS quencher or in an anaerobic atmosphere. This data demonstrates how salicylate-induced oxidative stress may contribute to permanence, indicating the ROS and its impact on the potential of cell membrane and metabolic activities could contribute in persister formation (Wang et al. 2017).

17.12 Cytokinin

In terms of ultraviolet B modulation, several hormones have indeed remained understudied. There is a considerable dearth of information about the control of strigolactone (SL) and CK specifically. The impact of ultraviolet B on CK in rice varies throughout time. Furthermore, CK and elongated hypocotyl-5 (HY5) interact to control flavonoid production, and it seems like it may be possible that UVR8 signaling interacts with one another. Generally, CK regulates the division of cells, stem commencement and development, leaf senescence, mineral absorption, apex supremacy, gametophyte, sink/source dynamics, vascular and phyllotaxis, and embryogenesis. Along with this CK are also responsible for the reaction to biotic and abiotic factors. The processes underlying the activity of this phytohormone in plants have been elucidated thanks to molecular genetic research in *Arabidopsis* (Vanhaelewyn et al. 2016). Cytokinin is known as a group of plant hormones that regulates cell division and differentiation in certain plant tissue cultures. Several free, natural CK have been efficiently refined via high-performance liquid chromatography (HPLC) and identified unequivocally by mass spectrometry (MS). Plant tissues are known to contain certain nonspecific phosphatases which hydrolyze CK nucleotides to their corresponding nucleosides. These enzymes are not completely inactivated during the usual extraction method of plant growth substances by the homogenization of plant tissues in ice-cold 80% methanol or ethanol. As CK are present in most plant tissues and some microorganisms in very small amounts, the isolation of a CK of sufficient purity for characterization has required extensive use of chromatographic methods such as paper (PC), thin layer (TLC), gas (GC), and HPLC. Cytokinin glucosides have been identified as the dominant metabolites of CK when fed to several plant tissues (Senbagalakshmi et al. 2017).

17.13 Conclusion

It is obvious that with the effects of other components of the solar spectrum on plant physiology, the effects of ultraviolet B on plant physiology are mediated through hormones. Some of these hormones (ABA, JA, SA, and NO) are upregulated in their action, and they appear to be primarily stress related and involved in photoprotection. A variety of phytohormones are available that can accelerate seed germination, the mobilization and transfer of nutrients, the improvement of stress tolerance and disease resistance, and the modification of all growth processes. Other hormonal mechanisms (which are suppressed and primarily cause morphological changes) are also affected. Ethylene can either be upregulated, as part of a stress response to high UVB levels or downregulated, as part of a morphogen response to high UVB levels, depending on the situation. Although the information on BR, AU, and SL in respect to UVB is limited, it has been demonstrated that they have a functional association with components of the UVR8 pathway, making them candidates for interaction with UVB-controlled photomorphogenic processes. It is anticipated that the existing shortage of knowledge will rapidly diminish because of the growing interest in this subject.

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Cereals and Phytohormones Under Ozone Stress

18

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Abstract

Increasing tropospheric ozone concentrations severely affect cereal crop production globally. Excess amounts of ground-level ozone interfere with different physiological and biochemical processes, and, thereby, affect crop plants' growth, yields, and production. On the other hand, phytohormones play a vital role in plant growth, development, and stress tolerance. Therefore, it is important to elucidate the role of different phytohormones in plants' defenses system against ozone stress. Several phytohormones, namely, abscisic acid, auxins, ethylene, gibberellins, salicylic acid, and jasmonic acid, have important roles in the ozone stress signaling cascade. Their upregulation and downregulation are critical for the growth and development of different cereals, namely, rice, wheat, maize, and soybean, under ozone stress. Thus, in this chapter, we discuss the potential roles of the abovementioned phytohormones, their crosstalk with ozone stress tolerance, and possible mechanism to reduce ozone-induced harmful effects, which will ultimately help to minimize ozone-induced yield reduction in cereal crops.

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Air pollution · Ozone · Cereals · Phytohormones · Antioxidant · Oxidative stress · Food security

18.1 Introduction

Tropospheric ozone is a volatile secondary air pollutant with a short life that has a negative impact on crop productivity both directly and indirectly, by way of oxidative stress. Tropospheric ozone significantly reduces crop productivity (Mauzerall and Wang 2001; Fuhrer and Booker 2003; Ashrafuzzaman et al. 2021). Ozone is one of the major damaging pollutants to plants because of its phototoxicity and availability in rural/agricultural regions (Ainsworth et al. 2012). As fossil fuels and nitrogen fertilizers are overused, the concentration of ozone has risen dramatically in recent years (Meehl et al. 2007). Nitrogen oxides (NO_x), methane (CH_4), carbon monoxide (CO), and other hydrocarbons undergo photochemical reactions in the presence of sunlight to produce tropospheric ozone (Schlesinger 1991). In the majority of cases, NOx is produced by the combustion of fossil fuel (63%). However, NO_x is also produced by lightning (10%), burning of biomass (14%), soils (11%), and other minor sources (Houghton et al. 2001). In natural vegetation, volatile organic compounds (VOCs) degrade into peroxy radicals (like RO_2, in there, R is an organic radical), which then react with NO and create nitrogen dioxide (NO_2) (Krupa and Manning 1988). While ozone production is generally VOC limited in metropolitan areas with high NO_x levels, ozone production is NOx limited in suburban or rural areas with low NO_x levels (Oltmans and Levy II 1994). Summer stagnant high-pressure systems, for example, are ideal conditions for ozone production because they combine high temperature and solar radiation (Mauzerall and Wang 2001). Natural ozone production, on the other hand, is expected to peak in early spring (Frei 2015).

In some parts of Australia and South America, ozone concentrations are as low as 20 parts per billion (ppb). In contrast, they are as high as 55–60 ppb in other zones of North America, Europe, Asia, and the Middle East (Ramankutty et al. 2008). This ozone map is visible when superimposed on a map of global cropland coverage, which shows that the croplands of India, China, and also the USA are exposed to considerably increased ozone concentrations than croplands in Brazil or Australia (Ramankutty et al. 2008). Over the last three decades, the amount of ozone in the atmosphere has increased at a range of around 0.5–2% each year at the middle latitudes in the Northern Hemisphere. This is due to rapid industrial and urbanized development (IPCC 2022). High ozone concentrations on the surface over large areas of North America as well as Europe are most common throughout the summer months, when the weather is dry and sunny. During seasons, with high light intensities in the United States, Japan, and Europe, ambient ozone levels typically range between 20 and 60 ppb, but ozone peaks surpassing 200 ppb are often observed around large cities (Tamaoki 2008) or during the hot summer episodes

(Pellegrini et al. 2007). Ozone and its precursors can be transported hundreds of kilometers from urban and industrialized areas to rural areas, resulting in elevated concentrations of ozone. More importantly, ground-level ozone concentrations are expected to rise by 20–25% by 2050, with increases reaching 40–60% by 2100 in countries such as India and China, due to the increased emission of ozone precursor gases (Pellegrini et al. 2016).

Ozone may accumulate in the troposphere under favorable meteorological conditions and reach a concentration that will cause a substantial reduction in the development, growth, and yield of sensitive plant species (Bhatia et al. 2012). High concentrations of background ozone throughout the growing season, called chronic exposure, and acute ozone stress are both possible in crops and both can result in the induction of cell death in crops (Ashrafuzzaman et al. 2018; Ainsworth 2017). In the 1950s, researchers discovered that ozone had harmful effects on plants. Today, ozone is the most significant secondary air pollutant which has an effect on human health and vegetation. High ozone concentrations are toxic to plants, and they have deleterious effects on physiological as well as biochemical processes and thereby affect the plants' biomass growth and yield of agricultural crops (Ashrafuzzaman et al. 2020; Krupa 1997; Feng and Kobayashi 2009).

18.1.1 Events After Ozone Exposure to Plant

Yield loss is the ultimate result of some sequential steps induced by ozone exposure to the leaves: At first, ozone enters the leaf apoplast through stomata. Then, due to the fact ozone degradation in the apoplast, various reactive oxygen species (ROS) are generated (Kangasjärvi et al. 2005). Hydroxyl radicals ($HO^{\bullet}$) can be formed as a result of hydrogen peroxide (H_2O_2) and superoxide (O_2^{-}), and $HO^{\bullet}$ can lead to the formation of lipid hydroperoxides (Schraudner et al. 1997). Rather than being detected by direct receptor-ligand interaction, intracellular ROS are more likely to be detected by their accumulation and altering the cell's redox balance (Lamb and Dixon 1997; Vranová et al. 2002). This can have a direct impact on enzymes, second messengers, and transcription factors in biochemical pathways (Kangasjärvi et al. 2005). Once the production of ROS in the apoplast surpasses the apoplast's antioxidative capabilities, an active, endogenous, and self-propagating ROS generation occurs. Programmed cell death (PCD) depends on this active oxidative burst, which persists after ozone exposure has ended (Kangasjärvi et al. 2005). In general, it is agreed that PCD is involved in the formation of ozone-induced lesions (Beers and McDowell 2001; Rao and Davis 2001).

The universal process of the mitogen-activated protein kinase (MAPK) signaling module is that it phosphorylates a MAPK kinase that is then phosphorylated and can activate the next MAPK kinase. The AtMPK6 and AtMPK3 molecules are two MAPKs, which are induced among other stresses, such as ozone exposure, in tobacco (Samuel et al. 2000; Samuel and Ellis 2002; Ahlfors et al. 2004; Joo et al. 2005). In addition to other oxidants, H_2O_2 and O_2^{-}can activate both AtMPK6/SIPK and AtMPK3/WIPK. Cell death and endogenous H_2O_2 production are induced by

AtMPK6 and AtMPK3 activation (Ren et al. 2002; Kangasjärvi et al. 2005). In the development of ozone lesions, plant hormones are important factors. There are some phytohormones, which play critical roles in the ozone sensitivity of plants and in the initiation, propagation, and containment of ozone lesions. These are abscisic acid (ABA), ethylene (ET), salicylic acid (SA), and jasmonic acid (JA) (Alam et al. 2021; Overmyer et al. 2003). These events associated with the formation of the ozone lesion can all be described as a self-amplifying loop, also known as the oxidative cell death cycle, which includes apoplastic antioxidants, stomatal control, and ROS perception (Van Camp et al. 1998; Overmyer et al. 2003). These sequential steps ultimately reduce yield in crop plants.

18.2 Effect of Absorbed Ozone at the Cellular and Metabolic Level

The pathways that lead to multiple forms of damage/disruption due to ozone are highly interconnected, and damage/disruption includes: (1) visible injury, (2) premature leaf senescence, and (3) reduced carbon assimilation. The first of these is commonly referred to as an acute response to ozone, while the second and third are stated as the chronic responses to ozone. All of these responses affect the cell to the leaf, and ultimately to the crop canopy, and finally crop productivity. The order of events are: (1) ozone enters the tissue; (2) then it produces ROS such as H_2O_2, $HO^\bullet$, and O_2^- that damage the leaf, and; (3) then ozone and other ROS come into contact with apoplastic antioxidants that can counteract the damaging effects of these "toxicants." There are a variety of potential processes that could impact the amounts of apoplastic antioxidants, including the following: (a) the activity of some enzymes (e.g., glutathione reductase, ascorbate peroxidase, and superoxide dismutase); (b) antioxidant compounds production (e.g., polyamines, ascorbic acid, glutathione, and β-carotene) and (c) by production of monoterpenes like volatile organic compounds (VOCs) released by some species of crop that can remove ozone in the atmosphere; (4) ozone and some related ROS can interact with the plasma membrane if the apoplastic antioxidant capacity is exceeded, which can occur either through the diminution of antioxidants or by the rapid access of ozone into the body. In the presence of ozone, slightly lower reactive and longer half-lived molecules may form. These reactions lead to a "cascade of responses" that will cause ozone injury to crop physiology, growth, and yield. These compounds may permeate further into the cell, producing metabolic alterations (Emberson et al. 2018).

Cellular alterations that occur owing to this include (a) change in cell wall composition, which can neutralize ozone as well as ROS, lowering the quantity of ozone existing at the membrane, and at the expense of ascorbate oxidation or loss; (b) shifts in both concentration of ions and solutes that give rise to membrane malfunction; (c) a transcription factor activation triggers protein cascades that result in the formation of new proteins; (d) ozonolysis of cell membrane unsaturated fatty acids; and (e) membrane lipids are peroxidized, generating organic radicals as well

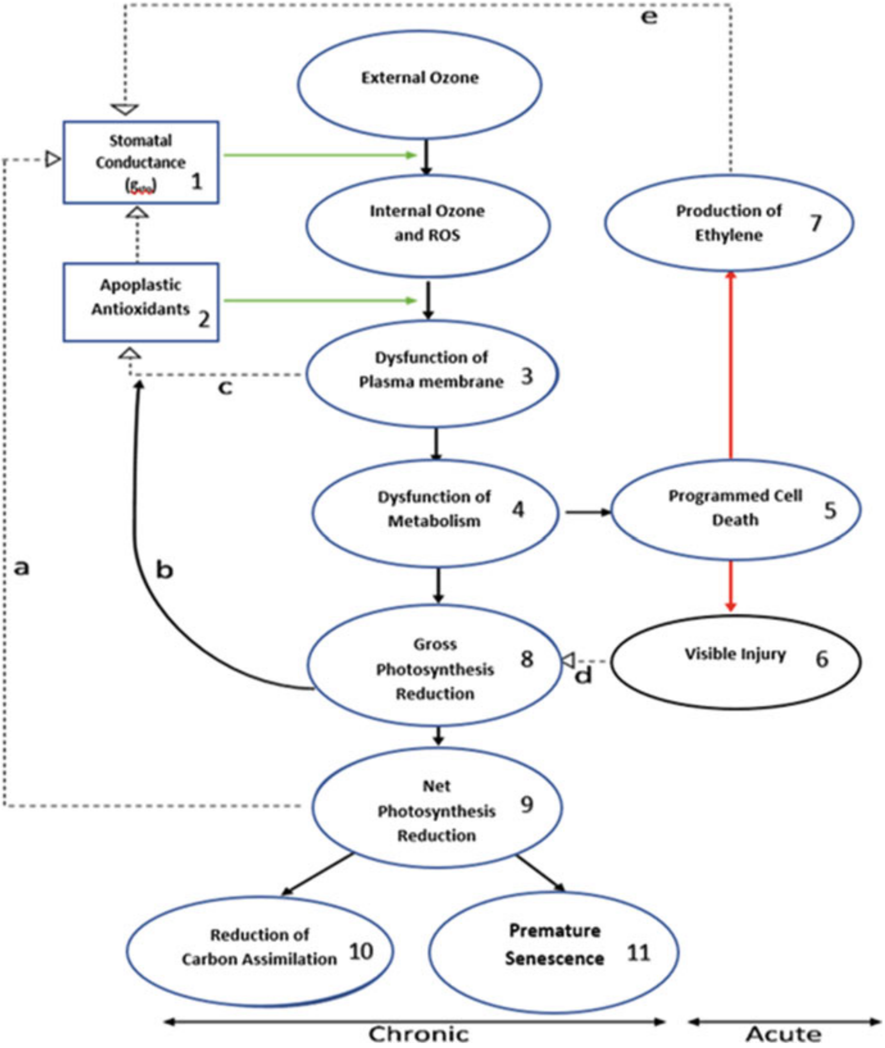

Fig. 18.1 The cellular as well as metabolic pathways of damage and injury (indicated by shaded boxes) in crops due to ozone (ROS and other derivatives) (Adapted from Emberson et al. 2018)

as organic peroxides, which can launch a cycle of free radical production. At high levels, ROS, which are generated via ozone, can result in cell death (shown in step 5, Fig. 18.1), a phenomenon similar to that which occurs when plant cells are attacked by pathogens. In the absence of cell death, the abovementioned biological alterations lead to altered communication and gene expression inside cells, leading to metabolic dysfunction (shown in step 4, Fig. 18.1). This leads to physiological changes such as reduced photosynthesis (shown in step 8, Fig. 18.1) and g_{sto}

(shown in step 1, Fig. 18.1), higher respiration rates, and early leaf senescence (shown in step 11, Fig. 18.1). As a result of these physiological changes, the plant's growth and development is affected (Emberson et al. 2018).

Ozone can attack the guard cells that constitute the stomatal complex. Short-term ozone exposures that result in increases in H_2O_2 have been accompanied by ABA-induced closing of the stomata, which is mediated by an increase in calcium influx in the guard cells (Emberson et al. 2018). Prolonged exposure, on the other hand, can cause the stomatal response to slow, which can have ramifications for the plants' response to water stress. Permeability of the guard cell membranes is hampered by high ozone fluxes and also by the formation of ROS derivatives. It ultimately causes the loss of osmotically active materials by the cell. This may increase the water potential, causing the guard cells to lose water. Control over a gas exchange is also expected to diminish (Fig. 18.1) (Emberson et al. 2018). Ozone and ROS also affect on plant proteins and enzymes if the amount of each protein is altered; activity is changed. These modifications are the "main drivers" of changes in net photosynthesis and gross photosynthesis (also known as carboxylation), respectively (shown in processes 8 and 9, Fig. 18.1). In addition to reducing net photosynthesis (shown in process 10, Fig. 18.1), ozone and its ROS derivatives in the apoplast can initiate unregulated cell death and hypersensitive responses, which can lead to programmed cell death (shown in process 5, Fig. 18.1), which can become apparent as the appearance of visible injury (Emberson et al. 2018).

18.3 Cereals Under Ozone Stress

Cereal grains have been critical to human civilization for thousands of years, and they are also one of the major components of the human diet. Rice (*Oryza sativa*), wheat (*Triticum aestivum*), and maize (*Zea mays*), as well as sorghum (*Sorghum bicolor*) and millets (*Panicum miliaceum*), play a critical role as daily survival staples for the people all over the world. Cereal grain consumption accounts for over half of the daily caloric intake of the world's population (Awika 2011). The three most important food crops around the world are rice, maize, and wheat. Approximately one-half of all calories consumed by humans are supplied by cereal grains (Awika 2011). A chart is given below showing the major cereal grain world production statistics (Fig. 18.2) and annual relative yield losses of different crops due to ozone (Fig. 18.3). A large amount of data indicates that important cereals like rice, wheat, and soybean suffer considerable yield losses under current ozone concentrations (Feng et al. 2003; Fishman et al. 2010). Over a year, wheat yields 4–15%, rice yields 3–4%, 2–5% of maize yields, and 5–15% of soybean yields are hampered due to ozone pollution in the world (Avnery et al. 2011; Betzelberger et al. 2012). Recent global modeling studies estimated that approximately 13% of soybean yield, 5% of rice yield, 7% of wheat yield, and 6% of maize yield is reduced by ozone globally (Mills et al. 2018) and annual economic loss of US$ 14–26 billion (Van Dingenen et al. 2009).

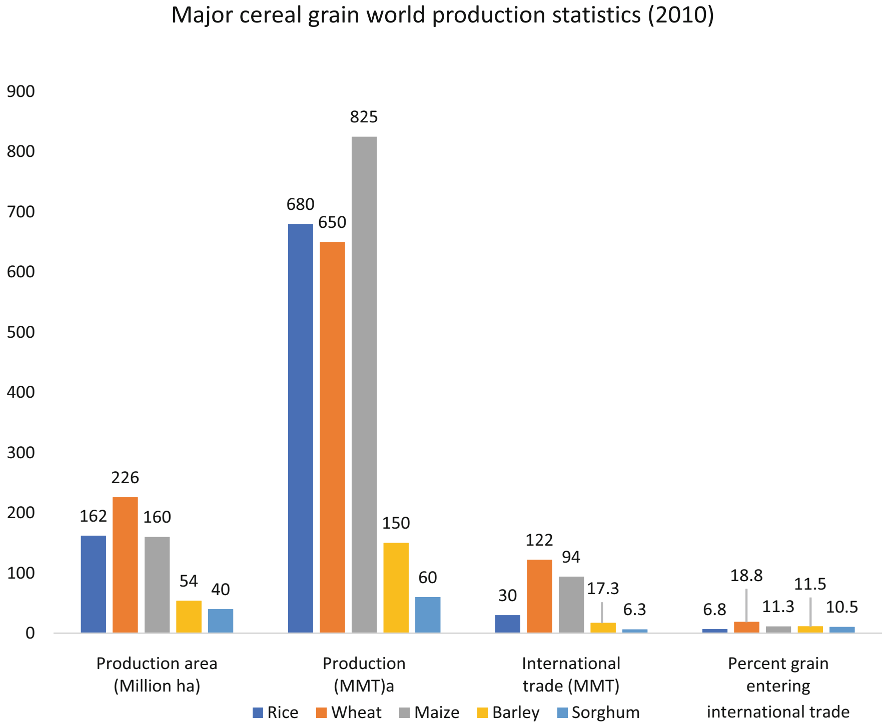

Fig. 18.2 Production of five major cereal grain worldwide statistics (2010) (data derived from Awika 2011)

18.3.1 Proposed Routes for Ozone-Induced Yield Reduction

High ozone levels have been linked to lower photosynthesis and plant growth, altered antioxidant metabolism, and smaller stomatal apertures as well as accelerated plant aging in numerous studies (Calatayud and Barreno 2004; Calatayud et al. 2007; Feng et al. 2008). Ozone's effects are determined by a number of factors (Fig. 18.4). Both a direct reaction in the sub-stomatal chamber and spontaneous conversion to ROS take place in the sub-stomatal chamber, ultimately resulting in the reduction of yield (Kanofsky and Sima 1995; Halliwell and Gutteridge 2015).

Most notably, ozone and the resulting ROS have the potential to react with the exposed proteins' sulfhydryl groups, which are found on the amino acids residues, primarily tyrosine, tryptophan, cysteine, histidine, and methionine. This has the potential to directly contribute to the reduction of overall plant vigor (Foyer and Noctor 2009). Furthermore, under high ozone levels, photosynthetic capacity and efficiency are reduced, which has resulted in significant yield loss in soybean cultivars in the United States that are particularly sensitive to ozone (Betzelberger et al. 2012).

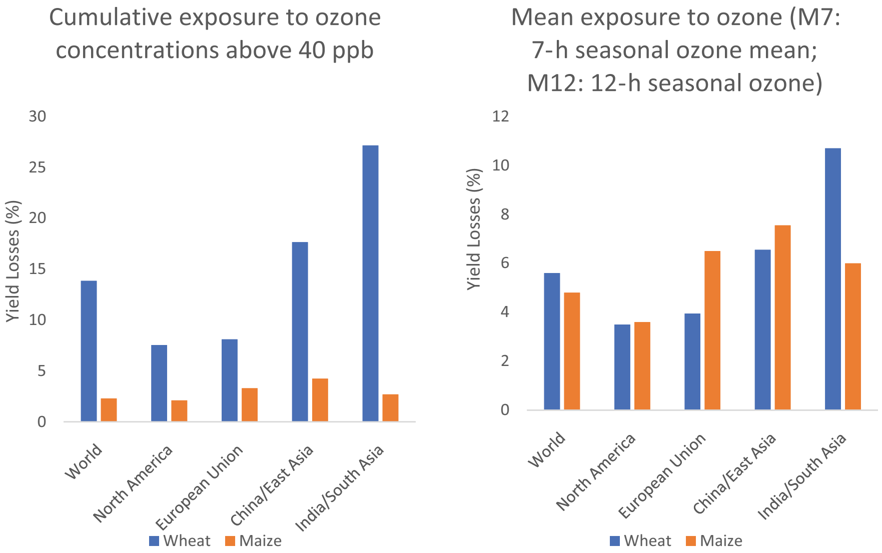

Fig. 18.3 Annual relative yield losses of different crops due to ozone (data derived from Ainsworth 2017)

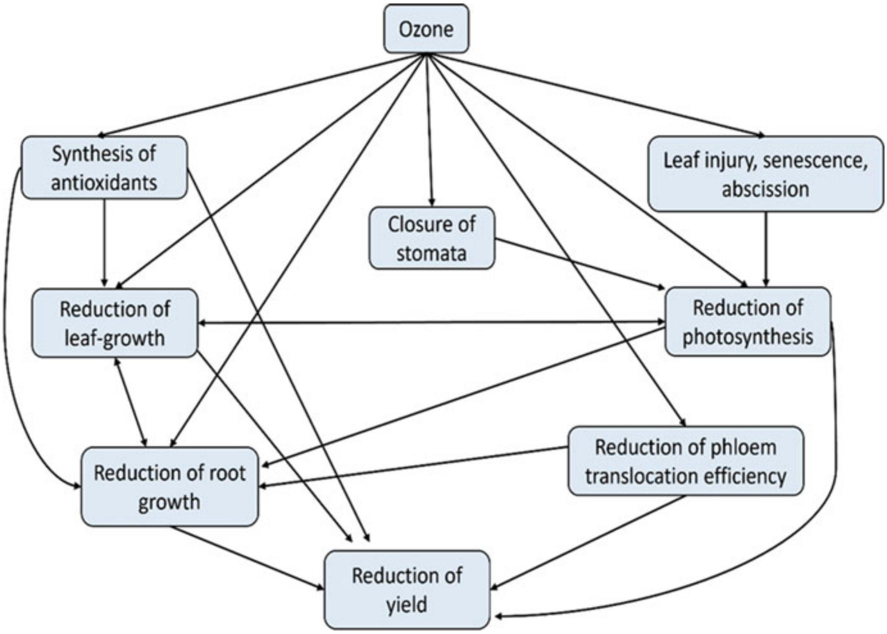

Fig. 18.4 Effects of ozone pollution on crop yield (Adapted from Wilkinson et al. 2012)

18.4 Phytohormones and Ozone Stress

Phytohormones are natural products, and they are also called plant growth regulators when they are synthesized chemically. They are chemical messengers synthesized in one area of the plant and transported to other parts, where they regulate plant responses to stress at extremely low concentrations (Javid et al. 2011). Phytohormones, despite their low concentration, regulate a diversity of cellular processes in plants. Phytohormone plays an important role as chemical messengers for communication between a variety of cellular and metabolic pathways (Voß et al. 2014). Phytohormones have a vital role in plant growth and development, as well as in response to abiotic stresses (Sikdar et al. 2012). Various developmental processes and signaling networks in plants are regulated by these hormones under different abiotic stresses (Raza et al. 2019). Ozone is one of the harmful abiotic stresses in cereals, and ozone has a significant impact on crop productivity (Feller and Vaseva 2014). Several aspects of crop growth and development are influenced by these stresses, including pigment components, water associations, membrane integrity, overall photosynthetic activity, and osmotic adjustments (Pathak et al. 2014). Plant hormones are biochemical molecules that play a role in the response of plants to ozone exposure. Phytohormones are a diverse class of signaling biomolecules that are present in cells in small amounts and are responsible for mediating responses to any internal or external stimuli that they are exposed to (Pathak et al. 2014). These biomolecules include abscisic acid (ABA), auxins (IAA), ethylene (ET), gibberellins (GAs), salicylic acid (SA), jasmonates (JAs), cytokinins (CKs), strigolactones (SLs), and brassinosteroids (BRs) (Wani et al. 2016). Endogenous ROS production is stimulated by ozone-derived radicals resulting in the accumulation of SA and the induction of programmed cell death. Cell death triggers the production of ET, which is necessary for the continuation of ROS production, which is responsible for the propagation of cell death. SA and ethylene both have the ability to promote cell death, and jasmonates work to slow the progression of this process. Abscisic acid has been shown to inhibit ET function, and it may also play a role in ozone-induced cell death (Fig. 18.5) (Pellegrini et al. 2016).

18.4.1 Abscisic Acid (ABA)

The phytohormone ABA has been determined as a critical biomolecule in responses to all abiotic stress, including ozone stress (Sharma et al. 2005). In plants, ABAs play an important role at various stages of their life cycle, including stomatal opening, embryo morphogenesis, dormancy and seed development, and accumulation of newly synthesized lipids and proteins, which all serve to mediate the responses of the plant to a variety of internal as well as external stimuli (Fahad et al. 2015). ABA also serves as the primary internal signal that allows plants to withstand adverse environmental conditions (Raza et al. 2019). Most of the time, drought and high salt stress result in increased endogenous ABA content, which alters gene expression and causes stomata to close (Shinozaki and Yamaguchi-Shinozaki 2007). The sensitivity

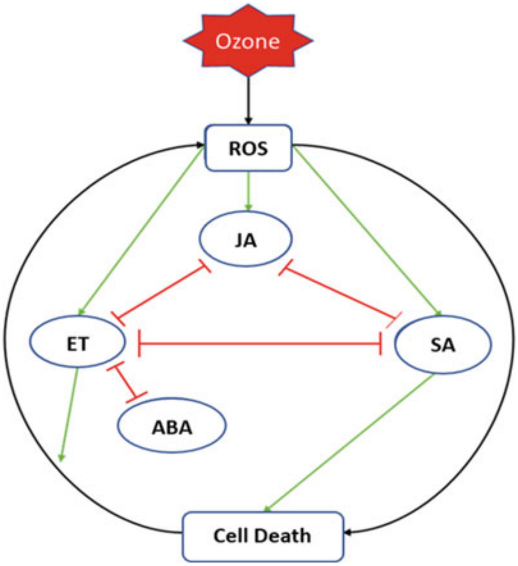

Fig. 18.5 The cycle of cell death caused by oxidative stress. Red bars indicate the mutually antagonistic interactions between ethylene, SA, and jasmonic acid (JA) (Adapted from Pellegrini et al. 2016)

of the ABA of stomata in ozone-sensitive plant species is altered by the ozone-induced ET production (Shinozaki and Yamaguchi-Shinozaki 2007). It has been reported that the breakdown of ozone in the apoplast results in the formation of a variety of ROS. Furthermore, ROS were predicted to cause an increase in the accumulation of free ABA as a result of reduced degradation (Daszkowska-Golec and Szarejko 2013; Song et al. 2014). A recent study suggested that an increase in apoplastic ROS levels could lead to an increase in the accumulation of ABA in guard cells. Increased ABA levels could lead to an increase in the production of ROS in guard cells, creating a positive feedback loop to promote stomatal closure (Mittler and Blumwald 2015). In addition, in response to environmental stimuli, endogenous ABA levels rise rapidly, triggering signaling pathways and, in addition, modifying different gene expression (O'Brien and Benková 2013). Ten percent of protein-encoding genes may be upregulated by ABA (Nemhauser et al. 2006).

18.4.2 Auxins (IAA)

There is a close connection between plant morphogenesis and hormonal homeostasis. IAA is a phytohormone that has a number of different functions. It is required for plant nutrition as well as growth regulation of the plant under different stress conditions (Kazan 2013). Auxin plays a critical role in the defense of plants by regulating gene involved in stress responses. Exogenous IAA causes the production of branching roots that do not elongate (Velada et al. 2020). Excess lateral roots are also produced by mutants which contain large quantities of auxin or mutants where the distribution of IAA is changed. Different hypotheses have been presented to account for stress-induced alterations in auxin metabolism and/or receptivity; however, a review of the literature revealed that stress-induced alterations in IAA transport and catabolism were the most often observed modifications. Furthermore, the catabolism of IAA is influenced by the presence or absence of stress (Velada et al. 2020). Under ozone stress, ROS have been found to be generated inside the leaf, and both ROS and IAA influence morphogenesis. These two signaling molecules should not be viewed separately because they have a significant impact on one another. By downregulating the production of auxin-inducible genes, ROS have the potential to regulate auxin sensitivity, a process that entails changes in MAPK activity (Potters et al. 2009). Antioxidant scavenging systems eliminate the toxicity caused by ROS and aid in the maintenance of ROS homeostasis. When plants encounter a variety of environmental stresses, the interaction between ROS and IAA has an impact on their growth and development. In order to adapt to abiotic stress, both the ROS and IAA networks should be activated. It is unraveled that plants are adapted and survive in harsh environmental stress circumstances by integrating ROS signaling pathways and auxin signaling pathways (Sharma et al. 2015).

18.4.3 Ethylene (ET)

Ethylene is a gaseous phytohormone required for several plant growth phases, including floral senescence, fruit ripening, and leaf as well as petal abscission. In addition to these, it also serves as a regulator of plant stress responses (Groen and Whiteman 2014). Several types of abiotic stress, including ozone stress, can cause changes in endogenous ET levels in plants. After the encounter of environmental stress, ET is accumulated, and the chances of a plant surviving in unfavorable conditions may increase (Ahmad and Prasad 2011). After exposure to ozone, plants produce ethylene from their shoot tissues (Kangasjärvi et al. 2005; Wilkinson and Davies 2009; Wilkinson and Davies 2010). Ozone causes an accumulation of ROS in plant cells, which consequently results in an oxidative burst within the cells. 1-Aminocyclopropane-1-carboxylic acid synthase (ACCS) is activated and phosphorylated by MAPKs in response to the oxidative burst that results from this event. When the ACC synthase is phosphorylated, it becomes more stable, which increases the production of ethylene (Fig. 18.6) (Iqbal et al. 2014).

18.4.3.1 Mechanism of Action of Ozone-Induced ET on ABA-Induced Stomatal Closure

The accumulation of ET also corresponds to the closure of the stomata (Wilkinson and Davies 2010). Ozone-induced ET can interfere with the stomatal closure defense mechanism of plants, which is induced in response to abiotic stresses such as drought. This is accomplished by altering the sensitivity of stomata to the plant hormone, ABA, which is produced in response to ethylene (Wilkinson et al. 2012). Soil drying causes ABA to be upregulated, which causes stomata to close and the leaves to retain more water. When ET is produced in response to ozone, it causes the

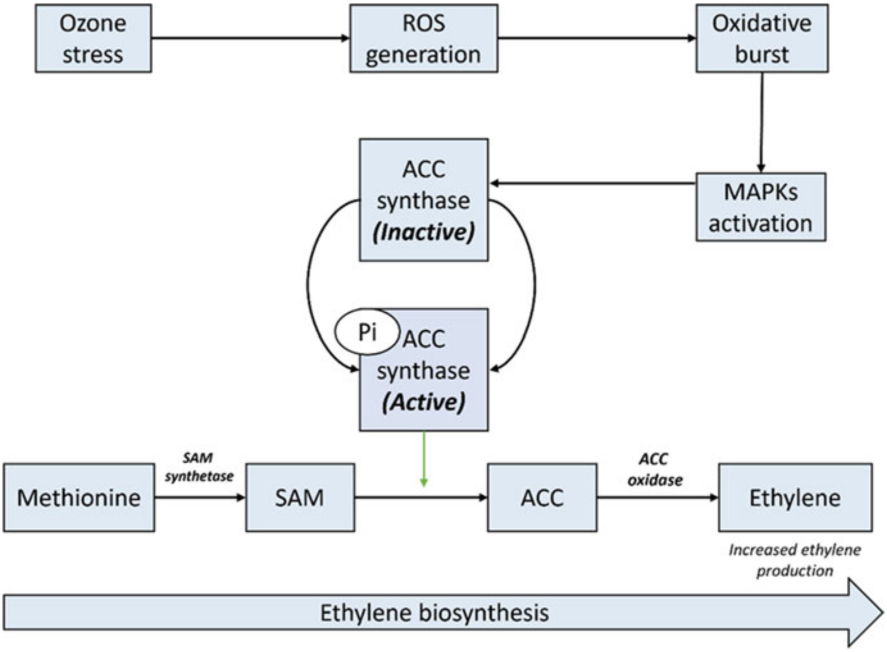

Fig. 18.6 Proposed ethylene biosynthesis pathways in plants exposed to ozone (Adapted from Iqbal et al. 2014). SAM, S-Adenosylmethionine

guard cell of stomata to lose their sensitivity to ABA, resulting in stomatal pores remaining more open in some sensitive genotypes. Therefore, plants will take up more ozone, and more water will be lost compared to plant not exposed to ozone (Fig. 18.7) (Wilkinson et al. 2012).

18.4.4 Gibberellins (GAs)

GAs are yet another type of phytohormone that aid in the processes of leaf expansion, stem elongation, seed germination, trichome initiation and development, and flower and fruit growth (Yamaguchi 2008). GAs are produced in response to stress, and it is accountable for plant growth in the face of specific abiotic stresses. Generally, GAs act positively toward the photosynthetic rate of plants, as well as leaf elongation and expansion, nutrient utilization efficiency, and light interception; they are responsible for regulating a variety of processes during plant growth (Khan et al. 2007). GAs can also mitigate the negative effects of environmental stresses (Yamaguchi 2008).

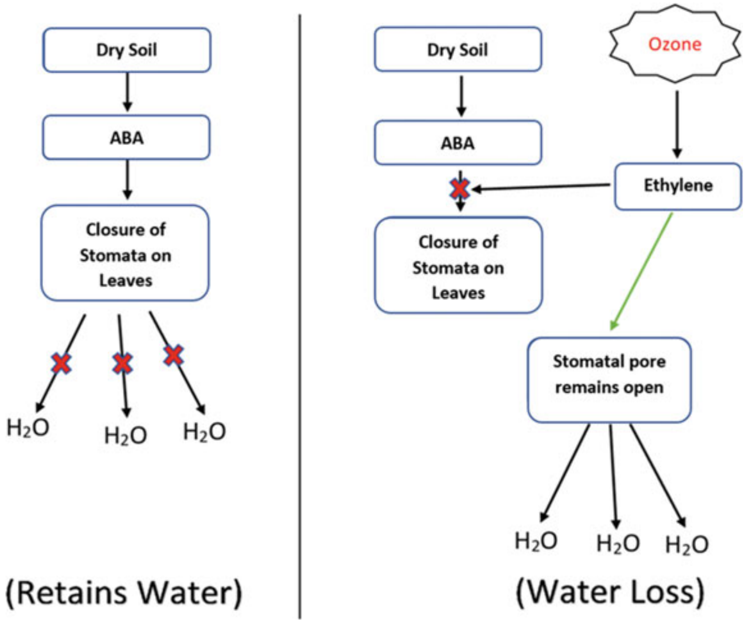

Fig. 18.7 Interactions and effects between ozone-induced ethylene production and ABA-induced stomatal closure

18.4.5 Salicylic Acid (SA)

SA is one kind of phenolic substance that can be found in plants (o-hydroxybenzoic acid) that are thought to resemble a hormone-like endogenous regulator (Iqbal et al. 2014). SA has been shown to support plant development, growth, and the cellular redox system of a cell through the activation of the GSH biosynthetic pathway (Yoshida et al. 2009). SA has received particular attention among signaling molecules due to its ability to govern a variety of aspects of plant responses to biotic as well as abiotic stresses. SAs regulatory role in plant-ozone stress tolerance has been thoroughly studied, and there are a number of reports available on the topic (Yoshida et al. 2009, Khan et al. 2012a, b, c, Kovács et al. 2014). In ozone-exposed plants, SA can act as a signal molecule. It can also promote cellular along with physiological changes (Tamaoki 2008). SA is also required to activate some processes against hypersensitive cell death, potentiate the antioxidant response and ozone sensitivity, and maintain cellular redox state (Rao and Davis 1999). It has been discovered that higher plants have two distinct SA synthesis pathways: (a) isochorismate and (b) phenylalanine ammonia-lyase (PAL) (Pellegrini et al. 2016).

It has been reported that tobacco leaves exposed to ozone metabolized 14C-labeled benzoic acid to SA, but ICS activity and mRNA levels did not increase (Ogawa et al. 2005). On the other hand, ICS activity increased in *Arabidopsis* that was exposed to ozone. So ultimately, it is reported that in tobacco leaves, SA is produced from phenylalanine by using benzoic acid, but in *Arabidopsis*, it is synthesized via isochorismate. However, the activation of SA biosynthesis routes in different plant species in the presence of ozone is still unclear (Tamaoki 2008). SA accumulates in plants that have been exposed to ozone, and excessive levels of SA are associated with the development of leaf lesions (Tamaoki 2008). SA can amplify the downstream signals that cause cell death in a manner similar to that which occurs in pathogen-infected plants, resulting in cell death (Tamaoki 2008). Although appropriate concentrations of SA are necessary to produce antioxidant defense responses and maintain an ideal cellular redox state, it has also been claimed that excessive levels of SA may activate the PCD pathway and cause ozone sensitivity (Tamaoki 2008). SA is also engaged in the signaling network that integrates other phytohormones such as JA and/or ET in plants that have been exposed to ozone (Rao et al. 2002). A research team discovered that both SA and ET is important to control ozone-induced cell death in *A. thaliana*. When ozone was applied to the same plant, it was shown that it might stimulate the production of jasmonate or methyl jasmonate, which was later found to play a key role in the reduced lesions generated by the exposure to ozone (Rao et al. 2000a, b). The buildup of ozone-accrued SA in *Nicotiana tabacum* plants has also been seen to be facilitated by ethylene-mediated control of the expression of the PAL and chorismate mutase (CM) genes in the presence of ozone (Ogawa et al. 2005).

It is identified that apoplastic ROS can interact with a number of other signaling pathways that are mediated by SA and can regulate cell death process (Overmyer et al. 2003). Endogenous as well as exogenous SA has been shown to participate in antioxidant metabolism and exert strict control over cellular ROS (Kang et al. 2014; Khan et al. 2014). Coordination of the SA-dependent and SA-independent signaling components by ROS signaling, on the other hand, resulted in an adequate defensive response. SA may operate as a signaling molecule for the establishment of systemic resistance (Beck et al. 2012) and can also activate a protein kinase (Mikołajczyk et al. 2000). SA has been implicated in the regulation of the metabolism of antioxidants, which has been shown to influence plant tolerance to key stimuli such as ozone, osmotic stress, UVB, metal, and heat (Wang et al. 2010; Nazar et al. 2011; Khan et al. 2012a, b, c; Khan et al. 2013a, b; Khan et al. 2014). It has been suggested that SA-mediated activation of superoxide dismutase (SOD), as well as GSH-based H_2O_2-metabolizing enzymes, for instance, glutathione peroxidase (GPX), and glutathione S-transferase (GST), improves the tolerance of plant to ozone (Abarca et al. 2001; Milla et al. 2003). In another study, the application of SA increased shoot Ca^{2+} (a second messenger) and resulted in a temporary rise in H_2O_2, which was believed to trigger antioxidant enzymes and ultimately result in a reduction in cellular ROS (Arfan 2009).

18.4.6 Jasmonic Acid (JA)

In recent years, JA has been identified as an endogenous regulator in the developmental processes and responses to a variety of environmental stressors (Okada et al. 2015). When plants are exposed to ozone, they produce more jasmonate (Rao et al. 2000a, b). During the oxidative cell death phase, jasmonates have a role in the prevention of lesion amplification resulting from ROS (Devoto and Turner 2005; Kangasjärvi et al. 2005) and protect tissues from cell death and also counteract the effects of ET and SA (Overmyer et al. 2000). It was revealed that JA levels in *M. officinalis* plants reached their maximum level at 8 h after the start of ozone exposure and remained high during the whole recovery time under ozone treatment (Pellegrini et al. 2013). The amount of JA in *A. thaliana* plants exposed to ozone (300 ppb, 6 h) increases only very late in the process, during the lesion development phase (Tuominen et al. 2004). Based on these findings, it appears that JA is predominantly produced in wounds as JA accumulation was only seen in plants that were severely damaged throughout the ozone exposure time period (Castagna et al. 2007). Furthermore, JA functions as a component of the anti-cell death pathway, which helps to restrict and modulate the progression of the lesion in its latter phases. In one study, it was shown that pretreatment of tobacco plants with jasmonates prevented the development of ozone-induced cell death (Örvar et al. 1997). A similar result was observed in *Arabidopsis*, where jasmonate treatment prevented the spread of ozone lesion and reduced the quantity of SA generated in response to ozone pollution (Rao et al. 2000a, b). It appears that JA plays at least two different functions in response to ozone: JA can counteract the promoting action of ET, resulting in the containment of lesion growth and dissemination, and inhibits the oxidative cell death process by encouraging lesion development and HR cell death, which ultimately leads to leaf senescence (Fig. 18.8) (Santino et al. 2013).

18.5 Phytohormones in Alleviating of Ozone in Cereals

18.5.1 Rice

In Asia, rice is among the most common staple food crop (Akhtar et al. 2010; Alexandratos and Bruinsma 2012). It is projected that 5% of global rice yields and over 10% of the regional yields are damaged that is likely to deteriorate further as ozone levels continues to rise (Ueda et al. 2015). With two major seasons in South Asia, rice is grown almost year-round, and both of these growing seasons can coincide with periods of high ambient ozone (Ashrafuzzaman et al. 2017). Crops are severely damaged by the photochemical oxidant tropospheric ozone (Pell et al. 1997). Crop yield loss in ozone exposed is caused by a decrease in photosynthetic activity, as well as growth inhibition induced by leaf damage (Frei et al. 2008; Akhtar et al. 2010). When rice is subjected to ozone stress, ascorbic acid serves as the primary antioxidant, preventing oxidative damage caused by the ozone (Frei et al. 2008).

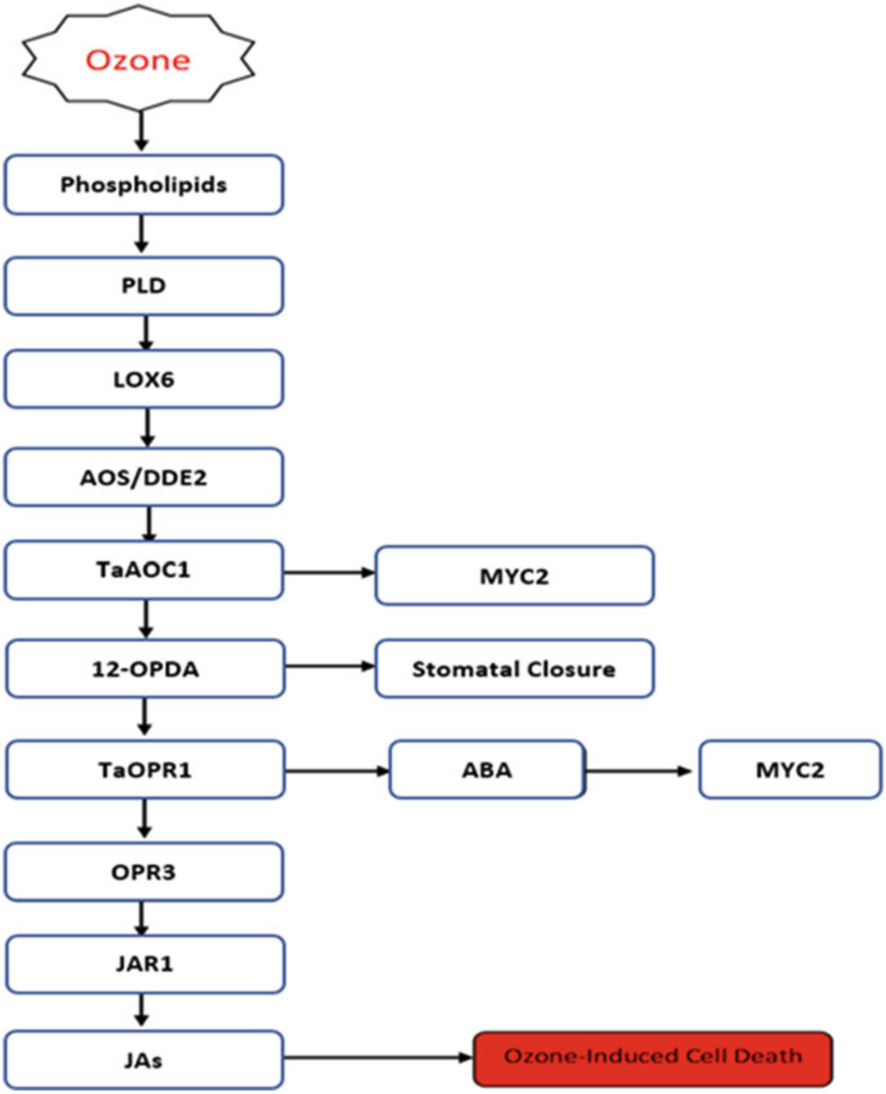

Fig. 18.8 Projected jasmonic acid biosynthesis pathways in plants exposed to ozone (Adapted from Pellegrini et al. 2016)

One experiment in Habataki demonstrated a vital role of phytohormones in relation to ozone damage in rice. It was reported that the levels of JA, as well as ABA are increased due to ozone exposure (Tsukahara et al. 2015). It was also observed that the levels of ABA, JA, and JA-Ile in inflorescence meristems of Sasanishiki (a rice variety) decreased by 31%, 73%, and 71% respectively, when exposed to elevated ozone but increased to two to three times the levels in Habataki when exposed to ambient air (Tsukahara et al. 2015). However, according to the findings, due to a reduction in the number of primary rachis branches, ozone-induced grain yield loss has been occurred (Tsukahara et al. 2015). Although the ABA-mediated mechanism is still unclear, however, it is suggested that ABA may reduce ROS production. It is also reported that during the elevated ozone in the panicle formation stage, JA and ABA are produced in the leaves to reduce leaf injury in rice (Woltering et al. 2003). It has been revealed that ozone signal(s) suppress APO1 (aberrant panicle organization 1) expression directly or suppress APO1 expression indirectly, ultimately leading to a decline in the number of primary rachis branches and, thereby, a reduction in grain yield in rice (Tsukahara et al. 2015).

18.5.2 Wheat

When it comes to vegetable protein in human food, wheat (*Triticum aestivum*) is the leading source worldwide (Mills and Harmens 2011). High ozone concentrations in the troposphere can significantly affect wheat development by decreasing photosynthesis and speeding up leaf senescence (Begum et al. 2020; Guarin et al. 2019). Daily ozone concentrations above 25 ppb reduced wheat yields by 0.26–0.95%, depending on the cultivar's ozone sensitivity (Guarin et al. 2019). Tropospheric ozone generally affects the grain protein concentration and baking quality in wheat. Ozone increases grain protein concentration, despite the fact that there is a considerable reduction of protein yield which is seen per plant or per ton of seeds (Mills and Harmens 2011). Ozone may affect not only the amount but also the type of proteins, which means that there are indications that its presence will change both the amount and type of proteins. In an open-top chamber experiment, the increase of dry gluten was stated at surrounding ozone levels in comparison to charcoal-filtered air (Vandermeiren et al. 1992). In addition, the zeleny value showed to be increased due to ozone compared to the protein concentrations (Piikki et al. 2008).

In addition, after being exposed to ozone, the starch content in wheat grains has been found to be reduced (Scotti et al. 1994). As ozone levels increase, the harvest index (the percentage of biomass in the seeds) decreases while the individual grain mass also decreases. Moreover, several nutritionally important minerals (P, Zn, K, Mg, Ca, Cu, and Mn), as well as protein, were impacted, but the yield was reduced as a result of ozone (Broberg et al. 2015). In terms of other minerals (S, Na, and Fe), no significant or inconclusive results were found. The positive influence of ozone was also observed on baking properties (Broberg et al. 2015). An experiment on wheat with five different levels of ozone exposure was conducted, and researchers found that grain mass at harvest was closely linked to grain filling duration and, in turn, to flag leaf duration as measured by chlorophyll content (Gelang et al. 2000).

18.5.3 Maize

Maize (*Zea mays* L.) is a C_4 plant, is the world's third-largest staple crop, and has a significant economic value (Singh et al. 2014). There is less information available about the effect of ozone on maize (Peng et al. 2020). Tropospheric ozone is predicted to cause yearly yield losses of approximately 10% in maize crops in the United States, resulting in crop losses of approximately $7.2 billion. Similar to other crops, maize is also sensitive to ozone stress, and it exhibits loss of photosynthetic capacity when exposed to polluted air throughout a long period of time (Choquette et al. 2019). In the initial stage, an advantageous effect was observed with the exposure of low doses of toxicant in maize quality protein (QPM) and non-quality protein (NQPM); however, growth traits were negatively affected by ozone at later stages. Under the influence of ozone stress, a variable pattern of photosynthate translocation has been observed. Higher concentrations of ozone initiated foliar injury like interveinal chlorosis, reddening of leaves, which was recognized to increase the production of photosynthetic anthocyanin pigments. Furthermore, a decline in the number of male flowers is observed at high ozone concentrations, indicating that ozone has a detrimental effect on reproductive structures and may be a contributing factor to productivity losses. Higher ozone doses were also found to result in substantial reductions in yield due to changes in carbon allocation patterns, specifically in husk leaves, as well as foliar damage and photosynthetic protein (Singh et al. 2014). It has also been reported that hybrids showed more sensitivity to ozone and impairment in photosynthetic traits compared to the parents (Choquette et al. 2019).

18.6 Phytohormone Signaling and Their Interaction

Plants must be able to recognize as well as respond to different environmental stresses coordinately and especially for their survival. When plants are stressed, the signal transduction cascade and variations in phytohormone levels are thought to be among the first line defense. To create a powerful defense system against stress or unwanted environmental stimuli, a number of plant hormones should act and collaborate together. SA and ABA are considered to be the key hormones that can act and can regulate the signaling pathways and networks. In such crosstalks, there are many signaling intermediates present for each hormone, and these signaling intermediates show their definite function. As a result, understanding the interactions between phytohormones and defensive signaling pathways is crucial. Potential targets for the development, host resistance mechanisms, and phytohormones may be revealed by this understanding (Grant and Jones 2009). SA, ET, and JA's roles in ozone-exposed plants if they act independently, the truth is that these substances act in mutually antagonistic or coordinated ways. The accumulation of SA against ozone stress appears to be negatively regulated by JA signaling and ET biosynthesis. A mutant of *Arabidopsis* plant that was both ozone sensitive and jasmonate semi-insensitive was found to have increased ethylene production while also having reduced jasmonate sensitivity (Kanna et al. 2003). Reduced ET production was observed due to treatment with JA in that mutant and showed lower ozone sensitivity. The level of ozone-induced ET production is decreased by the treatment of JA, which is seen in ozone-sensitive *Arabidopsis* mutant radical-induced cell death1 (rcd1) (Overmyer et al. 2000). These findings suggest that JA signaling is also involved in the regulation of ET biosynthesis and JA may be able to reduce the ozone sensitivity associated with high levels of ET production.

The interaction between SA and ET has also been explored in some plants that have been exposed to ozone. An increase in the production of ET, which is induced by ozone, was noticed in plants that had been pretreated with SA. In transgenic *Arabidopsis* plants over-expressing *salicylate hydroxylase gene (*NahG) that did not accumulate SA, the production of ET was found to decrease in response to ozone (Rao et al. 2002). These findings suggest that SA signaling is involved in the regulation of ET biosynthesis against ozone stress. Furthermore, lower levels of SA produced compared to wild type due to ozone in transgenic tobacco in which ET biosynthetic pathway is inhibited (Ogawa et al. 2005), indicating that ethylene signaling is regulating the SA biosynthesis in ozone stress. As previously stated, it has been demonstrated that the leaf damage which is induced by ozone can be declined by ET hormone by inducing defense-related genes (Tamaoki et al. 2003). In other words, in a plant, ET and SA signaling work together to promote growth. The induction of defense-related genes in this plant is decreased when SA production or signaling is reduced, which suggests that ET signaling is also reduced. As a result, SA signaling appears to be involved in the regulation of ET signaling in plant (Tamaoki 2008). Therefore, it is established that the ET and SA together act to increase ROS production and cell death against ozone stress (Overmyer et al. 2003). It is important to respond and regulate interactions between distinct phytohormones to control ozone-caused ROS production as well as leaf lesions (Overmyer et al. 2003). Thus, SA, ET, ROS, and cell death all contribute to regulating cell death. Besides these, JA is engaged in the prevention of the progression of lesion development. As a result, the levels of ET, JA, and SA production are dependent on the amount of ROS generation, and ozone-caused cell death is subsequently regulated by the functions of these distinct phytohormones (Tamaoki 2008).

18.7 Summary

Ozone-related crop yield reductions are underestimated globally by farmers and agronomists due to the lack of simple diagnostic tools and awareness. On the other hand, increasing ground-level ozone concentrations are threatening the food supply in many parts of the world as farmers have almost no management options. Therefore, assessment of all possible potential strategies is essentially needed to cope with ozone stress. A better understanding of ozone stress signaling pathways involving different phytohormones can be helpful to combat against ozone stress. These approaches may include lower accumulation or enhanced production of the phytohormones, which can interfere with the masking of ozone-induced harmful effects in crop plants. Therefore, elucidation of the functional characterization of different phytohormones and their crosstalk under ozone stress warrants further research to minimize the ozone-induced crop yield loss for ensuring food security in highly ozone-affected areas.

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Part IV

Improvement in Abiotic Stress Tolerance Through Biostimulants

Use of Biostimulants to Improve Salinity Tolerance in Cereals

19

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Abstract

Cereals are essential human foods in both developed and developing countries. They are a significant source of energy, carbohydrates, protein, and dietary fiber and contain a range of micronutrients. However, salinity is one of the main abiotic barriers to their productivity. Salt stress threatens 10% of the world's total land area (950 Mha), 20% of the world's arable land (300 Mha), and 50% of the total irrigated land (230 Mha). Further, it is expected to affect 50% of total cultivated land in 2050 at an alarming rate due to environmental changes and various inappropriate irrigation practices, especially in arid and semiarid climatic areas. The continuous rise in worldwide salinization makes these areas soil one of the most critical categories of degraded soils, with profound effects ranging from loss of biodiversity to total disappearance of vegetation and a loss of soil fertility. The high concentration of salts in the environment can also induce a series of

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alterations, from the genetic level to the morphological level of the cultivated plants.

Recently, biostimulants have gained considerable attention as natural and eco-friendly tools to maintain soil health and improve crops tolerance to (a)biotic stress such as salinity. The application of arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), organic amendment, algae extracts, and other active compounds as biostimulants has been recommended due, among others, to their capacity to enhance soil structure and porosity, fix atmospheric nitrogen for plant accessibility, improve nutrient uptake and solubilization, promote water absorption, and produce phytohormones. This chapter will explore plant biostimulants' potential roles in sustainable agricultural production systems, their protective effects against salinity stress, as well as the underlying mechanisms that control these effects in cereals.

Keywords

Cereals · Plant biostimulants · Stress tolerance · Organic components · Microorganisms · Nutrient uptake · Productivity · Sustainable agriculture

Abbreviations

ABA	Abscisic acid
AEs	Algal extracts
ACCD	1-Amino-cyclopropane-1-carboxylate-deaminase
AMF	Arbuscular mycorrhizal fungi
APX	Ascorbate peroxidase
CAT	Catalase
Chl	Total chlorophyll content
C_i	Intercellular CO_2 concentration
DM	Dry matter
EBIC	European Biostimulants Industry Council
EC	Electrical conductivity
EL	Electrolyte leakage
EPS	Exopolysaccharides
ESP	Exchangeable sodium percentage
ETC	Electron transport chain
F_v/F_m	Chlorophyll fluorescence
FW	Fresh weight
g_s	Stomatal conductance
GR	Glutathione reductase
GST	Glutathione S-transferases
GPX	Glutathion peroxidase
HC	Hydraulic conductivity
HS	Humic substances

H_2O_2	Hydrogen peroxide
IAA	Indole acetic acid
LWC	Leaf water content
MDA	Malondialdehyde
MLE	*Moringa oleifera* leaf extract
NUE	Nitrogen use efficiency
PGPR	Plant growth-promoting rhizobacteria
POD	Peroxidase
ROS	Reactive oxygen species
PSI	Photosystem I
PSII	Photosystem II
RWC	Relative water content
SAR	Sodium absorbable ratio
SOD	Superoxide dismutase
SOS	Salt overly sensitive
SSR	Simple sequence repeat
TSS	Total soluble sugar
WUE	Water use efficiency
WT	Wild-type

19.1 Introduction

One of the major challenges of this century will be to extend the food supply to meet the demands of a world population projected to reach 9.7 billion people by 2050, while accessible rural areas are losing their potential (Vargas et al. 2018). One major factor that limits food production is the decline in soil productivity. Available agricultural land continues to lose its potential due to the current management practices that rely on external inputs (e.g., inorganic fertilizers, herbicides, and pesticides) for higher crop yield (Gomiero 2016). In addition, climate change has accelerated the degradation process, mainly in arid and semiarid zones (Ait-El-Mokhtar et al. 2019a; Lyu et al. 2021). Saline sodicity causes degradation of soil structure, with adverse consequences ranging from biodiversity decrease to total disappearance of vegetation and loss of fertile land (Parihar et al. 2015). In addition to its detrimental effects on soil physicochemical and biological characteristics, the high concentration of salts in the environment can cause three types of stress, osmotic, ionic, and oxidative, which significantly reduce plant growth and yield.

Almost 953 million hectares of surface area worldwide are affected by salinity (Singh et al. 2018; Santander et al. 2021). One billion hectares are affected by the salinity problem in more than 100 countries (Fig. 19.1). The soil salinity phenomenon mainly affects arid and semiarid regions in Australia, Asia, Africa, and South America with about 357, 211, 209, and 129 million hectares, respectively (Singh

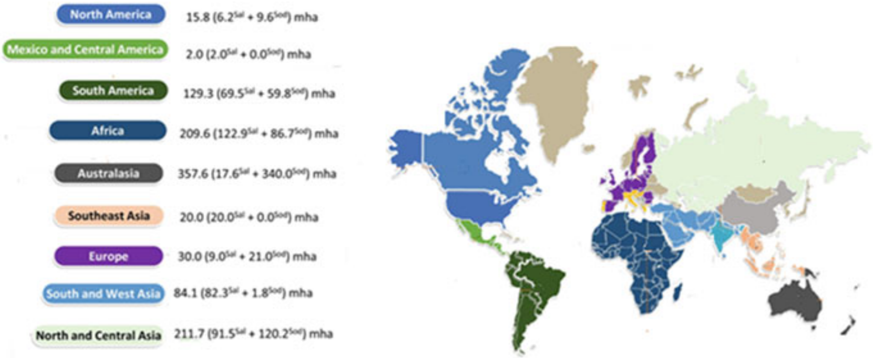

Fig. 19.1 Mapping the global saline and sodic soils distribution

et al. 2018) and poses an increasing threat to agriculture, especially cereals production (Ngara et al. 2012).

Cereal crops represent an essential source of minerals, energy, and protein for much of the world's population. Wheat, rice, and maize account about 50% of the world's plant-based food energy. Another 25% comes from sorghum, sweet potatoes, potatoes, and soybeans (Shiferaw et al. 2011; FAO 2021). However, the production of these cereal crops is negatively impacted by saline conditions, resulting in yield reduction. To reduce the impact of salinity on crop productivity, emphasis has been placed on the application of a wide variety of biostimulants such as the use of beneficial microorganisms (i.e., fungal, rhizobacterial), organic amendment, algae extract, and other active compounds constituting long-term and cost-effective alternative to face salinity constraints.

It is widely known that arbuscular mycorrhizal fungi (AMF) symbiosis increases the tolerance of plants to salinity by establishing mutualist associations with over 71% of vascular plants (Shamshiri and Fattahi 2016; Cosme et al. 2018; Ganugi et al. 2019). AMF grants several benefits to host plants by enhancing water and nutrient uptake (Ait-El-Mokhtar et al. 2019b; Ben-Laouane et al. 2019; Riaz et al. 2021), keeping a high K^+/Na^+ ratio (Porcel et al. 2012; Wang et al. 2021), greater photosynthetic capacity (Anli et al. 2020b; Toubali et al. 2020; Lahbouki et al. 2021), and higher osmoprotectants level (Garg and Baher 2013; Acosta-Motos et al. 2020) and enzyme activities (Ben-Laouane et al. 2019, 2020; Lahbouki et al. 2022). Likewise, plant growth-promoting rhizobacteria (PGPR) can contribute to the ability of plants to tolerate salinity through several synergistic processes, including mitigation of ionic stress and nutrient deficit by ensuring ionic homeostasis and enhancement of nutrient absorption (Li et al. 2020b), induction of osmolyte accumulation and phytohormone signaling (Ilangumaran and Smith 2017), and mitigation of oxidative stress by boosting photosynthesis and antioxidant capacity (Bharti et al. 2016; Anli et al. 2020b; Ben-Laouane et al. 2020).

Organic fertilizers may affect crop growth and yield under salinity (Abdallah et al. 2020). Their application can improve nutrient availability (Ait-El-Mokhtar et al. 2020) and stimulate plant respiration, chlorophyll content, and photosynthesis (Aridhi et al. 2020; Toubali et al. 2020; Ben-Laouane et al. 2021). Numerous studies revealed that these biostimulants can develop a series of activities including a higher cation exchange capacity (CEC), chelation ability, water retention capacities, and nutrient resource and enhance soil structure, aeration, and stability that may enhance the plant capacity to alleviate salt stress conditions and increase plant productivity (Cavagnaro 2015; Ben-Laouane et al. 2020; Bello et al. 2021; Castiglione et al. 2021; Machado et al. 2021; Naveed et al. 2021).

Algae extracts offer promising organic amendments to mitigate the impact of salt stress on cereal plant performance (El-Katony et al. 2021; Zou et al. 2021). The importance of algae extracts to plant development under (a)biotic stresses is associated with their high content of growth-promoting substances like phytohormones (e.g., auxins, gibberellic acid, cytokinin) and inorganic elements (Ca, Mg, K, Zn, Fe, Mo, Cu) and activation of the antioxidative systems (catalase and peroxidases), amino acids, and vitamins (Hashem et al. 2019; Mukherjee and Patel 2020).

Protein-based biostimulants, including protein hydrolysates, animal or plant origins, polyamines, glycine betaine, proline, glutamate, glutamine, and nonprotein amino acids (Teklić et al. 2021), boost plant growth and increase their tolerance to several abiotic stresses (Ilangumaran and Smith 2017).

The purpose of this chapter is to make available an overview of the negative impact of salinity on soil and cereals plants and the role that biostimulants could play to improve cereal tolerance to saline conditions.

19.2 Salinity: Types, Causes, and Salt Uptake from the Soil

There are two main groups of saline soils: saline soils and alkaline or sodic soils (Table 19.1). Saline soils are soils with a soil paste electrical conductivity (EC) > 4 dS/m, an exchangeable sodium percentage (ESP) < 15 or adsorbable sodium ratio (SAR) < 13, and a pH < 8.5 (Chhabra 2005). They contain abundant soluble salts to inhibit the growth of most crops (Munns and Tester 2008; Parihar et al. 2015; Kumar and Sharma 2020). Alkaline soils, most often associated with sodic soils, are soils with EC < 4 dS/m, ESP > 15 (or SAR > 13), and pH > 8.5.

Table 19.1 Classification of saline soils (adapted from USDA Salinity Laboratory, 1954) cited in Datta et al. (2019)

Soil type	EC (dS/m)	ESP	SAR	pH
Saline	>4	<15	<13	<8.5
Sodic	<4	>15	>13	<8.5
Alkaline	<4	>15	>13	>8.5
Salsodic	>4	>15	>13	>8.5

EC electrical conductivity, *ESP* exchangeable sodium percentage, *SAR* sodium absorbable ratio

These soils contain enough sodium to cause soil structure deterioration and limit crops growth. It is worth noting that soils with EC $>$ 4 dS/m, ESP $>$ 15, and pH $>$ 8.5 are considered saline-sodic soils (Chhabra 2005; Datta et al. 2019).

Soil is expected to be harmed by salinity when the EC is equivalent to a solution containing 40 mM NaCl (~4 dS/m), causing osmotic stress of about 0.2 MPa (Munns and Tester 2008). The development of most cultured species is affected by an external NaCl concentration of 50 mM. This concentration can even be lethal for some very salt-sensitive plants (Munns and Tester 2008). In semiarid regions, the soil solution's salt concentration can exceed 100 mM, reducing the growth of almost all crop plants (Shkolnik-Inbar et al. 2013).

Soil salinity can be classified into primary and secondary salinity (Vargas et al. 2018; Akhtar 2019). Eighty percent of salinized land has a natural origin (primary salinity) (Kumar and Sharma 2020). It results from a progressive accumulation of salts released during the weathering of rocks or from natural external inputs related to the intrusion of marine waters into coastal areas and/or soil surface evaporation associated with low precipitation and plant transpiration (Munns and Tester 2008; Akhtar 2019). Secondary salinity results from human or anthropogenic activities related to agricultural practices, overuse of fertilizers, and irrigation (Munns and Tester 2008; Devkota et al. 2015; Akhtar 2019). Indeed, irrigation is often practiced with poor water quality, which results in progressive salinization of soils, causing substantial losses in crop production every year by over 20% (Munns and Tester 2008; Porcel et al. 2012; Munns et al. 2012; Shahbaz and Ashraf 2013; Cox et al. 2018; Hirich et al. 2021).

Salinity primarily impacts soil physical qualities by causing flocculation, which binds fine soil particles into aggregates. Magnesium and calcium keep the soil flocculated, whereas large amounts of sodium cause the soil to disperse. Salinity transforms the soil into a hard cement-like material, causing low infiltration and hydraulic conductivity (HC) than forming a surface crust (Srivastava et al. 2019). Besides, the supply of water and essential nutrients for plants and microorganisms depends on the salt level in the soil. It has been shown that a high concentration of soluble salts in the soil often influences the soil stability and organic matter content (Mavi et al. 2012; Strehse et al. 2018). Saline soils contain limited mineral nutrients and organic matter as they become immobilized out of the reach of the plant root system. In addition, these soils can increase boron, aluminum, and carbonate toxicity (Imadi et al. 2016a, b). With enhancing salinity levels in soil, the concentration of chloride, cadmium, sulfate, and bicarbonate ions increases, while the levels of calcium and magnesium ions decrease, which negatively impacts the soil quality (Hashem et al. 2014).

19.3 Cereals Responses to Salt Stress

19.3.1 Salt Adverse Effects and Physiological Responses in Cereals

Cereal crops are grown in almost all world areas and play an essential role in satisfying global food and feed demands (Shiferaw et al. 2011; AbdElgawad et al. 2016; Mbinda and Mukami 2021). They are subjected to a large number of environmental stresses that severely reduce and limit their growth and yield (Saade et al. 2016; Abhinandan et al. 2018; Saddiq et al. 2021). Among the different abiotic stresses, salinity is one of the most significant threats to grain crops (Munns and Tester 2008; Shahbaz and Ashraf 2013; Hussain et al. 2017; Panuccio et al. 2018; Saddiq et al. 2021). Salt detrimental effects result in morphological, physicochemical, and molecular changes that negatively affect agricultural performance (Table 19.2) (Hanin et al. 2016; Mbinda and Mukami 2021). Salt accumulation leads to three adverse effects: osmotic, ionic, and oxidative stresses. Indeed, high Na^+ contents cause a water potential decrease and difficulty absorbing water, leading to stunted growth (osmotic stress) (Hanin et al. 2016; Negrão et al. 2017; Hussain et al. 2021). After the osmotic phase, an ionic phase appears in a time-dependent manner, which is caused by the accumulation of the toxic Na^+ and Cl^- ions at the leaf mesophyll, affecting thereby the plant growth and metabolism, where salt damages the lipid and protein structures located at plasma membranes (Parihar et al. 2015; Hanin et al. 2016; Saddiq et al. 2021). Oxidative stress is a disequilibrium between the creation and buildup of reactive oxygen species (ROS) in cells and the biological system's ability to eliminate these reactive products. This stress causes dysfunction of the photosynthetic apparatus and metabolic disorders (Kumari et al. 2019). The negative impacts of salinity on cereal growth depend, among others, on plant factors like variety, growth stage, and species (Nemati et al. 2011; Ali et al. 2020).

19.3.1.1 Effect of Salinity on Seed Germination

The germination stage is the most critical stage where most plants are severely affected by salt concentrations (Kubala et al. 2015). Salinity inhibits germination through the osmotic effect by decreasing water potential, making it inaccessible around the seeds (Islam et al. 2015; Panuccio et al. 2018). In addition, the reduced osmotic potential of the soil solution prevents seed imbibition due to enzyme activity decrease and high Na^+ uptake relative to K^+, resulting in embryonic toxicity and delayed metabolic processes (Soda et al. 2016; Day et al. 2019).

19.3.1.2 Effect of Salinity on Vegetative and Reproductive Stages in Cereals

Salinity suppresses plant growth through osmotic stress (the lowering of external water potential), adversely affecting the plant's capacity to uptake water. This process initiates multiple significant actions in plant tissues. Due to reduced turgor pressure, root and shoot cell expansion is immediately stopped at the macroscopic level (Zhao et al. 2020). The impact of salinity leads to height, leaf number, and leaf surface reductions. In wheat, soil salinity delays the growth of the shoot, more

Table 19.2 Effects of salt stress e on morphological, physiochemical traits in cereal plants

Cereals	Salinity level (mM)	Biochemical traits	Physiological traits	Mineral nutrition	Morphological traits	References
Wheat	496–621	– Increase of H_2O_2 and MDA – Increase CAT, POD, and APX	– Reduce WUE	– Overaccumulation of Na^+	– Reduction of shoot biomass	Khataar et al. (2018)
	60–120–180		–	–	– Reduction of agronomic traits: biomass, plant height, straw yield, number of spikes, number of grains per spike, 1000-grain weight, and grain yield	Chamekh et al. (2015)
	100	– Increase CAT, POD, APX – Accumulation of phenols – Increase MDA and H_2O_2	–	– Higher K^+/Na^+ ratio in leaves	– Decline in germination, growth and yield	Islam et al. (2015)
Maize	40–120	–	– Pigment reduction – Decrease of quantum yield of PSII	– Increase in Na^+ and Cl^-	– Reduction in FW	Qu et al. (2012)
	100	– Proline accumulation – Oxidative damage	– Decrease photosynthesis – Reduction in stomatal aperture – Decrease of stomatal conductance,	– Increased Na^+ and Cl^- accumulation – Reduce N, K, Ca^{2+}, Mg^{2+}, Fe uptake	– Shoot growth reduction – Reduction of total DM—Yield reduction	Kaya et al. (2010)

			– Reduction of pigments			
	25–50	Accumulation of proline in shoots and Na^+ in root	–	– Decrease in nutritional status	– Reduction in plant growth	Selvakumar et al. (2018)
Rice	40–80–120	– Decrease the chlorophyll content – Increase proline level – Reduce sugar, soluble protein, and free amino acid content	–	–	– Reduce plant yield	Hakim et al. (2014)
	100	– Decrease proline and TSS – Increase lipid, MDA, EL	– Decrease photosynthesis – Decease RWC	– Decrease in the accessibility of nutrients in the soil	– Decrease biomass	Chauhan et al. (2019)
Sorghum	50–100–200–300	– Reduce soluble sugar content in leaves	–	– Induce poorer mineral nutrition (N, P, K) and higher Na^+ absorption	– Increase mycorrhizal colonization rates – Reduce biomass	Wang and Shi (2019)
	100–200	– Decrease protein, APX, Chl b, and total chlorophyll	–	–	– Decrease root length, total dry weight	Ali et al. (2020)
	100–200	– Accumulation MDA in root – Increase CAT, SOD, APX, and GST activity	– Decrease of chlorophyll and carotene contents	–	–	Temizgul et al. (2016)
Barley	200	– Increase antioxidants activity (SOD, POD, CAT, APX)	– Reduce pigments (Chl a, Chl b, total Chl)	–	– Decrease fresh and dry biomass of shoots and root	Noreen et al. (2021)

(continued)

Table 19.2 (continued)

Cereals	Salinity level (mM)	Biochemical traits	Physiological traits	Mineral nutrition	Morphological traits	References
		-Increase ascorbic acid, proline, and α-tocopherol				
	23–46	–	– Decrease chlorophyll pigment – Decrease transpiration rate	–Accumulation Na^+ contents in roots and shoots – Reduce K^+ and Zn^{2+} uptake	– Decrease shoot and root fresh and dry weights – Reduce yield	Harris et al. (2010)

APX ascorbate peroxidase, *CAT* catalase, *Chl* chlorophyll, *EC* electrical conductivity, *EL* electrolyte leakage, F_v/F_m photochemical efficiency, *FW* fresh weight, *GST* glutathione S-transferases, g_s stomatal conductance, H_2O_2 hydrogen peroxide, *MDA* lipid peroxidation, *POD* peroxidase, *RWC* relative water content, *SOD* superoxide dismutase, *TSS* total soluble sugar, *WUE* water use efficiency, *GR* glutathione reductase sensitive to salt stress than root, but it accelerates the plant toward maturity (Khalilzadeh et al. 2018). Plants sustain relatively a strong root development under high-saline stress; a large amount of photosynthetic energy is devoted to rooting production to keep high water levels, water seeking and/or water loss reduction. Iqbal et al. (2018) showed that salinity reduced nitrate reductase, water and turgid potentials, stomatal conductance, transpiration, and photosynthetic rate, as well as nutrient absorption while it increased glycine betaine, proline, total soluble sugars, and total free amino acids in maize.

Furthermore, studies have shown that those yield parameters in wheat are reduced by salt stress (Setter et al. 2016; Siddiqui et al. 2017). Cereal crops subjected to salt stress at heading or ear differentiation decreased the number of spikelets per ear and grains (Khataar et al. 2018), negatively affecting the mobilization of reserves at the grain filling phase. Similarly, Khalilzadeh et al. (2018) showed that yield and grain weight are significantly affected in salt-stressed wheat and that salinity harms the remobilization of reserves during the grain filling phase.

19.3.1.3 Salinity Effects on Mineral Nutrition and Plant Physiology

Salinity negatively affects the leaf physiological activity, especially photosynthesis, which is the leading cause of the reduction in plant production (Hanin et al. 2016; Hussain et al. 2021). The reduction in photosynthesis is associated with the restriction of stomatal conductance caused by the decrease of leaf water potential (Ait-El-Mokhtar et al. 2019b; Ben-Laouane et al. 2020; Boutasknit et al. 2021; Mbinda and Mukami 2021). The more stomata restrict the diffusion of CO_2 between the substomatal cavities and the sites of carboxylation within chloroplasts, the lower the intercellular CO_2 concentration (Ci) will be. Accumulation of Na^+ and Cl^- ions in soil restricts the absorption of mineral nutrients like N, P, K^+, and Ca^{2+} (Parihar et al. 2015; Hussain et al. 2017), which induce cytoplasmic toxicities and disrupt cellular ion homeostasis (Wang et al. 2003; Farooq et al. 2017). Na^+ and Cl^- ions are the major elements producing several physiological perturbations and adverse effects on plants. However, Na^+ is the primary ion since it interferes with the absorption of K^+ and disrupts the various processes in which K^+ is involved, including the activity of many enzymes, stomatal regulation, and photosynthesis stimulation (Parihar et al. 2015). Moreira et al. (2020) reported that maize leaf and root decreased K^+ and Mg^{2+} under salinity, while Na^+ and Cl^- increased (Moreira et al. 2020).

19.3.1.4 Effect on ROS and Carbohydrate Metabolisms

Under physiological conditions, low concentrations of intracellular ROS have an essential role in normal redox signaling to maintain metabolic function and integrity. However, under adverse conditions of (a)biotic stresses, increased levels of ROS contribute to tissue dysfunction and remodeling through oxidative damage (Mittler et al. 2004; Porcel et al. 2012; Siddiqui et al. 2019). Oxidative stress is defined as a perturbation between the ROS compounds production and their removal. The substantial reduction of CO_2 fixation, electron transport chain (ETC), and photorespiration in the mitochondria and chloroplast are the leading causes of stress-related ROS production (Mittler et al. 2004; Hasanuzzaman et al. 2020). Thus, salinity induces stomatal closure, which reduces the accessibility of CO_2 fixed by the rubisco enzyme, and leads to the accumulation of excess reducing power (Porcel et al. 2012; Talaat 2021). This accumulated reducing power inhibits the transport of electrons from photosystem II (PSII) to photosystem I (PSI), and the resulting excess electrons are captured by oxygen molecules, resulting in the production of excess ROS, including superoxide radical (O_2^-), hydroxyl radical (OH^-), and hydrogen peroxide (H_2O_2) (Mittler 2002; Devireddy et al. 2021). ROS cause oxidative damage to cereals plants. Indeed, excess ROS can alter various organic and inorganic molecules present in cells, including DNA, proteins, lipids, amino acids, and sugars (Nedjimi 2014; Temizgul et al. 2016). They act in three ways: tearing off either an electron or a hydrogen atom or adding double bonds. As a result, they induce a reduction in crop growth and productivity or even cell death (Nath et al. 2016; Al Kharusi et al. 2019).

19.3.2 Strategies for Coping with Salinity in Cereal Cultures

Salt tolerance is the capacity of plants to survive and terminate their life cycle on soil containing high levels of soluble salt (Meng et al. 2015; Volkov 2015). Those plants that can resist high salt concentrations in the rhizosphere and grow successfully are named halophytes. Salt tolerance is a complex characteristic involving several interacting factors (Reddy et al. 2017; Meng et al. 2018; Zhao et al. 2020). Like other crops, cereals also have complex regulatory mechanisms regulating their salt stress response, ranging from cell morphology and composition changes to molecular signaling and genome variation (Ganie et al. 2019) (Fig. 19.2).

19.3.2.1 Growth Regulation and Membrane Transport Systems Control

The decrease of growth is an adaptive ability necessary for the plant survival subjected to salt stress since this development delay allows the plant to accumulate

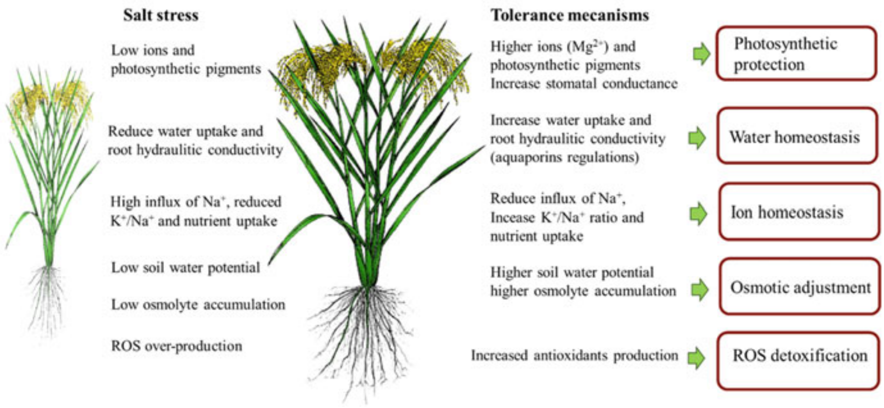

Fig. 19.2 Main salinity effects and possible mechanism(s) for salinity tolerance induction in cereals

energy and resources in order to minimize the stress effects before imbalance between the interior and exterior of the organism rises to a threshold level where the damage is irreparable (Chamekh et al. 2015; Ganie et al. 2019). To cope with the adverse effects of salinity on growth, plants need to make osmotic adjustments. The majority of the root cell turgor is recuperated within 40–60 min through increased absorption of mineral ions, and growth recovers, but at a reduced rate. That is most probably due to the change in cell wall constitution resulting from the linking of Na^+ to cell wall components. As a result of osmotic stress, stomata also close rapidly, reducing the plant's capacity to take up CO_2 (Zheng et al. 2008; Rehman et al. 2021). The fast stomatal closure can be attributed to the quick fall accompanying salt stress. In maize subjected to a NaCl solution of 100 mM, the roots xylem pressure reaches values of 0.05 MPa (Zhao et al. 2020). Stomatal closure may also increase abscisic acid (ABA) concentration due to increased salt stress. Parveen et al. (2021) observed an increase in ABA levels in wheat under salt stress, resulting in stomatal closure to minimize water leakage caused by salinity-induced osmotic stress, ultimately causing stunted growth and plant decline.

Adaptation to salt stress also takes place at the cell membranes level. In terms of ion transport, the strategy of tolerance to salinity is quantitative and qualitative. The ions selectivity at the entrance presents the qualitative component, well-defined from the various recent membrane transporters (Na^+/H^+ antiport) (Munns and Tester 2008; Deinlein et al. 2014; Lei et al. 2018). In facilitated diffusion and active transport, membrane proteins could be particular to specific solutes. Furthermore, various solutes (Na^+ and K^+) might compete for the same transport protein. Membrane permeability to Na^+ and the activity, number, and sensitivity of membrane Na^+/H^+ antiports evolve to adapt to long-term sodium stress on a quantitative level (Volkov 2015; Srivastava et al. 2019).

19.3.2.2 Na^+ Exclusion

The plant avoids salt from translocating to the leaves through an internal layer of root cells at the endodermis (Nemati et al. 2011). The ability to exclude Na^+ and/or Cl^- from the stems is well linked with the salt tolerance degree (Yang et al. 2020). Maintaining a low Na^+ concentration in the leaves could be due to the exclusion mechanism that leads to Na^+ accumulation in roots, preventing excessive translocation to stems (Farooq et al. 2015). Munns and Tester (2008) showed that in addition to sodium exclusion through the presence of Kna1, a responsible gene for Na^+ exclusion, barley plants can use another salinity tolerance mechanism by trapping salt ions in a specific leaf compartment. This avoids the toxic effects of high Na^+ and counterbalances the osmotic pressure of the soil. Osmotic tolerance and the exclusion of ions are two mechanisms mainly involved in rice plants tolerance to salt (Munns and Tester 2008).

19.3.2.3 Osmoregulation

One of the key mechanisms of tolerance to abiotic stresses such as salt is the osmotic adjustment, especially during the first phase of salt stress (Harris et al. 2010; El Moukhtari et al. 2020). This is completed by accumulating osmoregulatory compounds, including ions such as K^+, Na^+, and Cl^- and/or organic molecules like soluble sugars (glucose, fructose) and certain amino acids (glycine betaine, proline). The accumulation of osmoregulators reduces the osmotic potential and maintains the turgidity potential (Kubala et al. 2015). This phenomenon helps preserve a wide range of physiological activities (such as transpiration, photosynthesis, and growth) and can affect plants at any stage of development (Jaramillo Roman et al. 2020). It protects membranes and enzymatic systems, especially in developing organs (Hanin et al. 2016). It's important to note that proline may play an essential function in cytosol vacuole pressure maintenance and pH regulation. Kaya et al. (2010) showed that proline accumulation enhances in maize plants subjected to high-salt stress (400 mM NaCl). Maize leaves accumulated more than 600 mol g^{-1} of proline, which could assist plants to cope with osmotic stress caused by salt.

19.3.2.4 Antioxidant Defense System

Plants have a range of reactions to salt stress, including osmotic and ionic homeostasis, and cellular detoxification, primarily provided by antioxidant defense mechanisms (Zhu 2001; Mittler 2002; Rao and Chaitanya 2016). To support the adverse effects of ROS, cereals induce an effective enzymatic antioxidant system, including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), glutathione reductase (GR), glutathione peroxidase (GPX), and ascorbate peroxidase (APX) (Islam et al. 2015; Panuccio et al. 2018). The increased ascorbic acid and glutathione production is also a critical substrate for detoxifying reactive oxygen entities with potential oxidant scavengers (Das and Roychoudhury 2014). It has been shown that salt stress boosted antioxidant enzyme activity in maize plants by upregulating CAT, SOD, APX, POD, and GR in both roots and leaves (Abd-Elgawad et al. 2016). Maintaining high antioxidant activity is positively correlated with decreasing lipid peroxidation as well as cell membrane stability (Begum et al. 2020; Shareef and Al-Khayri 2021) . Islam et al. (2015) showed that in salt stress-tolerant wheat, the highest are antioxidant enzymes activity (CAT, POD, and APX) and phenolic accumulations; the lowest is lipid peroxidation H_2O_2 contents. Similar findings were observed in sorghum plants showing a positive correlation between antioxidants and salt resistance (Wang and Shi 2019).

19.3.2.5 Genetic Basis of Salt Stress Response in Cereals

The ability of cereals to withstand salinity depends on genetic variability since certain species are more resistant to this type of abiotic stress than others (Volkov 2015; Yasmin et al. 2016; Srivastava et al. 2019). Tolerance to salt stress is mainly known as a compound characteristic controlled by numerous genes (Reddy et al. 2017). The high accumulation of Na^+ and Cl^- in the cytoplasm is metabolically toxic to plants (Munns and Tester 2008), implicating essential genes related to salt tolerance. For instance, the salt overly sensitive (SOS) pathway is maintained in rice and an Na^+/H^+ antiporter, *OsSOS1*, and decreases the Na^+ content in the cell (Porcel et al. 2016; Reddy et al. 2017).

A substantial upregulation in the expression of genes linked to cellular ion balance, osmolytes accumulation, and abscisic acid was observed in two new salt-tolerant bread wheat, named "Maycan" and "Yıldız," which may improve salt tolerance (Aycan et al. 2021). Interestingly, it has been recently reported the substantial maternal effects in a comparative analysis of reciprocal F2 hybrids in wheat, which offspring of tolerant maternal plants had more remarkable emergence and higher salinity tolerance (250 mM NaCl) than sensitive maternal hybrids, suggesting substantial potential for maternal genetic effects, extending across generations, to contribute to stress tolerance. Simple sequence repeat (SSR) markers screening of the reciprocal hybrid genotypes and parents' nuclear genomes and Sanger sequencing of low-, medium-, and high-dominant markers revealed insignificant changes in the nuclear genome among offspring and parents (Aycan et al. 2021). The rice variety BRRI dhan 28 with *OsSOS1* showed an enhanced salt resistance level at 150–200 mM NaCl (Yasmin et al. 2016). Also, Shen et al. (2015) showed that *OsHAK21* could mediate plasma membrane K^+ uptake and played crucial roles in maintaining Na^+/K^+ homeostasis in rice under salinity. Takagi et al. (2015) developed a line named "Kaijin"—practically equivalent to the elite cultivar "Hitomebore" and differed by only 201 SNPs from wild type (WT)—that showed 0.75% NaCl tolerance. Recently, Rana et al. (2019) developed a high-salt tolerant rice variety, named YNU31-2-4, carrying the *hst1* gene and had the same agronomic traits to the WT under normal growth conditions but significantly higher survival rate and increased shoot and root biomasses than the WT under salt stress (125 mM NaCl).

19.4 Biostimulants as Alleviators of Salt Stress in Cereals

As reported by European Biostimulants Industry Council (EBIC), plant biostimulants are a varied group of substances or microbes that, when applied to plants, seeds, or rhizosphere, stimulate natural processes of plants by enhancing nutrient uptake and efficiency, crop growth and yield, and tolerance to (a) biotic stress (Xu and Geelen 2018).

Seminal studies have focused on exploiting biostimulants for many years to increase plant growth and productivity and reduce synthetic fertilizers and pesticides (Aseri et al. 2008; Bhardwaj et al. 2014; Youssef and Eissa 2014; Nabti et al. 2017). Recently, biostimulants have become key factors in mitigating (a)biotic stresses (Berruti et al. 2016; Esringü et al. 2016; Van Oosten et al. 2017; Paymaneh et al. 2019; Ben-Laouane et al. 2020; Del Buono 2021). Although plant biostimulants are typically applied to facilitate nutrient uptake, many of them also have preventive effects against environmental stresses. The application of biostimulants has been suggested as one of the most promising and practical approaches to achieve higher yield stability and mitigate the negative salt effect in several plants (Rouphael and Colla 2018). The essential role of biostimulants in mitigating salt stress has been reported in many cereals like quinoa (Ramzani et al. 2017; Cai et al. 2021), wheat (Fileccia et al. 2017; Oljira et al. 2020), sorghum (Desoky et al. 2018), rice (Aybeke 2016; Hafez et al. 2019), and maize (Estrada et al. 2013a; Lashari et al. 2015; Moreira et al. 2020). Specifically, biostimulants could enhance salinity tolerance in cereals through direct and indirect mechanisms, resulting in higher germination rate, roots and shoots growth, quality, productivity, and crop yield (Table 19.3 and Fig. 19.3).

Based on their source, biostimulants are divided into two main groups: microbial and nonmicrobial biostimulants. Microbial-based biostimulants include, among others, AMF and PGPR, while the nonmicrobial ones encompass humic and fulvic acids, algae extracts, protein-based biostimulants, and other active compounds such as biopolymers (Rouphael and Colla 2020a).

19.4.1 Microbial-Derived Biostimulants

PGPR are the most studied microbial-derived biostimulants (Calvo et al. 2014). They are found in the rhizosphere and play a crucial role against salt stress in different crops, including cereals, through several physiological and molecular mechanisms. These include fixing atmospheric N, solubilizing soil nutrients, secretion of growth-promoting molecules (indole 3 acetic acid (IAA), 1-aminocyclopropane-1-carboxylate-deaminase (ACCD), and ammonia and hydrogen cyanide (HCN)), production of exopolysaccharides (EPS) and siderophores, inducing antioxidant machinery, modulation of plant stress markers, and osmolytes synthesis (Van Oosten et al. 2017; Kumar Arora et al. 2020; Del Buono 2021). This discovery has led to multifunctional PGPR-based preparations for commercial agriculture that can be used for seeds treatment (bio-priming) or applied in the plant rhizosphere, where they colonize and provide nutrient benefits to the host plant (Pathania et al. 2020). PGPR application is an environmentally friendly and durable approach to substitute chemical fertilizers with a severe environmental impact on soil biodiversity (Vejan et al. 2016; Basu et al. 2021). It has been shown in rice that the long-term application of inorganic fertilizers alters the bacterial community structure, resulting in the alteration of soil biodiversity and rice productivity (Kumar and Verma 2018). Thus, PGPR application is a safe technology that ensures durable agricultural production worldwide and promotes the productivity of saline agroecosystems (Basu et al. 2021). Dal Cortivo et al. (2020) revealed that PGPR application enhances plant performance in seed germination, shoot and root development, biomass, soil structure and water retention capacity, and alleviation (a)biotic stresses.

Several species of PGPR, including *Azospirillum* sp., *Pseudomonas* sp., *Serratia* sp., *Klebsiella* sp., *Pseudomonas*, *Enterobacter*, *P. pseudoalcaligenes*, and *Bacillus pumilus*, have been reported to boost salt stress in cereals. PGPR diversity is dependent on the soil quality, host plant, and nutrient availability in the rhizosphere (Tian et al. 2020).

Singh et al. (2015) showed that the inoculation of salt- and heat-stressed wheat plants with salt-tolerant *Klebsiella* sp. strain increased biomass, chlorophyll content, K^+ uptake (84%), and reduced plant growth inhibition (10¯100%) and Na^+ absorption (65%) compared to untreated plants. Furthermore, treatments with *Trichoderma* isolates can stimulate net photosynthesis, WUE, and biomass accumulation in wheat

Table 19.3 Biostimulant-mediated salinity stress tolerance in cereals plants

Cereals crop	NaCl level (mM)	Biostimulant composition	Effect/mechanism	References
Wheat	124–496	*Bacillus siamensis* (PM13) *Bacillus* sp. (PM15) *Bacillus methylotrophicus* (PM19)	– ACCD activity and EPS production – Increase germination rate – Enhance root and shoot length and pigments – Sequestration of Na^+	Amna et al. (2019)
	31–465	*Pseudomonas putida* (N21), *Pseudomonas aeruginosa* (N39) and *Serratia proteamaculans* (M35)	– Activate ACCD activity – Increased DM and grain yield – Increased chl and K^+/Na^+ content – Reduce ethylene level	Zahir et al. (2009)
	22–453	Fulvic acid + licorice root extract	– Enhance plant morphological and physio-biochemical characteristics – Improve antioxidant defense system	Elrys et al. (2020))
	146–292	Mixture of *Glomus* spp.	– Enhanced metabolism of carbon and nitrogen	Talaat and Shawky (2014b)
	146–292	Mixture of *Glomus* spp.	– Increase production of enzymatic and nonenzymatic antioxidants – Detoxify ROS	Talaat and Shawky (2014a)
	200	*Trichoderma*	– IAA production – Enhance net photosynthesis, WUE, and biomass production	Oljiraet al. (2020)
	150–200	*Klebsiella* sp.	– Enhance ACCD activity – Increase plant biomass and chlorophyll content – Reduction in plant growth inhibition (10–100%) – Exclusion of Na^+ (65%) and increased K^+ uptake (84%) in the host plant	Singh et al. (2015)
	200	*Arthrobacter nitroguajacolicus*	– Upregulation of 152 genes (cytochrome	Safdarian et al. (2019)

(continued)

Table 19.3 (continued)

Cereals crop	NaCl level (mM)	Biostimulant composition	Effect/mechanism	References
			P450s, nicotianamine synthase gene (NAS), oligopeptide transporters (OPTs), ATP binding cassette (ABC) transporters, sugar/inositol transporter)	
	150M	Brown seaweed polysaccharides	– Promote plant growth – Decrease membrane lipid peroxidation – Stimulates the photosynthetic machinery – Induce antioxidant activities	Zou et al. (2019)
	60–120	Salicylic acid and melatonin	– Promote growth and grain yield – Modulate the photosynthetic capacity	Talaat (2021)
	150	Halotolerant PGPR Dietzianatronolimnaea STR1	– Modulate ABA signaling, SOS pathway, ion transporters, and antioxidant machinery	Bharti et al. (2016)
	100	Sulfated chitooligosaccharide	– Decrease the content of malondialdehyde – Increase the chlorophyll contents Modulate fluorescence characters – Adjust antioxidant enzyme activities – Modulate the gene expression of several antioxidant enzymes	Zou et al. (2016)
Maize	250	*Pseudomonas putida* UW4	– ACCD activity – Modulate protein expression	Cheng et al. (2012)
	25–75–150	Hydrolysate-based biostimulants from alfalfa containing triacontanol and IAA	– Improve plant biomass – Increase leaf proline Increase phenylalanine ammonia-lyase activity – Increase salinity-related gene expression	Ertani et al. (2013)

(continued)

Table 19.3 (continued)

Cereals crop	NaCl level (mM)	Biostimulant composition	Effect/mechanism	References
	100	Humic acid	– Increase plant biomass, chlorophyll contents, mineral nutrients, and key antioxidant enzyme activity	Kaya et al. (2018)
	100	Chitosan	– High growth – Activate alternative respiration at the biochemical and molecular levels	Turk (2019)
	100	*Rosmarinus officinalis* L. + *Artemisia* L. leaf extracts	– Increase germination percentage and germination indexes	Panuccio et al. (2018)
	0–66–100	*Rhizophagus intraradices*, *Claroideoglomus etunicatum*, and *Septoglomus constrictum*	– Increase of shoot dry biomass, K^+ and K^+/Na^+ ratio – Reduce Na^+ accumulation – Regulation of *ZmAKT2*, *ZmSOS1*, and *ZmSKOR* genes expression	Estrada et al. (2013a)
	0–85	*Pseudomonas reactans* EDP28, *Pantoea alli* ZS 3-6, and *Rhizoglomus irregulare*	– Increase the content of K^+ – Decrease of Na^+	Moreira et al. (2020)
	0–40–80	*Rhizophagus intraradices* + *Massilia* sp. RK4	– Promote AMF root colonization and nutrient uptake	Krishnamoorthy et al. (2016)
	25 and 50	*Gigaspora margarita* S–23 *Claroideoglomus lamellosum* *Pseudomonas koreensis* S2CB35	– Reduce the accumulation of proline in shoots and Na^+ in roots. – High K^+/Na^+ ratio – Alter *ZmAKT2*, *ZmSOS1*, and *ZmSKOR* genes expression to maintain K^+ and Na^+ ion homeostasis	Selvakumar et al. (2018)
	23–42	Humic acid	– Increase soil macroaggregates – Improve soil nutrient availability and nutrient uptake	Liu et al. (2019b)

(continued)

Table 19.3 (continued)

Cereals crop	NaCl level (mM)	Biostimulant composition	Effect/mechanism	References
	25	Protein hydrolysates (APR®, ILSA S.p.A., Arzigano VI, Italy)	– Regulate nitrate transport and ROS metabolism gene expression	Trevisan et al. (2019)
Rice	200	*Bacillus amyloliquefaciens* NBRISN13 (SN13)	– Modulate 14 genes (*NHX1*, *SOS1*, *BZ8*, *GIG*, and *BADH*) – Stimulate osmoprotectant	Nautiyal et al. (2013)
	100	*Bacillus amyloliquefaciens*-SN13	– Increase biomass, RWC, proline, and total soluble sugar – Decrease lipid peroxidation and electrolyte leakage – Modulate photosynthesis, hormone, cell wall, lipid metabolism-related genes	Chauhan et al. (2019)
Sorghum	93–383	Humus substances (HM) + *Moringa oleifera* leaf extract	– Increase growth characteristics, photochemical activity, phytohormones contents, osmoprotectants, and enzymatic/nonenzymatic antioxidants	Desoky et al. (2018)
	100–200	Humic acid + jasmonic acid	– Increase root length, total DM, salt tolerance index, seedling vigor index, shoot length, protein content, APX, chl b, and total chl	Ali et al. (2020)
Quinoa	400	*Enterobacter* sp. (MN17) + *Bacillus* sp. (MN54))	– Improve plant water relations – Decrease Na^+ uptake	Yang et al. (2016)
	300	*Pseudomonas* sp. strain M30-35	– Increase biomass production, root activity, and photosynthetic pigment – Stabilize P content – Increase saponin content	Cai et al. (2021)

(continued)

Table 19.3 (continued)

Cereals crop	NaCl level (mM)	Biostimulant composition	Effect/mechanism	References
Barley	138	Humic acid	– Increase soil pH and organic matter – Enhance plant nutrients, total chlorophyll and dry biomass	Rekaby et al. (2020)
	100	Humic acid	– Limit Na^+ uptake – Enhance syringic acid, alanine, proline, ascorbate, glutathione, and phytochelatin	Jarošová et al. (2016)
	50–200	Foliar fertigation of ascorbic acid and zinc	– Improved biomass production, photosynthetic pigments, nutrient uptake – Enhance enzymatic and nonenzymatic antioxidant biosynthesis, and harvest index	Noreen et al. (2021)

ACCD 1-aminocyclopropane-1-carboxylate-deaminase, *Chl* chlorophyll, *DM* dry matter, *EPS* exopolysaccharides, *IAA* indole 3 acetic acid, *RWC* relative water content, *WUE* water use efficiency

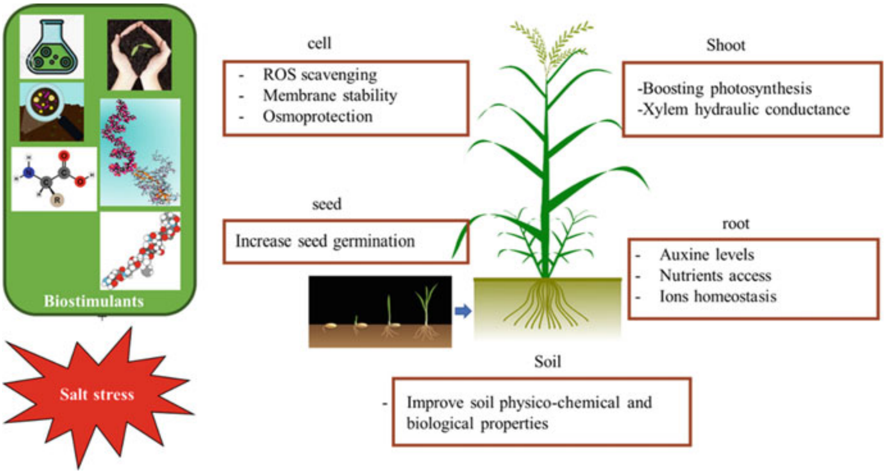

Fig. 19.3 Summary of the main mode of action targeted by biostimulants in cereals under salt stress

cultivars (Oljira et al. 2020). Transcriptome data of inoculated wheat roots with *Arthrobacter nitroguajacolicus* under salt stress revealed the upregulation of 152 genes belonging to flavonoid phenylpropanoid, terpenoid porphyrin and chlorophyll metabolism, stilbenoid, and diarylheptanoid metabolism pathways (Safdarian et al. 2019). Bharti et al. (2016) showed that inoculation of wheat with halotolerant PGPR *Dietzia natronolimnaea* STR1 protects plants from salt stress by adjusting ABA signaling, salt overly sensitive (SOS) pathway as well as ion transporters, and antioxidant machinery. Inoculation of quinoa plants with *Pseudomonas* sp. strain M30-35 mitigates salt stress by increasing biomass production, root activity, photosynthetic pigment content, and saponin, a crucial secondary metabolite in quinoa (Cai et al. 2021). Inoculation of maize with *Azotobacter* strains has been revealed to have generally positive impacts under salt stress by facilitating N, P, and K^+ uptake and Na^+ exclusion (Rojas-tapias et al. 2012).

The microbial-derived biostimulant category also contains arbuscular mycorrhizal fungi. AMF were reported as the world's oldest plant partners, with a partnership dating back 500 million years (Kistner and Parniske 2002; Ganugi et al. 2019). They form a close relationship with around 90% of terrestrial plants, delivering many benefits to their hosts (Smith and Read 2008; Wu 2019). Symbiotic AMF has a substantial impact on the cultivation effectiveness of crops. Several studies corroborated that AMF-based biostimulants could alleviate the harmful salinity effects in cereals (Estrada et al. 2013a; Talaat and Shawky 2014a; Selvakumar et al. 2018; Moreira et al. 2020). AMF can reduce the impact of excessive soil salinity and stimulate plant growth by promoting nutritional uptake and water status, enhancing soil structure, and contributing to salt stress resilience in agricultural and salt-exposed areas (Evelin et al. 2019). In maize, inoculation with native AMF revealed a significant increment of shoot dry matter (DM), K^+, and K^+/Na^+ ratio at different salinity levels and reduced Na^+ accumulation (Selvakumar et al. 2018). These favorable impacts were linked with the regulation of the gene in the roots such as *ZmAKT2*, *ZmSOS1*, and *ZmSKOR*, contributing thereby to K^+ and Na^+ homeostasis of inoculated maize (Estrada et al. 2013a). Co-inoculation with AMF and plant growth-promoting bacteria (PGPB) further leads ion homeostasis to maintain (K^+ and Na^+) in leaves of maize at the transcriptional level (Moreira et al. 2020). Selvakumar et al. (2018) found a similar effect after co-inoculating with *Gigaspora margarita* S–23, *Claroideoglomuslamellosum*, and *Pseudomonas koreensis* S2CB35. Likewise, Krishnamoorthy et al. (2016) showed that salt-stressed maize co-inoculated with *R. intraradices* and *Massilia* sp. RK4 promotes AMF colonization and mineral nutrient uptake. Talaat and Shawky (2014a) reported that AMF symbiosis protected wheat against the damaging effect of salinity and significantly enhanced plant productivity, gas exchange capacity, N, K^+, nitrate, chlorophyll, RWC, carbohydrates, protein, and the activities of carbonic anhydrase as well as nitrate reductase. The increase of free amino acids, soluble sugars, proline, and glycine betaine concentrations under saline conditions was marked in inoculated wheat. Furthermore, a lower degree of membrane peroxidation in AMF-treated plants was detected. Increased production of enzymatic and nonenzymatic antioxidants by AMF inoculation to eliminate the toxic effects of ROS would further improve wheat adaptation to saline soils and increase productivity (Talaat and Shawky 2014a).

19.4.2 Organic Amendment

Organic amendments, such as compost or vermicompost, are classified as biofertilizers. However, they are a source of agrochemicals or microbes that potentially have biostimulant properties, such as humic and fulvic acids, phytohormones, and amino acids. These substances interact with plant signaling processes and reduce the negative response to stress (Yakhin et al. 2017; Xu and Geelen 2018).

Humic substances (HS) are generated by the biodegradation of organic matter, producing ultimately a mixture of acids containing phenolate and carboxyl groups. According to Ouni et al. (2014), HS are divided into three fractions fulvic acids, humic acids, and humin. Fulvic acids contain higher oxygen content and lower molecular weight (Van Oosten et al. 2017). The algae represented by humic acids are considered to have gained importance as biostimulants because of their ability to enhance germination, plant growth, productivity, and nitrogen use efficiency (NUE) and tolerance to a diverse range of abiotic stresses, including salinity. Kapoore et al. (2021) reported the presence of humic acid (10 ± 1% of dry weight) in the brown alga *Pilayella littoralis* filamentous. Humic substances-based biostimulants have been reported to contribute to a protective role under salinity in cereals (Van Oosten et al. 2017; Liu et al. 2019a, b; Malik et al. 2020). Humic acid biostimulants improve soil texture, physical, chemical, and biological traits. Liu et al. (2019a, b) reported that HA fertilizer increased soil macroaggregates by 78–126%, affecting the fungal and bacteria community structure, improving soil nutrient availability and nutrient uptake. Foliar application of HA or pre-sowing seed treatment effectively improved salinity tolerance of maize plants by enhancing plant biomass, chlorophyll content, nutrients uptake, and activities of antioxidant enzymes (Kaya et al. 2018). Similar mitigating effects by HA application have been detected in barley grown under saline stress. Data indicate the potential of foliar or hydroponic HA application to limit Na uptake and positively impact the number of specific molecules (alanine, syringic acid, proline, glutathione, ascorbic acid, and phytochelatin) (Jarošová et al. 2016). Under salt stress conditions, sorghum treated with *Moringa oleifera* leaf extract (MLE) increased growth characteristics, photochemical activity, phytohormones content, and antioxidant system (Desoky et al. 2018). HA also play a protective role at different stages of the plant. Ali et al. (2020) showed that, at 200 mM NaCl salinity level, sorghum seeds treated with humic acid had higher root elongation, total DM, salt tolerance index, seedling vigor index, shoot height, protein concentration, APX activity, chlorophyll *b*, and total chlorophyll than untreated plants. The combination of HA and jasmonic acid was more effective in protecting early seedlings from salt stress damage and alleviating abiotic stress. Elrys et al. (2020) reported that the dual application of fulvic acid and licorice root extract significantly enhanced wheat morphological and physio-biochemical characteristics under saline stress. Furthermore, these treatments significantly improved the antioxidant defense system and reduced ROS, enhancing wheat growth performance under saline conditions.

19.4.3 Algae-Derived Biostimulants

Algae are classified generally into two main groups: (1) macroalgae (commonly known as seaweeds) are multicellular, marine, or freshwater organisms. Macroalgae are frequently divided into three categories: brown, red, and green algae. (2) Microalgae, which comprise blue-green algae, are evolutionarily diverse unicellular photosynthetic organisms, virtually present in all aquatic ecosystems and soils' surfaces (Carillo et al. 2020). Different species of algae, mainly seaweeds, are generally used for biostimulants production. The dominating microalgae species with biostimulatory action are *Ascophyllum nodosum*, *Ecklonia maxima*, *Durvillea potatorum*, *Fucus serratus*, *Durvillea antarctica*, *Himanthalia elongata*, *Laminaria digitata*, *L. hyperborea*, *Macrocystis pyrifera*, and *Sargassum* spp. (Sharma et al. 2014).

Over the past few decades, it has become clear that algal extracts (AEs) can impact crops owing to their richness in bioactive compounds, signaling molecules, and mineral and organic nutrients. AEs boost plant growth in stressful circumstances such as saline environments, which has recently led to increased use as plant biostimulants (Carillo et al. 2020).

Several studies detailed the biological activity of microalgal extracts and how their use could help reduce the harmful effects of abiotic conditions, including salt stress (Nabti et al. 2010; Zou et al. 2019, 2021; El-Katony et al. 2021). AEs affect plant defense and pathways involved in plant resistance to salt stress (Sharma et al. 2014; Zou et al. 2019; Carillo et al. 2020). Zou et al. (2019) revealed that polysaccharides from brown seaweed promoted plant growth, decreased membrane lipid peroxidation, and stimulated photosynthetic machinery under saline conditions. Besides, it has been shown that EPS extracted from the halophilic microalgae had a significant effect on wheat germination and growth (El Arroussi et al. 2016). It improved the wheat germination rate by 83–96% under salt stress. EPS improved the root height by 133–444% and the coleoptiles height by 105% (El Arroussi et al. 2016). Fucoidan, an acid heteropolysaccharide extracted from the brown algae *Macrocystis pyrifera* with an MW= 11.1 kDa, can enhance the salt stress tolerance of wheat seedlings (Zou et al. 2021). Application of seaweed *Ulva Lactuca* extracts to plants inoculated with *Azospirillum brasilense* further enhanced durum wheat salt tolerance and reduced proline and total sugar content (Nabti et al. 2010).

Furthermore, algal extracts have been demonstrated to improve the colonization of durum wheat roots by *A. brasilense* under salt stress conditions. In rice, brown algae *Dictyota dichotoma* extracts (Hudson J.V. Lamouroux) enhanced the germination rate by ca. 100% and alleviated salinity stress (El-Katony et al. 2021).

19.4.4 Protein-Based Biostimulants

Protein-based biostimulants are divided into two main categories: (1) protein hydrolysates consisting of mixtures of peptides and amino acids with other nitrogenous molecules, like betaines, polyamines, and nonprotein amino acids (Teklić et al. 2021), and (2) individual amino acids including glutamate, glutamine, proline, and glycine betaine (Calvo et al. 2014). Protein-based biostimulants may increase salt stress tolerance in cereals (Ertani et al. 2013; Trevisan et al. 2019). Alfalfa-based hydrolysate biostimulants containing triacontanol and IAA alleviated salt stress in maize by improving plant growth and increasing leaf proline and phenylalanine ammonia-lyase activity and modulating genes involved in salinity tolerance (Ertani et al. 2013). Trevisan et al. (2019) revealed the positive action of protein hydrolysates biostimulant (APR®, ILSA S.p.A., Arzigano VI, Italy) as an enhancer of the response to salinity in maize by regulating the transcription of a set of genes implicated in nitrate transport and ROS metabolism. In wheat, exogenous co-applied salicylic acid and melatonin through spraying could counteract the salt stress effect, promote growth and grain yield, and modulate the photosynthetic capacity (Talaat 2021).

19.4.5 Chitosan

Chitosan is a deacetylated form of biopolymer chitin produced naturally or industrially (Turk 2019; Azmana et al. 2021). The physiological effects of chitosan oligomers in plants under stressful conditions are contributed to the polycationic compound that binds to a vast amount of cellular molecules, including the plasma membrane, DNA, cell wall constituents, and specific receptors implicated in the activation of defense genes and plant elicitation (du Jardin 2015). Under saline stress conditions, chitosan-treated maize exhibited higher growth promotion than unstressed seedlings (Turk 2019). Chitosan can activate alternative respiration, thereby increasing the mitochondrial respiration rate, cytochrome respiration, and alternative respiration capacities (Turk 2019). In addition, AOX1, encoding alternative oxidase, was significantly upregulated by chitosan (Turk 2019). Chitosan could decrease superoxide anion and H_2O_2 content and lipid peroxidation level (Turk 2019). Zou et al. (2016) showed that sulfated chitooligosaccharide (SCOS) helped plants decrease the MDA and increase chlorophyll content, modulate fluorescence characters, and adjust the antioxidant enzyme activities in wheat under 100 mM NaCl, resulting in better crop performance. The impact of SCOS on wheat seedling photochemical efficiency was linked to its increased antioxidant enzyme ability, which reduced photosynthetic apparatus structural deterioration during NaCl stress.

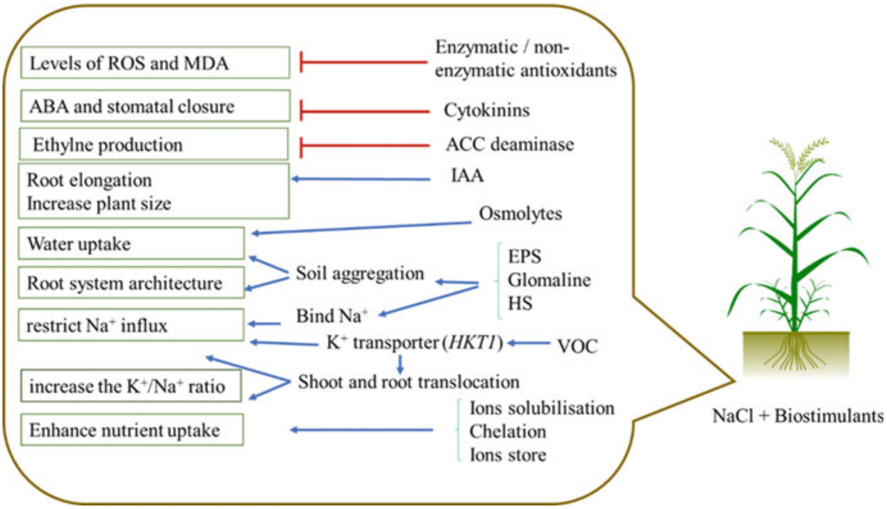

Fig. 19.4 General overview of biostimulants' underlying mechanism(s) to help cereals cope with salt stress

19.5 Role of Biostimulants in Improving Cereals Under Salt Stress

Under adverse environmental conditions such as salinity, biostimulants react with plants and alter their local and systemic mechanisms in different ways, allowing them to survive with these environments through diverse adaptation mechanisms (Cataldo et al. 2022). The biostimulants could mitigate salt stress and protect plants via several physiological, biochemical, and molecular approaches that can be activated during different stages of plant growth, either simultaneously or sequentially (Malik et al. 2020; Nephali et al. 2020; Rouphael and Colla 2020b; Irani et al. 2021) (Fig. 19.4).

19.5.1 Improvement of Mineral Nutrition

Salt stress affects the diffusion and mobility of soil nutrients owing to the poor soil structure caused by salinity. Biostimulants could improve macro- and micronutrient uptake and promote plant growth in stressful environments. PGPR can enhance the nutrient availability in the rhizospheric soil by fixing nutrients, thus preventing them from leaching out, resulting in mitigation of salt stress effects and increased plant biomass (Vejan et al. 2016; Oleńska et al. 2020). Certain PGPR can enhance atmospheric N fixation and solubilization of inorganic P (Anita et al. 2017; Liu et al. 2019a) and K^+ (Tan et al. 2014; Kaushal 2019), resulting in their availability and absorption by plants.

It is well known that AMF symbiosis enhances explicitly plant growth and mineral nutrient uptake (Baslam et al. 2013; Alqarawi et al. 2014; Panneerselvam et al. 2017; Evelin et al. 2019; Santander et al. 2019). The improvement of nutrient status in the mycorrhizal plant is mainly due to the enhancement of soil structure and a rise in the extraradical hyphae's absorption surface, enabling a more extensive investigation of soil nutrients. Under salt stress, AMF inoculation enhanced stomatal conductance, pigment (chlorophyll) content, and photosynthetic efficiency of host plants, resulting in a considerable increase in P, N, and Mg content (Panneerselvam et al. 2017; Evelin et al. 2019). In turn, AMF requires photosynthates transferred from the host plant, leading to ca. 20% drainage of C from the host plant to the soil (Juge et al. 2012; Parihar et al. 2020). This indirectly supports the carbon sequestration in the soil (Walley et al. 2013; Parihar et al. 2020). AMF can help to stabilize soils for up to 5 months after the host plant has died (Soka and Ritchie 2014; Gujre et al. 2021). Besides, AMF play an essential role in the flux of other significant nutrients (e.g., N and P).

One of HS's most studied physiological effects is enhancing ion absorption by improving the synthesis and function of membrane proteins, particularly proton pumps, which enhance the electrochemical gradient of protons across the plasma membrane (Canellas et al. 2020). Humic and fulvic molecules are not only a key source of soil organic C but also can have a phytohormone-like activity that induces nutrient uptake (Jindo et al. 2020). The main beneficial effect of these substances on plants under salt stress is due to changes at physiological and anatomical levels in both roots and shoots that assist plants to better uptake and spread nutrients along with the increment in nutrient accessibility via chelation (Van Oosten et al. 2017; Jindo et al. 2020; Malik et al. 2020).

The positive impact of algal-derived biostimulants on the growth, yield, and salt stress tolerance of cereal crops has been mainly attributed, among others, to the provision of essential nutrients (Zou et al. 2019, 2021). Algae are rich in macronutrients, mainly N, P, and K (Sharma et al. 2014). They can store minerals in soluble forms (Carillo et al. 2020).

19.5.2 Regulation of Ion Homeostasis and Mitigation of Deleterious Effects of Ion Toxicity

Salinity negatively affects plant growth and development by producing specific ion toxicity, which impairs mineral ion balance. Plant tolerance systems are built to maintain ionic homeostasis. Reducing Na^+ and Cl^- uptake and enhancing K^+ absorption, resulting in a lower Na^+/K^+ and Na^+/Ca^{2+} ratio, are considered among the key possible strategies of improving plant growth, productivity, and tolerance under salt stress circumstances (Hurtado et al. 2021).

Mycorrhizal plants exhibit higher K^+/Na^+ levels than non-mycorrhizal ones under salinity (Evelin et al. 2019; Ait-El-Mokhtar et al. 2020; Ben-Laouane et al. 2020; Toubali et al. 2020). Mycorrhizal plants can control the translocation of Na^+ to aerial parts and regulate its internal concentration. This is attributed to AMF ability in sequestering Na^+ in vacuoles or excluding it from the cytosol. The toxicity of sodium in the apoplast is minor compared to the cytoplasm. In addition, AMF allows the host plant to withdraw Na+ from the xylem and redirect it to the roots from photosynthetic regions (Evelin et al. 2019; Paymaneh et al. 2019). These changes offered by mycorrhizal symbiosis are accomplished through upregulating genes that encode Na^+ and K^+ transporters (i.e., *ZmAKT2*, *ZmSOS1*, *ZmSKOR*) charged for the upkeep of K^+/Na^+ balance in roots (Fileccia et al. 2017). Such transporters promote Na^+ exclusion from the cytosol and sequestration in the vacuoles resulting in improved salt tolerance. Rice accumulates more Na^+ in root than the aboveground due to a decrease in Na^+ distribution between both organs, suggesting the root-to-shoot communication as one of the critical approaches to reduce salt stress and maintain plant development under salinity (Porcel et al. 2016).

EPS secretion by PGPR plays a critical role in Na^+ extrusion and K^+ absorption in plants to maintain a higher K^+/Na^+ ratio (Kumari et al. 2019). EPS produced by PGPR boost biofilm production on the root surface, which help to maintain photosynthetic activity and plant growth (Naseem et al. 2018) and prevent Na^+ penetration into the roots (Kohler et al. 2006; Upadhyay et al. 2012). This mechanism was studied in many cereals, such as wheat (Upadhyay et al. 2012) and maize (Moreira et al. 2020).

Inhibition of Na^+ uptake is part of the protective mechanisms of humic acid against salinity. Khaleda et al. (2017) showed that salt-induced destruction of *HKT1* was inhibited by the humic acid application that enhanced the *HKT1* protein richness in the root, resulting in significant Na^+ reabsorption from xylem bundles into cells of the root parenchyma and, consequently, less Na^+ translocation to the shoot. Similarly, barley showed a decrease in Na^+ uptake following the humic acid application (Jarošová et al. 2016).

19.5.3 Production of Phytohormones

PGPRs can directly enhance plant growth under salt stress by forming compounds similar in structure and function to phytohormones. PGPR can decrease ethylene content in the host plant by producing ACCD, catalyzing the conversion of ACC (ethylene biosynthesis' precursor) to ammonia and α-ketobutyrate (Goswami et al. 2016; Anita et al. 2017; Nascimento et al. 2018).

It was revealed that humic acid could be utilized as a growth biostimulant to control hormone balances, boost plant growth, and improve stress tolerance. Humic matter's complex biological activity is influenced by its concentration, chemical properties, molecular weight, and size (Ouni et al. 2014). Muscolo et al. (2007) showed a similar effect of humic acid to IAA application.

Algae-derived biostimulants are a source of phytohormones and play essential roles in plant response to environmental stimuli (Sharma et al. 2014; Carillo et al. 2020). Auxins, cytokinins, gibberellins, betaines, abscisic acid, jasmonic acid, polyamines, ethylene, and brassinosteroids are the main phytohormones detected in macroalgal species, and they are also considered essential factors by which algae improve plant growth performance, yield, and defense response, particularly against abiotic stress (Stirk et al. 2013a, b).

19.5.4 Accumulation of Osmoprotectants

The accumulation of sodium chloride sodium, hydrogen carbonate, and sodium carbonate in the soil leads to high pH and alkalinity, which ultimately causes osmotic stress and nutrient deficiency in cereals due to interference in nutrient uptake. This adversely affects the physiological functioning of cereals (Munns et al. 2015). PGPR and AMF can accumulate large amounts of organic osmolytes, including trehalose, sucrose, proline, and glycine betaine. The accumulation of these osmolytes offers an adaptation strategy under high salinity through promoting cellular osmotic regulation, ROS detoxification, membrane integrity preservation, and enzyme/protein stability (Kumari et al. 2019).

19.5.5 Induction of Antioxidant System

Plant adaptation to salt stress has been linked to maintaining a strong antioxidant capacity to scavenge the harmful ROS. Plants develop a complex connection of many enzymatic (i.e., SOD, CAT, POX, APX, GPX, and GR) and nonenzymatic molecules (i.e., flavonoids, carotenoids, glutathione, tocopherols, and ascorbate) as a defensive strategy to remove ROS (Porcel et al. 2012; Hasanuzzaman et al. 2020).

PGPRs can protect plants from oxidative stress and induce ROS-neutralizing mechanisms by boosting the level of antioxidants and other compounds that act as ROS scavengers, compared to non-treated plants (Kohler et al. 2009; Ojuederie et al. 2019). Several reports revealed the role of PGPR in inducing the antioxidant system and removal of free radicals generated during high salt conditions in cereal plants (Bharti et al. 2016; Bharti and Barnawal 2019; Ilyas et al. 2020; Kumar Arora et al. 2020). Thus, the application of PGPR plays a crucial role in enhancing the oxidative stress tolerance capacity of cereals plants (Garg et al. 2019).

Mycorrhizal cereal plants exhibit less oxidative damage than non-mycorrhizal ones subjected to salt stress, either through improved antioxidant enzymes or antioxidant compounds (Ruíz-sánchez et al. 2011; Estrada et al. 2013b; Talaat and Shawky 2014a). Several studies have confirmed that enhanced antioxidant activity by mycorrhizal symbiosis is linked with reduced osmotic stress in plants (Evelin et al. 2009, 2019; Ben-Laouane et al. 2019, 2020; Ait-El-Mokhtar et al. 2020; Anli et al. 2020a). These studies reported that by increasing antioxidant activity, mycorrhizal symbiosis reduces the accumulation of toxic metabolites, such as MDA and H_2O_2, and ensures cell membranes' integrity and stability. However, the exact mechanism by which PGPR or AMF influences host plant ROS metabolism and the underlying mechanisms are not well elucidated.

The physiological mechanisms of humic substances to prevent salt stress have been associated with reducing ROS concentration and increasing enzymatic/

nonenzymatic antioxidants defense to avoid ROS-induced oxidative damage. The potential function of humic acids in preventing oxidative stress in cereals plants has been suggested in many crops such as maize (Kaya et al. 2018; Canellas et al. 2020), wheat (Elrys et al. 2020), sorghum (Desoky et al. 2018; Ali et al. 2020), and barley (Jarošová et al. 2016).

Algae as biostimulants can have an essential role to prevent plants against salinity by inducing the antioxidant system. It is well documented that marine algae contain a large concentration of phenolic substances. Compared to vascular plants, the phenolic compounds in marine macroalgae are diverse, ranging from essential compounds like phenolic acids to highly complex and specialized ones (Carillo et al. 2020). These molecules are often produced under stressful situations, scavenge ROS, and stabilize membranes and proteins (Audibert et al. 2010; Blanc et al. 2011; Malik et al. 2020).

19.5.6 Maintenance of Water Homeostasis

Long-term salinity exposure creates water stress conditions that perturb plant performance. Due to reduced soil water potential, plant growth is principally impacted in the osmotic stage. Alleviation of this effect requires a set of molecular and cellular and physiological alterations.

PGPR are revealed to have the ability to increase aquaporin gene expression, directing water uptake by plants under salt and salt-associated drought stresses. PGPR such as *Azospirillum brasilense*, *Pantoea agglomerans*, and *Bacillus megaterium* induced *PIP2*, *ZmPIP1-1*, and *HvPIP2-1* genes implicated in aquaporin synthesis (Kumar Arora et al. 2020). This gene upregulation stimulates water absorption and sustains water potential. An increment in water accessibility was shown in quinoa inoculated with *Enterobacter* sp. MN17 and *Bacillus* sp. MN54, which therefore reduced osmotic and ionic stress (Yang et al. 2016).

Under salinity, inoculation with AMF enhances plant water use status owing to the "extra absorption" of water by the extracellular hyphae. Furthermore, AMF change the number of important compatible organic substances that help enhance osmotic adjustment (Augé et al. 2014; Al-Arjani et al. 2020). AMF symbiosis improves active solute transport to maintain water flowing through plant roots. Furthermore, modulation of hydraulic root characteristics by AMF are reported to be linked to aquaporin genes expression (Aroca et al. 2007; Hajiboland 2013; Ding et al. 2019; Cheng et al. 2021). Aquaporin genes such as *LjNIP1* and *LjXIP1* are upregulated in AMF plants, generating a considerable increase in the water uptake ability in salt-affected cereals (Hajiboland 2013; Cheng et al. 2021). However, Fileccia et al. (2017) revealed that the expression level of the (a)biotic stress-related genes *DREB5*, *AQP4*, *AQP1*, *PIP1*, and *DHN15.3* which was detected in the AMF-stressed wheat was significantly lower compared to non-AMF-stressed plants and similar to the observed values in the non-stressed control plants. They explain that AMF association did not improve plant tolerance to salinity but instead created a situation where plants were exposed to a lower salt stress level than non-mycorrhizal plants.

19.5.7 Restoration of Soil Structure and Quality

Salt stress deteriorates soil characteristics such as pH and EC. Excessive Na^+ ions affect soil porosity and nutrient composition by destroying the bonds between these different particles. Application of biostimulants such as PGPR could alleviate the deleterious impacts of salinity by boosting soil structure through EPS secretion that binds soil particles (Naseem et al. 2018). A significant increment in soil aggregation around roots was revealed in the maize rhizosphere treated with an EPS-producing bacterial strain under salt stress (Nadeem et al. 2021). The secretion of this substance plays a critical role in Na^+ exclusion and K^+ uptake by plants (Kumari et al. 2019).

AMF directly impact the soil and root system architecture by regulating pH and EC and improving soil structure, aggregation, and root biomass (Rillig et al. 2015). Mycorrhizal association decreases pH and rhizospheric soil EC by releasing organic substances into the soil and the selective nutrients uptake (Liu et al. 2016). Due to their mycelial network extent and thickness, AMF could access the pores surrounding microaggregates and form stable aggregates that help air and water diffusion and prevent soil degradation (Bhardwaj et al. 2014; Berruti et al. 2016; Gałązka et al. 2020). In addition, glycoproteins (glomalin) produced into the soil by AMF may have an essential role in this process(Aalipour et al. 2021). Glomalin—hydrophobic and thermotolerant glycoprotein—has a slow biodegradability by soil microorganisms. Glomalin binding to clay particles allows a strong cohesion, more resistance to microbial degradation, providing the excellent structural integrity of soil (Pal 2014; Gałązka et al. 2020). Glomalin's capacity to improve the structural stability of saline soils has previously been documented(Hammer and Rillig 2011; Garcia et al. 2019; Kaushal 2019; Li et al. 2020a).

Accumulation of HS due to organic matter supply controls soil physicochemical properties. In particular, HS provides the energy for the beneficial organisms, influencing soil water holding capacity and structure, releasing plant nutrients from soil minerals, trace minerals availability, and fertility of salt-affected soils (Ouni et al. 2014). HS can indirectly decrease soil pH, Na^+, and EC, likely owing to the high Ca^{2+}, Mg^{2+}, and K^+ supplies that keep the cation exchange sites on soil particles and enhance Na^+ leakage losses through precipitation occurrence (Lakhdar et al. 2008; Ouni et al. 2014).

Biostimulants improve the K^+/Na^+ ratio via selectively increasing K^+ absorption and preventing harmful Na^+ translocation in saline circumstances. Such biostimulants can increase the antioxidative structures in plants for ROS scavenging, like enzymatic compounds of SOD, CAT, APX, POD, and GR and nonenzymatic components, including glutathione, cysteine, and ascorbic acid. PGPR-producing ACCD decreases the overproduction of ethylene in plants due to salt stress and eliminates ethylene's negative impact on roots. Production of phytohormones improves plant growth and promotes root characteristics to facilitate water and nutrient uptake. IAA increases root elongation and aerial parts size. Biostimulants-treated cereals produced osmoprotectants (i.e., proline, polyamines, total free amino acids) that contribute to salinity tolerance. EPS binds the toxic Na^+ and restricts Na^+ influx into roots. Due to EPS, glomalin, or humic substances production, soil aggregation helps enhance water and nutrient uptake. Volatile organic compounds (VOCs) may induce a high affinity of *HKT1* in shoots and reduce *HKT1* in roots, reducing Na^+ access into roots and promoting Na^+ recirculation from shoots to roots.

19.6 Conclusions and Perspectives

Biostimulants have gained worldwide interest due to their revolutionary benefits of sustainable agriculture. The microbial inoculants and natural substances may ensure crops productivity, including cereals, even under changing environments. Biostimulant application is an efficient alternative to boost cereals tolerance in saline soils and reduce the impact of this constraint on productivity. Under the saline condition, biostimulants can improve the growth and productivity of cereals and soil health directly and indirectly via a network of strategies. Applying these biological inputs mitigates the salt-induced effects in cereals by maintaining water and nutrient homeostasis, producing phytohormones and organic osmolytes, reducing ions toxicity, stimulating antioxidant system defense, regulating fundamental gene expression, and improving soil structure and fertility. Although there are many exciting opportunities associated with adopting biostimulants, there are also clear challenges. Though more research is required, it demonstrates that concerns about the effectiveness of some biostimulants are perhaps valid. Since biostimulants enhance (cereal) crops' ability to acquire and assimilate what they need from the surrounding environment instead of directly supplying the plants with what it needs, it is critical, therefore, to understand the interactions between these biostimulants and the environment (e.g., application timing relative to plant growth stage or to establish standard microbial soil amendments in the presence of other soil microbiota). In addition, the interaction between different microorganisms and/or nonmicrobial biostimulants is still to be elucidated. Besides, the exact mechanisms implicated in the positive effects of biostimulants are not fully understood. Molecular approaches may shed light on understanding the whole picture of the biostimulants' mode of action in alleviating the deleterious impact of stresses on cereal crops.

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Use of Biostimulants to Improve Drought Tolerance in Cereals

20

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Abstract

Abiotic stresses present the most constraints, negatively affecting plant growth performance and productivity. Climate change variations and agricultural mismanagements such as the overuse of chemical fertilizers and pesticides have heightened abiotic stresses that impact crop productivity and, therefore, caused

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agroecosystem degradation. Nowadays, the improvement of crops productivity has become a global concern to a grown population. Research on sustainable tools to increase plant production, especially cereal crops, is needed to respond to this challenge. However, it is crucial to manage environment-friendly techniques sustainability like biostimulants to improve cereal crop productivity under harsh conditions. Moreover, it is generally believed that biostimulants are more effective in offering tolerance to cereal crops against numerous abiotic stresses, including drought stress. Several biostimulants like arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), *Trichoderma* spp., endophytes, and seaweed extracts (SWE) are used to increase cereal crop production and boost their tolerance to drought stress conditions. These biostimulants could assist cereal crop tolerance mechanism upregulation and avoid the central metabolic pathway downregulation. These biostimulants provide essential mineral nutrients to cereal crops and increase fitness and productivity under drought stress. These biostimulants could potentially support plants' adaptability to avoid the adverse impacts of drought stress by stimulating the antioxidant defense system and photosynthetic activity. Therefore, more investigations focusing on the biostimulant-mediated cereal crop quality and productivity promotion are needed. The current chapter will make a comprehensive knowledge of AMF, PGPR, *Trichoderma* spp., endophytes, and SWE, their effects on cereal crop growth stages and productivity, their applications and advantages, and the potential mechanisms employed to improve their tolerance under drought stress.

Keywords

Climate change · Drought · Biostimulants · Crop productivity · Tolerance · Agricultural ecosystem

20.1 Introduction

Cereals occupy an important place in the agricultural production system globally. The Food and Agriculture Organization of the United Nations (FAO) has forecast an increasing world cereal production in the coming years. Global cereal production and utilization have been steadily increasing for the past 3 years, marking a net increase near 2800 million tons for 2020/21 (Fig. 20.1) (FAO 2021). Cereals are a crucial part of the world's agricultural production system, providing a food staple for a considerable part of the global population (Rouphael and Colla 2020). Cereal grains constitute an important carbohydrates source for human food. Cereals including rice, wheat, maize, barley, and sorghum represent the main crops cultivated worldwide, being also widely cultivated in arid and semiarid regions where drought, salinity, soil poverty, erosion, high temperatures, and heavy metal are the most abiotic constraints limiting plant's growth performances, quality, and productivity (Ghatak et al. 2017; Hussain et al. 2020; Anli et al. 2021). Drought is common in

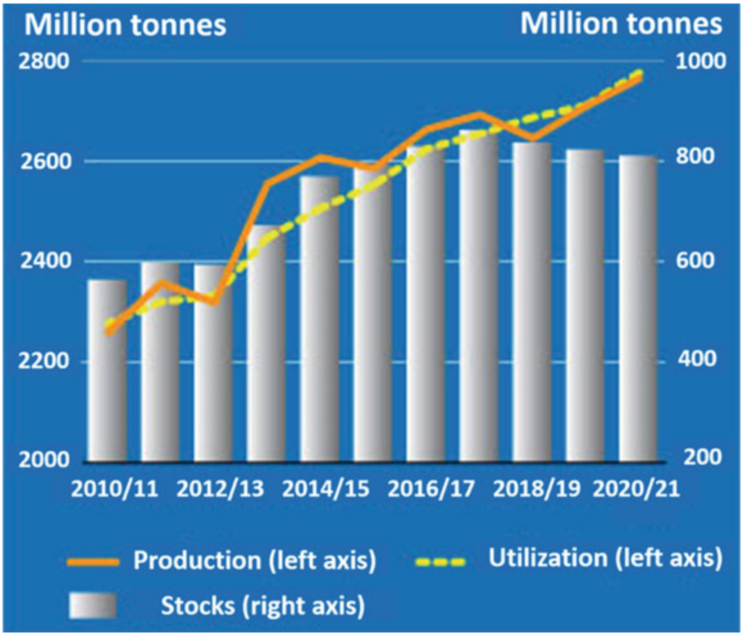

Fig. 20.1 World cereal production, utilization, and stocks from 2010 to 2021 (Source: FAO 2021, http://www.fao.org/worldfoodsituation/csdb/en/)

virtually all climatic areas, and the loss of cereal crop production due to drought is reported to be the most significant agricultural loss (Daryanto et al. 2016, 2017).

The negative impacts of climate change-driven (a)biotic stresses and the relative degradation of croplands are increasing the vulnerability of crops adaptation (Abdel Latef et al. 2019a, b, 2020; Rodríguez-Berbel et al. 2020), threatening thereby the global food homeostasis and restricting the expansion of crops production (Fahad et al. 2017; Hasanuzzaman et al. 2020; Torabi Haghighi et al. 2020; Abdelhameed et al. 2021). Globally, the crop yield reduction by abiotic stresses is estimated at 50–70% (Francini and Sebastiani 2019). Among abiotic stresses, drought is one of the key contributors to the plants' production, quality and quantity, decline, and food insecurity (Ojuederie et al. 2019; Ait-El-Mokhtar et al. 2022) by adversely reducing plant growth performances, physiology, and reproduction (Trivedi et al. 2018; Irani et al. 2021). Drought causes a set of agro-physiological, biochemical, nutritional, and molecular variations that lead to plant growth and development disruption (Carillo et al. 2019; Khan and Bano 2019; Baslam et al. 2020). The metabolic processes, gas exchange variables, including stomatal conductance and internal CO_2 concentration, and cell membrane permeability are damaged by drought stress (Augé et al. 2015; Kanwal et al. 2017; Boutasknit et al. 2020). Under drought conditions, the first plant reaction to drought stress is stomatal closure, which results in limited plant growth performance, water loss linked to internal CO_2 concentration decrease, and photosynthetic activity inhibition (Fullana-Pericàs et al. 2018;

Symanczik et al. 2018; Hao et al. 2019). In addition, drought causes oxidative stress by overproducing reactive oxygen species (ROS) (Hasanuzzaman et al. 2020; Boutasknit et al. 2021a). To overcome their sessile lifestyle, plants have developed specific strategies that give them an exceptional range of plastic development. Plants adapt to adverse natural conditions by coordinating a complex network of sensing mechanisms. Under such conditions, genetic and molecular mechanisms for avoiding stress-induced detrimental alterations are critical for plant survival (Anli et al. 2020a; Ben-Laouane et al. 2020; Teklić et al. 2021).

Besides, drought stress can affect soil structure and productivity and reduce water supply to plants directly via microbial communities and/or indirectly through the changes in soil physical and chemical characteristics (Vimal et al. 2017; Nguyen et al. 2018). Due to intensive agricultural practices, soil fertility, productivity, and quality have deteriorated. Soil fertility depletion is currently considered one of the most critical emerging challenges due to the increasing global population, abiotic stresses, pollution, and disruption of natural resources under climate change conditions (Vimal et al. 2017; Trivedi et al. 2018; Dubey et al. 2019). Recently, attention was devoted to evaluating the various adverse effects of drought on cereal grain quality and understanding the potential mechanisms underlying stress-alleviating strategies and the possible positive effects of biostimulants (Kanwal et al. 2017; Boutasknit et al. 2021a). To this end, the utilization of microbial and nonmicrobial biostimulants such as arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), endophytes, *Trichoderma* spp., and seaweed extracts (SWE) has emerged as a valid technology to increase agriculture production and soil fertility to render the existing traditional agricultural system better adapted to meet long-term rising demand, with appropriate access to food now and in the future (Ripa et al. 2019; Rouphael and Colla 2020). In contrast, unplanned use of chemical inputs in agricultural soils decreased telluric microorganisms diversity and negatively impacted soil health (Sun et al. 2015; Vimal et al. 2017; Xue et al. 2017).

Plant-microbe associations in the rhizosphere are critical in the transformation, mobilization, solubilization, and subsequent uptake of vital nutrients by plants in order for plants to reach their full genetic potential in the era of sustainability. These beneficial microbes can offer a defense system to plant under adverse environmental constraints (Frioni et al. 2018; Gangwar and Singh 2018; Ait-El-Mokhtar et al. 2020; Anli et al. 2020a). The management of plant-microbe interaction is crucial to coping with plants against drought stress and understanding mechanisms involved in microbe-driven drought tolerance, promoting crop productivity in a harsh environment (Khan and Bano 2019; Yaseen et al. 2019; Polcyn et al. 2019; Boutasknit et al. 2021b). The engineering of these soil microbial inoculants is an emerging sustainable agricultural technology that can improve crop productivity and soil fertility/health by boosting the communication of plant-beneficial microbes under stressful conditions (Gangwar and Singh 2018). Indeed, applying the beneficial microorganisms (AMF, PGPR, endophytes, and *Trichoderma*) to droughted plants can enhance the plant response mechanisms and promote stress tolerance and adaptation (Oyewole et al. 2017; Gangwar and Singh 2018; Bernardo et al. 2019;

Khan and Bano 2019). PGPR can regulate drought tolerance via exopolysaccharides, phytohormones, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and volatile compounds production and by regulating stress-responsive genes related to the root morphology (Khan and Bano 2019; Kaushal 2019). AMF-mediated drought tolerance is not only by enhancing mineral and water absorption from the surrounding soil but also by activating plant's aquaporins to provide better hydration, increasing osmotic adjustment, antioxidant defense system, phytohormones, and improving soil structure and aggregates by glomalin (Bernardo et al. 2019; Symanczik et al. 2020). Endophytes—microorganisms colonizing symptomless the healthy living tissues of the plant—may be an essential tool in managing (a)biotic stresses by promoting hosts' growth, adaptation, development, and stress tolerance via the large amount of biologically active substances produced. Indeed, endophytes are a significant source of physiologically active metabolites under drought conditions, such as soluble sugars, organic acids, and amino acids (Hosseyni Moghaddam et al. 2021). Plant growth-promoting fungi (PGPF) such as *Trichoderma* spp. have been recommended to boost plant growth and production. *Trichoderma* spp. has evolved various approaches for establishing a mutually beneficial association with plants. Furthermore, *Trichoderma*-mediated plant growth control might directly impact secreted substances on plants or an indirect influence by altering the local environment, such as the soil microbiota or soil pH-inducing nutrients available for plant growth. Chemical signaling, in which fungi produce chemical substances that change plant metabolism, is used to achieve this type of cross-kingdom communication. Recent studies revealed *Trichoderma*-mediated global proteome and transcriptome modification in plants and their impact on growth regulation and defense (Coppola et al. 2019; La Spada et al. 2020; Ho et al. 2016). Mitigation of ROS damage, water-use efficiency, and secretion of phytohormones are the three main strategies utilized by the avirulent plant symbionts in promoting plant growth under drought conditions or other abiotic stressors (Fahey et al. 2020; Abdullah et al. 2021).

Together with beneficial microbes, applications of nonmicrobial biostimulants were shown to boost plant growth and development and macro- and micronutrient uptake and translocation in several crops, resulting in increased biomass production and yield. Seaweed extracts are considered an essential category of nonmicrobial plant biostimulants owing to their use on several agronomic and horticultural crops under conventional and organic farming systems. Since ancient times, SWE have been utilized widely in agriculture farming as a soil amendment to boost crop productivity (Nabti et al. 2017; Malik et al. 2020). In recent years, SWE gained an important attractiveness globally as biostimulants (Khan et al. 2009). SWE stimulate several characteristics of plant and development. Under drought, SWE mitigate oxidative stress by decreasing cell membrane leakage and lipid peroxidation resulting in an increment of antioxidant enzymes activities. SWE may positively impact phytohormones and mineral status responsible for reactivating the photosynthetic activity and, consequently, the agronomic performance (Trivedi et al. 2018; Kumar et al. 2020). SWE application in agriculture as biostimulants extends to their original use as soil conditioners to boost soil quality and productivity. However, recent trends in organic agriculture and greater demands for biobased feeds have created an ample opportunity for reinvestigating SWE positive effects as soil conditioners and/or biofertilizers/biostimulants (Khan et al. 2009; Malik et al. 2020). SWE contain various organic compounds, especially carbohydrates, phytohormones, proteins, and fatty acids, which have a beneficial effect on moisture and nutrient retention in the soil (Malik et al. 2020). The beneficial impacts of SWE on soils and plant growth have been linked to enhancing water holding capacity, boosting microbial activity, and improving soil texture. Under stress conditions, algal-based fertilizers were found to help create an appropriate soil habitat for root development by improving microbial activity and diversity, including respiration, nitrogen mobilization, and mineral nutrient mineralization (Battacharyya et al. 2015).

This chapter aims to provide an overview of the research related to the potential effects of AMF, PGPR, and SWE on the different development stages and productivity of cereal crops. Moreover, the progress in clarifying the potential strategies underlying biofertilizer-inducing drought tolerance in cereal crops is discussed.

20.2 Cereal Production Under Drought Stress

20.2.1 Drought Stress Effects on Rhizosphere

Drought stress can negatively impact the soil structure and productivity (Lal 2014; Anli et al. 2020a). Water deficit decreases the telluric microbial community’s rate, structure, and activity (Hueso et al. 2012; Geng et al. 2015). The shortage of soluble nutrients and their unavailability in dry soils reduce microbial mobility and access to these nutrients, ultimately reducing microbial activity (van der Heijden and Wagg 2013; Zia et al. 2021). The rhizosphere microbiome has a vital role in plant functioning by integrating several metabolic processes, including the decomposition of organic matter and the nutrient cycle (Akinola et al. 2021; Munoz-Ucros et al. 2021). In addition to limiting the spatial distribution of nutrients and microorganisms in the soil, water deficit also decreases soil respiration and increases the adaptation of specific microbial communities to stressful conditions (Suseela et al. 2012; Karimzadeh et al. 2021). Extreme and frequent drying and rewetting episodes can lead to the selection of microbial taxa which are more resistant to desiccation, and these modifications can provide a community that reacts differently, stress-tolerant species, to moisture stress (Schimel et al. 2007; Fuchslueger et al. 2016; Begum et al. 2019) (Fig. 20.2). Fungi and bacteria exhibit a large scale of tolerance to water stress. Fungi are inherently more drought-tolerant than bacteria (Fuchslueger et al. 2016; Poudel et al. 2021) and have used several strategies to overcome this stress (Poudel et al. 2021), whereas bacteria grow faster and outcompete fungi for access to labile substrates. Since the water potential of the soil enhances quickly after rainfall, the microorganisms have to release solutes before the cells are burst by osmotic pressure (Vafa et al. 2021; Lahbouki et al. 2022). Therefore, knowing the effect of drought on root-associated microbial communities is a critical stage in evolving drought control

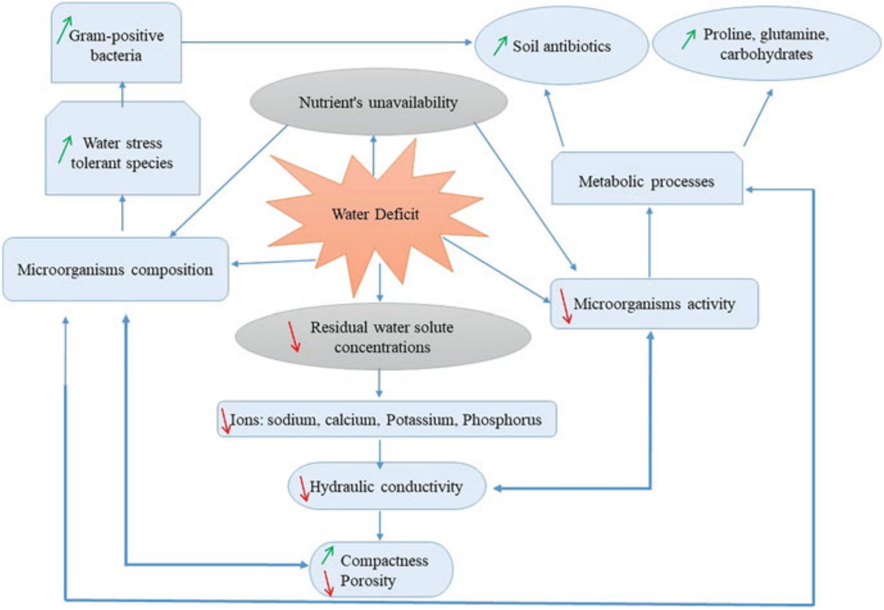

Fig. 20.2 Effects of drought stress on agricultural soil

solutions (Naylor and Coleman-Derr 2018). Water deficit changes the proportional abundance in the soil microbiome without deleting existing taxa, demonstrating that drought does not affect microbial alpha diversity but its composition. In addition, it was observed that the ratio of Gram-positive to Gram-negative bacteria increased under stressful conditions (Acosta-Martínez et al. 2014; Chodak et al. 2015; Fuchslueger et al. 2016). The difference in sensitivity to drought between Gram-positive and Gram-negative bacteria is probably due to their different metabolic capacities and substrate choices (Kurm et al. 2017). Dry soils are generally "oligotrophic"—lack nutrients and have an excess of oxygen (Kurm et al. 2017)—and the proliferation of the bacteria (oligotrophic bacteria) is made through the degradation of plant polysaccharides (Bouskill et al. 2016; Martiny 2016). Gram-positive bacteria have the characteristics of oligotrophs because they can produce extracellular enzymes capable of degrading complex organic compounds in dry soils by using inorganic N and recalcitrant C (Treseder et al. 2016; Hartmann et al. 2017), whereas Gram-negative bacteria are more likely to be copiotrophs since they use labile C and organic N (Treseder et al. 2016). The change in bacterial community composition due to water stress may also be related to sporulation, allowing bacteria to enter dormancy during drought stress periods (Hayden et al. 2012; Acosta-Martínez et al. 2014). Indeed, Gram-positive bacteria are more resistant to water stress due to their ability to sporulate and the thickness of their walls than Gram-negative bacteria (Schimel et al. 2007; Tocheva et al. 2016).

Water deficit can cause existing microorganisms to release a range of substances that impact the community's stability. Droughted soils have abundant antibiotics, thought to be released by drought-resistant bacteria as a physiological reaction to competing with other bacteria for restricted resources or perhaps as signals to stimulate drought-response pathways, including biofilm formation (Bouskill et al. 2016). In addition, several bacteria synthesize compounds during the drought period, such as proline, amino acids, glutamine and glycine betaine, and carbohydrates (Bouskill et al. 2016) that affect soil aggregate stability in the rhizosphere (Kohler et al. 2009) and hydrophobicity (Ahmed et al. 2021). The accumulation of these molecules in soils influences the equilibrium of the rhizosphere and protects macromolecular structures (Kohler et al. 2009) (Fig. 20.2). The physical and chemical properties of the soil also change under water stress and may influence the composition of microbial communities (Lauber et al. 2009; Gunnigle et al. 2017; Hartmann et al. 2017). Drought stress increases the residual water solute concentrations (Schimel et al. 2007; Karandish 2017). Dry soils contain low ions, sodium, calcium carbonate, potassium, phosphorus, iron, and aluminum (Bachar et al. 2010; Bouskill et al. 2016). Decreased nutrient cycling in low-moisture soils causes a decrease in existing soil nitrate and P forms (Sardans and Peñuelas 2004; Fuchslueger et al. 2014) and an increase in complex organic C (Saradadevi et al. 2017; Fang et al. 2020; Shen et al. 2020). Soil hydrological characteristics control soil water fluctuations downhill toward the groundwater level or laterally to stream connections, and they allow to predict the parameters affecting the agronomic operations (Fang et al. 2020). Water stress reduces hydraulic conductivity and total soil porosity owing to decreased plant aerial biomass in stressed soils (Zhang et al. 2018). Drought-inducing reduction in soil organic matter negatively impacts the soil structure, more compact and less porous (Wu et al. 2016) (Fig. 20.2).

20.2.2 Effects of Drought Stress on Physiological Traits in Cereals

Drought stress induces many physiological and biochemical changes that alter cereal metabolic status, influencing adaptation and survival (Hasanuzzaman et al. 2020). Cereal crops have evolved many strategies at agro-physiological, biochemical, and molecular levels to overcome drought stress. Generally, plants respond to drought stress by avoiding periods of water shortage, keeping high water potential through various protective mechanisms, and maintaining metabolic activity (Fahad et al. 2017; Bernardo et al. 2019). Cereal crops maintain a high water status during drought stress to avoid dehydration, minimizing water loss through stomatal closure, leaf area reduction, root elongation, and leaf senescence (Augé et al. 2015; Zafar-Ul-Hye et al. 2019). Despite implementing such strategies, water stress affects the physiology of cereals at several levels. In periods of drought, plants show a decrease in growth due to a disruption of photosynthetic activity (Table 20.1). When water availability is limited, plants are negatively affected through a decrease in stomatal conductance, photosynthetic pigments content, production of ROS and disruption, and degradation of membrane cells (Trivedi et al. 2018). Furthermore, many studies

Table 20.1 Drought stress effects on cereal crops

Plants	Drought	Impacts/mechanisms	References
Maize	DS (14 days after irrigation) and the recovery phase (1 day after irrigation)	Reduction of stomatal conductance, transpiration rate, CO_2 uptake, and leaf mineral nutrients (N, Mg, and Ca)	Zoppellari et al. (2014)
Maize	75 and 55% (relative soil water content) during 4 weeks	– Decrease the dry weight – Increase plant damage by improving MDA content and membrane relative permeability	Zhu et al. (2011)
Maize	Moderate and severe DS for 30 days	– Plant growth and photosynthetic activity decrease – ROS generation enhancement	Begum et al. (2019)
Maize	WW and DS conditions	– Decrease in stomatal conductance and photosynthetic pigments – Overproduction ROS – Disruption and degradation of membrane cells	Trivedi et al. (2018)
Maize	WW and DS conditions	– ROS accumulation increment – Cell death – Protein degradation	Huang et al. (2019)
Maize	DS during 7 days	– Decrease in biomass production, phytohormones (indole 3-acetic acid and gibberellic acid) and photosynthetic pigments – Increase in ABA production, proline content, and antioxidant activities (SOD, CAT, and POX)	Yasmin et al. (2017)
Maize	WW, 60% (soil water content) DS 30%	– Decrease in biomass accumulation, carbohydrates concentration, amino acids, and flavonoids – Increase in protein oxidation and H_2O_2 and MDA content	Selim et al. (2019)
Wheat (tolerant and sensitive cultivars)	WW, moderate and severe DS	*Sensitive cultivar*: – Decline in membrane stability, photosynthetic activity, and plant water relations – Increased ROS generation, lipid peroxidation, and membrane injury *Tolerant cultivar*:	Abid et al. (2018)

(continued)

Table 20.1 (continued)

Plants	Drought	Impacts/mechanisms	References
		– Enhanced enzymatic and nonenzymatic antioxidant activity and buildup of soluble sugars, proline, and free amino acids – High photosynthetic activity under drought than the sensitive variety	
Wheat (tolerant and sensitive varieties)	DS for 10 days	– ABA-regulated proteins are more expressed in the sensitive variety	Alvarez et al. (2014)
Wheat (tolerant and sensitive varieties)	15% PEG-6000, moderate DS and 30% PEG-6000, severe DS for 5 days	*Sensitive variety*: – Reduction of photosynthetic activity, grain number, and yield – Increase in ABA production *Tolerant variety*: – Increase in antioxidant activity (SOD and POX) – Physiological performance promotion, photosynthetic rate, carbohydrate accumulation, pollen sink strength, development, and fertility	Dong et al. (2017)
Wheat	DS after 30 days of germination	Decrease in soil and plant RWC and photosynthetic activity	Mathur et al. (2018)
Wheat	50% (moderate DS) and 25% (severe DS) of the optimal water supply (100%)	– Decrease in growth performances and grain yield, water potential reduction, stomatal conductance, photosynthetic activity – Increase in proline accumulation	Silletti et al. (2021)
Wheat	Irrigation and dry farming	– Reduction of grain yield and growth performances	Vafa et al. (2021)
Wheat	0, 15, and, 25% PEG-6000 during 15 days	– Decrease in plant biomass – Photosynthetic activity perturbation	Hussain et al. (2014)
Rice (tolerant and sensitive varieties)	20% PEG-6000 during 48 h	– Severe damages (chlorophyll degradation, protein oxidation, and increased H_2O_2, MDA and lipoxygenase) in drought-sensitive variety	Basu et al. (2010)

		– Antioxidant enzymes increment (flavonoids and phenolics) in a drought-tolerant variety	
Rice	10 days of DS	– Biomass and grain yield reduction – Increase in antioxidant activity (SOD, CAT, POX, and APX)	Joshi et al. (2020a)
Rice (transgenic line)	DS during 25 days, followed by a recovery until maturity	– Increase in RWC, photosynthetic efficiency, chlorophyll content, and stomatal conductance – Overproduction of trehalose, sugars, amino acids, and organic acids	Joshi et al. (2020b)
Rice	WW and DS during 0, 8, and 10 days	– Chlorophyll degradation – ROS accumulation increment	Gusain et al. (2015)
Sorghum	WW, 80–100% FC DS, 35–55% FC during 12 weeks	– Stomatal conductance decrease, – Decrease of dry weight and N and P concentrations	Symanczik et al. (2018)
Sorghum	WW, moderate and severe DS stress during 3 months	– Decrease in RWC, chlorophyll, protein, amino acid, and N content – Decrease number of panicles, grain number per panicle, 1000-grain weight and yield	Kamali and Mehraban (2020)
Sorghum	WW (100% FC) Moderate DS (75% FC) Severe DS (50% FC)	– Decrease in plant growth performances – High accumulation in proline and sugars content and improvement of lipid peroxidation	Kour et al. (2020a)

ABA abscisic acid, *APX* ascorbate peroxidase, *CAT* catalase, *DS* drought stress, *PEG* polyethylene glycol, FC field capacity, *MDA* malondialdehyde, *POX* peroxidase, *ROS* reactive oxygen species, *RWC* relative water content, *SOD* superoxide dismutase, *WW* well watered reported that drought is among the most inducing environmental constraints to cereal growth performances, development and productivity, and grains quality (Fahad et al. 2017; Khan and Bano 2019). Drought stress reduces cereal productivity and grain quality during the grain developmental stage, the most sensitive stage. In addition, drought negative impacts on seed quality were studied in cereals, including wheat, maize, rice, barley, and sorghum (Karim and Rahman 2015; Hasanuzzaman et al. 2020; Symanczik et al. 2020). Mineral nutrition is a crucial factor in the development and productivity of cereal crops. However, under drought, the mineral nutrition of cereal crops is negatively affected (Kumar et al. 2020). Drought can disrupt ion homeostasis in plant cells, which negatively affects plant mineral nutrition. Generally, the decline in soil water availability limits the availability of mineral elements in the soil and leads to a decrease in their uptake and consequently to a reduction in their concentrations in different plant tissues (Siddiqui et al. 2021). Moreover, the mineral nutrition of plants is intimately linked to the stability of the roots cell membrane as the first target of environmental constraints such as drought (Layek et al. 2015; Trivedi et al. 2018). The disruption of ionic homeostasis in plants caused by drought is due to their cell membranes and transpiration damage. Therefore, conserving membrane stability is essential in plants' resistance and/or tolerance to drought (Teklić et al. 2021; Siddiqui et al. 2021). Besides, drought stress can cause imbalances in plant mineral uptake, leading to secondary effects on plant growth and evolution. For instance, drought can significantly inhibit mineral uptake in wheat and maize, resulting in reduced yields and mineral concentrations of grains (Karim et al. 2012; Kumar et al. 2020).

Water represents essential support for biochemical interactions that occur in plant cells. Water scarcity affects the cellular water potential and turgor and cellular homeostasis. Drought-induced changes in the pool gene expression result in modifications to protein biosynthesis machinery. A translation elongation factor eEF-1α was observed in a tolerant barley variety than a sensitive one under drought stress conditions (Ashoub et al. 2013).

A comparative proteomic study of ABA-regulated proteins revealed a significant increase in translation-related proteins in a drought-tolerant wheat variety, while a downregulation was recorded in the drought-sensitive variety (Alvarez et al. 2014). Modifications in many ribosomal proteins belonging to cytosolic ribosomes (40S, 60S) were commonly identified in drought-treated barley and wheat studies (Ghabooli et al. 2013; Kausar et al. 2013; Nemati et al. 2019; Harb et al. 2020). Alterations in the protein degradation machinery components, namely, proteasome subunits and ubiquitin ligase complex enzymes (components E1 to E3), have been identified in several proteomic studies in barley and wheat (Ghabooli et al. 2013; Alvarez et al. 2014; Awasthi et al. 2019; Kumar et al. 2020).

Amino acids are traditionally known as the precursors and components of proteins and other N-containing compounds and play an essential role in plant metabolism and development. Various amino acids act as osmolytes. For instance, proline is an essential osmolyte in an osmotic adjustment under stress conditions in cereals, while glutamic acid is an essential precursor of proline and chlorophyll (Kour et al. 2020a; Fardus et al. 2021). Both glutamic acid and glutamate play a significant role in N assimilation. Glycine is a precursor of glycine betaine, which acts as an osmolyte under stress conditions (Kausar et al. 2013; Faghani et al. 2015; Annunziata et al. 2019). Phenylalanine serves as a precursor for a wide range of aromatic substances (e.g., flavonoids and lignin components) produced via the phenylpropanoid channel and regulated by phenylalanine ammonia-lyase (PAL). Different amino acids can also be deaminated to produce oxoacids; Krebs cycle intermediates.

Several nonprotein amino acids like γ-amino butyric acid (GABA) are essential factors in the drought response. Under water shortage, a metabolomic investigation in wheat revealed an increase in many amino acids, especially tryptophan, proline, tyrosine, phenylalanine, isoleucine, leucine, and valine conditions (You et al. 2019). Besides, tryptophan has the potential to act as a ROS scavenger. The increased amino acids suggest an increment of secondary metabolites such as flavonoids, terpenoids, glycosides, and lignin, which can improve the plant tolerance under drought stress conditions (Kausar et al. 2013; Alvarez et al. 2014; Ibrahim and Abdellatif 2016; You et al. 2019).

Studies showed an upward tendance of phytohormones, including ABA, salicylic acid, and jasmonic acid under drought. A significant expression of the 9-cis-epoxycarotenoid dioxygenase (NCED) gene, which mainly encodes an enzyme involved in ABA biosynthesis, was identified in wheat plants (Dong et al. 2017; Ghatak et al. 2017). ABA cannot traverse the plasma membrane at the leaf cells and translocate to the stomatal cells by transpiration through the leaf apoplast. Its translocation toward the stomata leads to both stomatal closure and a decrease in stomatal conductance capacity. Increased stomatal resistance of the leaves leads to a decrease in water loss from the leaf surface, which represents one of the most advanced reactions of the plants to drought stress. Further, low CO_2 assimilation through the stomata provokes a decrease in plant photosynthesis efficiency (Alvarez et al. 2014; Ghatak et al. 2017).

20.2.3 Current Advances and Limitations for the Genetic Improvement of Drought-Tolerant Genotypes of Cereals

Drought stress causes genetic infertility and embryo abortion during the reproductive phases. It is essential to understand how plants respond to drought stress to produce drought-resistant genotypes. Depending on the plant's growth stage, drought stress may result in yield reductions. This decrease in yield can be mitigated by implementing various programs to help farmers ensure optimum cereal output to maintain global yield levels.

Plants expressing an array of genes linked with morphological and physiological traits contributing to drought stress tolerance have been demonstrated (Sahebi et al. 2018). Morphological adaptations include increases in root length and thickness and delayed leaf senescence. Physiological changes include stomatal closure, condensed transpiration rate, the relationship between flowering and mature phases, and biomass and yield partitioning (Zafar-Ul-Hye et al. 2019). Drought stress has been studied widely; however, improving plants' drought tolerance is still challenging to achieve due to its characteristics' diversity. Because they react differently to drought stress, genetic diversity across cereal cultivars is a significant element in creating more drought-resistant cultivars. Drought-tolerant genotypes are frequently used to explore drought tolerance and are the best source of drought tolerance genes for creating drought-tolerant agricultural cultivars (Quiroga et al. 2017; Nemati et al. 2019).

Functional genomics information is required for the effective creation of drought-resistant cereals. Drought resistance is a complicated character, crucial to figure out how essential genes operate in the growth of cereal plants for drought tolerance and, ultimately, better grain output. Most research has focused on plant survival rates under extreme water stress, which is rarely relevant for grain crops (Passioura 2012; Khan et al. 2019). Several genes should be considered to modify the built-in feedback regulation mechanism and avoid the excessive accumulation of intermediate products. To get a high yield, negative interactions between drought tolerance and other characteristics such as photosynthetic rate must be considered. The majority of the experiments that showed an increase in transgenic plant production were done in greenhouses under controlled circumstances, but the reaction of the given transgene might be different under field conditions (Khan et al. 2019; Sallam et al. 2019). Moreover, despite scientific progress in genetics, plants are still challenged by drought problems that continuously reduce agricultural productivity. For this reason, it is precious to develop other biotechnological approaches, such as the use of natural biostimulants to improve drought tolerance and productivity of crops with high economic value.

20.3 Biostimulants as a Tool for Improving Cereal Productivity Under Drought Risk

Natural biostimulants are substances or microorganisms that can be applied to plants to improve the nutritional efficiency, tolerance to abiotic stress, and/or quality/functionality attributes of the crop, independently from its nutrient content (Rouphael et al. 2020).

20.3.1 Microbial Biostimulants and Cereal Drought Tolerance

Various microbial biostimulants are used in cereal growth performances and productivity. These types of biostimulants contain a functional compound range, which can influence the plant metabolic pathways. In contrast, research on cereals response to drought stress and microbial biostimulants application is gaining interest; there is a need to elucidate the interactions between drought and biostimulants at plants metabolic level, notably from the point of view of functional food production. The PGPR, AMF, endophytes, and *Trichoderma* spp. comprise a fundamental category of biostimulants to promote agricultural sustainability. These biostimulants were used in the world through their importance to improve agriculture management and soil restoration and conservation under drought stress conditions (Table 20.2) (Bitterlich et al. 2018; Kumar et al. 2020; Malik et al. 2020; Rouphael and Colla 2020; Hosseyni Moghaddam et al. 2021).

The PGPR bacteria can reduce the drought stress damage by producing enzymes such as ACC deaminase and thus protect the plants (Zafar-Ul-Hye et al. 2019; Nadeem et al. 2021). These beneficial microorganisms can ensure plant growth and viability by inducing roots elongation, promoting branched roots formation, and mitigating the drought stress negative impacts. PGPR play a key role in the interactions between plants and microbes owing to their capacity to induce phytohormones production and phytostimulation promotion efficiency (Kanwal et al. 2017; Yasmin et al. 2017). The PGPR can exhibit several mechanisms to promote plant growth performances, including phosphate and potassium solubilization, iron sequestration, phytohormones production, and mineral nutrient uptake improvement to mitigate drought stress damages and benefit plants (Yaseen et al. 2019; Zafar-Ul-Hye et al. 2019). PGPR can produce plant growth regulators, i.e., cytokinins, to alleviate the harsh effects of drought stress. Also, the auxin produced by PGPR promotes plant root elongation and architecture under drought stress (Zafar-Ul-Hye et al. 2019; Carlson et al. 2020). PGPR can produce ABA and GA to improve tolerance, which is linked with an increment in plant growth under stressful conditions (Table 20.2) (Khan et al. 2019; Mishra et al. 2020).

Plant inoculated with AMF can address the demand for food production sustainability strategies. AMF can also protect cereal crops against drought stress. AMF represent a crucial factor of beneficial soil microorganisms that regulate plant growth performances and water and mineral nutrient absorption. Similarly, AMF improve soil structure and porosity and stabilize soil aggregates, making the soil less susceptible to degradation and erosion ultimately (Symanczik et al. 2018; Šarapatka et al. 2019). The potential positive impacts of AMF combined with plant roots are well discussed. AMF inoculation improves mineral nutrient uptake and translocation, root architecture system, photosynthetic apparatus, and water absorption capacity under drought stress (Bernardo et al. 2019; Symanczik et al. 2020). The impacts of AMF in promoting osmotic responses to drought stress are associated with promoting plant hydration and physiological activities. In fact, the fine network of AMF extraradical hyphae could increase the absorption of water and mineral nutrients from the adjoining soil (Zhang et al. 2018; Symanczik et al. 2020). Furthermore, the positive effects of AMF inoculation were related to enhancing intrinsic water-use efficiency and the modulation of plant hormonal, e.g., ABA levels under drought stress conditions (Table 20.2) (Dong et al. 2017; Kumar and Verma 2018).

Microbial endophytes are a symbiotic group of microorganisms that live within plant tissues and interact with their hosts without causing illness. According to available research, endophytes are thought to be present in all terrestrial plants. Endophytes have been demonstrated to play a role in increasing drought resilience (Sahebi et al. 2018). The host plant supplies protective niches for the microorganisms, which in turn release metabolites that enhance nutrient absorption,

Table 20.2 Example of biostimulants application in cereal crops under drought stress

Biostimulants	Plants	Drought	Impacts/mechanisms	References
AMF, *Glomus versiforme*	Maize	Moderate and severe DS for 30 days	DS alleviation through the improvement of plant growth, chlorophyll content, mineral nutrients uptake and assimilation, accumulation of osmolytes (sugars, proline, amino acids), and activation of antioxidant enzymes	Begum et al. (2019)
AMF, *Glomus etunicatum*	Maize	75 and 55% FC during 4 weeks	Cell damages decrease through the enhancement of antioxidant enzymes (SOD, CAT, and POX)	Zhu et al. (2011)
Indigenous AMF, *Rhizophagus arabicus* and Exotic AMF strain, *R. irregularis*	Sorghum	WW: 80–100% FC DS: 35–55% FC during 12 weeks	Increase of stomatal conductance, N and P concentrations and ^{15}N transport rate, and ^{15}N concentration	Symanczik et al. (2018)
PGPR, *Pseudomonas* sp.	Sorghum	DS once weekly during 3 successive weeks	– Increase in antioxidant activity – Root architecture and growth promotion – Upregulation of the GA, IAA, and CKs – Systemic tolerance activation through the hormones (BRs, Jas, and SAs) and other molecules (sphingosine and psychosine) signaling and decreased ethylene levels due to ACC deaminase activity – Osmolytes accumulation (proline, glutamic acid, and choline)	Carlson et al. (2020)
AMF, *Funneliformis mosseae*	Wheat	WW and DS during 29 days	– Improvement of carbohydrates, mannosylfructose phosphate, 3-propylphosphoenolpyruvate – Upregulation of phytohormones, indole-3-acetyl-valine, indole-3-acetyl-methionine, gibberellin A29-catabolite, gibberellin A34-catabolite, and tuberonic acid glucoside organic osmolytes	Bernardo et al. (2019)

PGPR, *Pseudomonas helmanticensis* and *P. baetica*	Wheat	88 and 55% FC	– Increase shoot P – Increase of grain yield, shoot and root dry weights – P solubilization and IAA production	Karimzadeh et al. (2021)
PGPR, *Rhizobium leguminosarum*, *R. phaseoli*, and *Mesorhizobium ciceri*	Wheat	PEG-6000-simulated DS (0, 15, and 25% PEG) during 15 days	– Seedlings biomass improvement – Drought tolerance index increment –IAA production capacity > boost root development and alleviate DS	Hussain et al. (2014)
PGPR, *Pseudomonas fluorescens*, *P. jessenii*, *P. synxantha*, *Bacillus cereus*, *Arthrobacter nitroguajacolicus*	Rice	WW and DS during 0, 8 and 10 days	– Growth promotion – Cell damages decrease – Enhancement of antioxidant enzymes production	Gusain et al. (2015)
Native AMF consortium and PGPR (*B. subtilis* and *Halomonas* sp.)	Maize	DS phase (14 days after irrigation) and the recovery phase	Improvement of stomatal conductance, transpiration rate, CO_2 uptake, and leaf mineral nutrients (N, Mg, and Ca)	Zoppellari et al. (2014)
AMF and PGPR	Sorghum	WW, moderate and severe DS	– Increase in grain yield – Increase the photosynthetic pigments and soluble protein content – Electrolyte leakage reduction	Kamali and Mehraban (2020)
SWE, *Kappaphycus alvarezii*	Wheat	WW and DS	– Overexpression of genes involved in protein synthesis, cell wall, hormone synthesis, lipid, amino acid, nucleotide, and N metabolisms	Kumar et al. (2020)
SWE, *Kappaphycus alvarezii* seaweed extract	Maize	WW and DS	– Increase in seed yield, cob length, grain length, and number of grains – Increase in activities and concentrations of antioxidant enzymes – Reduction in ROS and H_2O_2 levels	Trivedi et al. (2018)

ACC 1-aminocyclopropane-1-carboxylic acid, *AMF* arbuscular mycorrhizal fungi, *BRs* brassinosteroids, *CAT* catalase, *CKs* cytokinins, *DS* drought stress, *FC* field capacity, *GAs* gibberellins, *IAA* indole-3-acetic acid, *JA* jasmonic acid, *PGPR* plant growth-promoting rhizobacteria, *POX* peroxidase, *RWC* relative water content, *SA* salicylic acid, *SWC* soil water content, *SOD* superoxide dismutase, *SWE* seaweed extract, *WW* well watered thus increasing the plant's growth and biomass gain (Sadeghi et al. 2020). Endophytes offer plants' nutritional advantages and other benefits such as protection against abiotic stress, including drought stress (Bakhshandeh et al. 2020). Drought-induced endophyte-mediated plant responses include increased plant growth and vigor, improved photosynthesis, osmotic balance, water-use efficiency, gas exchange, antioxidant activities, and changes in the expression of drought-related genes (Sahebi et al. 2018; Sadeghi et al. 2020). The endophytic bacteria have three metabolic pathways, which induce plant development. They are biofertilization, phytostimulation, and biological control and are interrelated in the plant's physiological processes (Gaiero et al. 2013; Srebot et al. 2021).

Trichoderma spp. are one of the essential groups of the microbial rhizosphere. *Trichoderma* can impart beneficial effects on promoting plant growth and development. *Trichoderma* spp. has been shown to improve plant growth under abiotic stressors and reduce oxidative stress in osmotic-treated plants (Gangwar and Singh 2018; Jiménez-Arias et al. 2021; Silletti et al. 2021). *Trichoderma* spp. can also increase plant growth and vigor, solubilize plant nutrients, and produce abiotic stress tolerance molecules. They can also help plants grow and develop resistance to various abiotic stresses, such as water stress (Shukla et al. 2012; Silletti et al. 2021).

Molecular research of beneficial microorganisms paved a new way to understand their implication in plant defense systems under drought stress conditions. A good understanding of the diverse mechanisms implicated in plant-microbe interactions represents a criterion for increasing innovative approaches for boosting cereal crop yields and adaptation. Inoculation of beneficial microbes in plants has economic importance, as they increase the yield of agricultural production and requires low-cost farming techniques, resulting in low environmental impact. Thus, it is necessary to improve management methods and the application of microorganisms to maximize the beneficial interactions provided by their association with the plants.

20.3.2 Nonmicrobial Biostimulants

Several biostimulants are used in modern biological agriculture to improve crop productivity under different environmental systems. Seaweed extracts (SWE) have recently gained importance as biostimulants for several crops owing to their possession of bioactive substances, including amino acids, vitamins, and phytohormones, and macro- and micronutrients that can boost plant growth and affect cellular metabolism (Khan et al. 2009; Anli et al. 2020b). When used in small amounts, positive impacts of SWE on crop growth were ascribed to plant growth regulators, and eventually, micronutrients that improve root elongation and architecture, mineral nutrient uptake, and photosynthetic activity (Khan et al. 2009). Under water stress conditions, SWE can improve physiological traits and plant performance. Application of SWE under drought conditions showed a significant improvement in maize and wheat physiological processes related to mineral uptake, seed yield, photosynthetic activity, antioxidant defense system activation, and a decrease in lipid membrane peroxidation and ROS production (Stamatiadis et al. 2015; Trivedi et al. 2018). Such modifications induced by the SWE application suggest that this type of biostimulant presents a biological factor necessary for the adaptation of cereal crops and would boost the potential mechanisms at cellular and molecular levels necessary for the tolerance of these crops under water shortage. The application of SWE has been shown to improve the drought tolerance and yield of several cereal crops (Layek et al. 2015; Trivedi et al. 2018; Kumar et al. 2020; Malik et al. 2020). A recent study on the effect of SWE application on the transcriptome response of maize roots subjected to water stress (Table 20.2) (Kumar et al. 2020) revealed a positive effect on the expression of several genes involved in several biological processes: RNA, DNA, cell wall, protein, transport, stress, hormone and lipid amino acid, nucleotide, and N metabolisms. In fact, upregulation in genes involved in root growth and seed development, auxin and GA signaling, nitrogen metabolism and transport, and antioxidant enzymes activity like the glutathione S-transferase and the peroxidase have been observed. In contrast, starch and sucrose degradation-related transcripts have been downregulated (Kumar et al. 2020).

20.3.3 Single, Dual, and Multi-combination of Biostimulants Against Drought

Biostimulants, including SWE and beneficial microorganisms, i.e., AMF, endophytes, *Trichoderma* spp., and PGPR bacteria, could be used alone or combined to boost crop productivity under stressful conditions (Sadeghi et al. 2020; Yadav et al. 2020; Vafa et al. 2021). The microorganisms can be effective in recycling soil nutrients and their uptake by plants. Application of these biostimulants alone or in combinations improves the mineral nutrition and photosynthetic activity of the plant under water stress conditions and the biological activity of the microorganisms (Pereira et al. 2020). Plants, in turn, receive many advantages from the beneficial microbes, including growth enhancement and reduction of damage induced by stress (Kaushal 2019; Kumar et al. 2020). A single application of biostimulants can be beneficial, neutral, or negative for plant growth. Ngoroyemoto et al. (2020) demonstrated that SWE application alone significantly improved growth and pigment content, while PGPR bacteria alone showed a significant adverse effect on amaranth plants' growth and chlorophyll pigment content.

Furthermore, a recent study found that *Trichoderma* sp. can help reduce the detrimental effects of drought-stressed rice plants by lowering lipid peroxidation and ROS production while increasing proline concentration (Begum et al. 2019). Endophytic fungal inoculation improved wheat growth and drought tolerance by controlling antioxidant enzymes and the concentration of suitable solutes like soluble sugars and proline. Furthermore, wheat plants treated with this endophytic fungus showed enhanced photosynthetic, C, and N accumulation, resulting in a favorable connection between plant dry biomass and water shortage and re-watering circumstances (Qiang et al. 2019). However, the combination of biostimulants to improve the vigor and development of cereals under water stress conditions is understudied. It was reported recently that the combined treatment

(SWE + PGPR) significantly improved wheat growth and photosynthetic pigment content (Vafa et al. 2021). The same study revealed that the tripartite combination of AMF, PGPR, and SWE improved the agro-physiological traits of wheat, spike length, and number of seeds per spike under water deficit conditions.

20.3.4 Biostimulants: Beneficial Effects and Mode of Action in Cereals Under Drought

Recent studies reported the effects of biostimulants under drought stress conditions. Several mechanisms were described to clarify the roles of the biostimulants in cereals' drought tolerance at physiological, biochemical, and molecular levels (Fig. 20.3). The main physiological mechanisms of enhancing cereal crops under drought conditions can be attributed to the increase of the hydraulic conductivity of the roots or the water relations and the mineral nutrients availability (Mathur et al. 2018; Pereira et al. 2020; Kamali and Mehraban 2020). Among the microorganisms involved in water uptake and nutrient translocation, especially under drought conditions, are AMF via extraradical hyphae (Fig. 20.3) (Zhao et al. 2015; Kamali and Mehraban 2020). These hyphae can invade soil pores impermeable to root hairs (Klamer et al. 2019). The extensive hyphal network of AMF increases the contact surface in the soil around the plants, which leads to an improvement in the leaf water potential and relative water content of the cereal plants under drought conditions (Talaat and Shawky 2014). Furthermore, glycoprotein glomalin production by AMF presents an essential role in the water relations of plants during drought stress

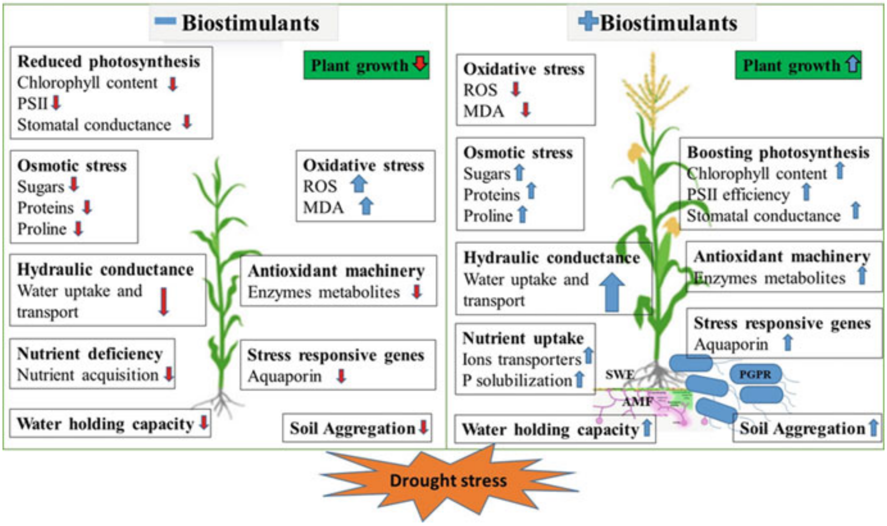

Fig. 20.3 Effect of drought stress in the absence (left panel) or presence (right panel) of biostimulants on plant growth

(Ji et al. 2019). Glomalin is involved in soil aggregates that promote better water retention (Fig. 20.3) (Sekaran et al. 2021). AMF establish microchannels that serve as narrow water passages through air zones directly connecting to the roots (Kaushal 2019).

Similarly, numerous studies have shown that exopolysaccharides in PGPR-inoculated cereals increase the water holding capacity (Hussain et al. 2014; Naseem and Bano 2014; Yaseen et al. 2019; Pereira et al. 2020). The production of exopolysaccharides by bacterial strains plays an essential role in improving the relative water content of cereals such as maize (Naseem and Bano 2014; Yasmin et al. 2017) and wheat (Hussain et al. 2014; Kanwal et al. 2017) under drought conditions through the formation of hydrophilic biofilms around roots (Naseem and Bano 2014; Naseem et al. 2018). The production of exopolysaccharides and glomalin by PGPR increases the soil-adherent/root tissue ratio and macroaggregate stability by increasing soil water and nutrient uptake in the proximity of the roots, which can alleviate drought stress in wheat (Fig. 20.3) (Mathur et al. 2018; Khan and Bano 2019), maize (Nadeem et al. 2021) and rice (Joshi et al. 2020a) plants. Furthermore, AMF, endophytes, *Trichoderma* spp., and PGPR symbiotic plants respond to the reduction in soil water potential by lowering the water potential of leaves and xylem, which alters stomatal conductance, hydraulic conductivity, transpiration rate, and photosynthetic efficiency under drought conditions (Bárzana et al. 2012; Gangwar and Singh 2018; Zafar-Ul-Hye et al. 2019; Sadeghi et al. 2020). Drought decreases soil water volumes, which leads to stomatal closure and, consequently, reduced transpiration rate due to a decreased CO_2 diffusion through stomata. When AMF has colonized cereal crops, root hydraulic conductivity increases due to the hyphal network, resulting in turgidity of guard cells (stomata opening) and increased CO_2 diffusion into leaf mesophyll cells and, consequently, enhanced photosynthesis under water stress conditions (Fig. 20.3) (Zoppellari et al. 2014; Ouyang et al. 2017; Begum et al. 2019). The enhanced photosynthesis in cereal plants inoculated with PGPR, endophytes, *Trichoderma* spp., or AMF may be due to efficient photosynthetic machinery (Ruiz-Sánchez et al. 2010; Begum et al. 2019; Zafar-Ul-Hye et al. 2019; Fahey et al. 2020; Hosseyni Moghaddam et al. 2021). The enhancement of photosynthesis in plants could be strongly related to the chlorophyll content and the increase in N and Mg^{2+} contents (major components of chlorophyll molecules) of mycorrhizal plants under water stress conditions. Mathur et al. (2018) reported that AMF hyphae are likely to increase Mg uptake, promoting chlorophyll pigment content in mycorrhizal wheat plants subjected to drought conditions. An effective photosystem II (PS II) reaction centers lead to efficient energy transfer that results in quantum yield increase in mycorrhizal cereal plants under water stress conditions (Fig. 20.3) (Quiroga et al. 2017; Mathur et al. 2018). Additionally, AMF-mediated drought responses are likely related to aquaporins' expression and/or signaling molecules. Quiroga et al. (2017) indicate that AMFs could help maize plants to improve their tolerance to drought by regulating the expression of a wide range of aquaporins. Aquaporin genes expression (GintAQPF1 and GintAQPF1) cloned from *Rhizophagus irregularis* was upregulated in cortex cells of maize roots inoculated by *Glomus intraradices*, indicating the role of AMF aquaporins in improving water transport by AMF hyphae to plant (Symanczik et al. 2020). In addition, osmotic adjustment and accumulation of compatible solutes such as proline, sugars, polyamines, betaines, quaternary ammonium compounds, polyhydric alcohols, amino acids, and proteins are involved in reducing water loss and maintaining water absorption during drought periods in cereals (Abid et al. 2018; Tabbasum et al. 2021). Cell water potential decreases due to the accumulation and aggregation of compatible osmolytes, which maintain cell turgor at a higher level and protect enzymes, proteins, and biomembranes from oxidative damage (Fig. 20.3) (Huang et al. 2014). During water deficit, soil microorganisms (PGPR, endophytes, *Trichoderma* spp., or AMF) participate in the production of osmolytes in cereals to mitigate damage to cell turgor (Qiang et al. 2019; Kour et al. 2020b; Sedaghat et al. 2020). The accumulation of proline in plant cells during osmotic stress is imperative for primary metabolic processes since it acts as a molecular chaperone by quenching reactive oxygen species that reduce lipid peroxidation and preserve proteins and membranes from oxidative damage (Evelin et al. 2019). Several investigations in cereal plants have suggested that plants treated with PGPR and/or AMF contributed to osmotic adjustment by increasing proline and flavonoid levels (Basu et al. 2010; Kolupaev et al. 2019; Selim et al. 2019; Carlson et al. 2020). Zhu et al. (2011) and Qiang et al. (2019) showed that increasing proline levels in AMF-inoculated plants provides cereal plants with greater resilience and adaptability to cope with drought. Trehalose stabilizes wheat and rice plant cell structures and proteins under drought conditions (El-Bashiti et al. 2005; Ibrahim and Abdellatif 2016; Joshi et al. 2020b). Sharma et al. (2020) reported that the trehalose-6-phosphate synthase gene showed upregulation of genes involved in stress tolerance in inoculated plants compared to non-inoculated counterparts. Similar findings were recorded in maize plants under drought stress conditions (Rodríguez-Salazar et al. 2009). Soluble sugars can enhance osmotic tolerance, especially in plants inoculated with AMF, endophytes, *Trichoderma* spp., and/or PGPR under drought conditions (Naseem and Bano 2014; Qiang et al. 2019; Boutasknit et al. 2020).

Several strategies are used to cope with drought stress, including the production of phytohormones. The changes in phytohormonal levels in plants inoculated with beneficial microbes ensure plant survival and growth and regulate plant tolerance against drought stress. On the other hand, drought can negatively affect the metabolic process of roots and the plants' photosynthetic capacity. Plants treated with PGPR, endophytes, or *Trichoderma* spp. showed a root system with a highly reshaped architecture and with a well-developed surface (Carlson et al. 2020; Sadeghi et al. 2020; Pan et al. 2020; Silletti et al. 2021) to increase the nearby area for water absorption and hydraulic conductivity and nutrient supply during stress (Dimkpa et al. 2009; Kaushal 2019). IAA is among the essential regulators of plant growth because it intervenes in the cellular division of the shoots, the apical dominance, and the roots' branching (Siddiqui et al. 2021). Changes in IAA levels in wheat plants inoculated with *Azospirillum* improved leaf water potential and increased leaf water levels (Arzanesh et al. 2011). PGPR-treated maize plants can synthesize IAA, which leads to increased water uptake, improves nutrition, and influences the plant's physiology, leading ultimately to drought stress tolerance

(Vacheron et al. 2013; Yasmin et al. 2017). Due to rhizobacteria-induced IAA production, wheat seedlings increase the length and density of root hairs and lateral roots (Timmusk et al. 2014; Raheem et al. 2018).

ABA plays a significant role in the drought stress response as it regulates transpiration rate, root hydraulic conductivity, and aquaporin expression (Barooah et al. 2021). The ABA responses regulate stomatal conductance by inducing stomatal closure and reducing water loss in wheat genotypes under drought stress (Saradadevi et al. 2014, 2017). Roots and leaves of mycorrhizal wheat and maize showed lower ABA concentrations than non-mycorrhizal plants under drought stress (Bernardo et al. 2019). The maize plant inoculated with PGPR and AMF can influence the stomata function by regulating ABA (Ren et al. 2019; Nadeem et al. 2021). De Ollas and Dodd (2016) demonstrated that ABA interacts with jasmonic acid (JA) for plant tolerance to water stress conditions. JA hormone plays an essential role in regulating the expression and abundance of aquaporins and water absorption and transport. Other studies have shown that AMF symbiosis and salicylic acid (SA) regulate aquaporins and root hydraulic properties in maize plants under drought conditions (Quiroga et al. 2018). Other phytohormones involved in regulating drought stress in cereals include strigolactones and auxin (Sedaghat et al. 2017). Strigolactones are considered stimulators of AMF metabolism, hyphal branching, plant growth, and root architecture (Lanfranco et al. 2018; Nasir et al. 2019). Plants inoculated with AMF can enhance strigolactone and auxin responses to drought stress (Huang et al. 2021). In addition, gibberellic acid plays a crucial role in plant growth through its involvement in stem elongation, germination, flowering, senescence, and fruit ripening (Cheng et al. 2020). Various studies have indicated that inoculation with gibberellin-producing bacteria alleviates the effects of drought stress on the host plants. Previous observations showed a significant increase in gibberellins in maize plants primed with *Azospirillum lipoferum* (Abdel Latef et al. 2020). Cytokinins (CKs) play a fundamental role in cell division, stem growth, photosynthetic activity preservation, and stomatal opening maintenance under drought conditions. Furthermore, a positive effect of CKs on the survival of PGPR-treated plants under drought stress conditions has also been reported (Arkhipova et al. 2007; Zafar-Ul-Hye et al. 2019; Carlson et al. 2020).

Exposure of cereal plants to drought leads to the generation of reactive oxygen species (ROS) that can react with proteins, lipids, and other essential macromolecules and denature macromolecules' structure and function (Abid et al. 2018; Qureshi et al. 2018; Huang et al. 2019). The enzymatic (superoxide dismutase (SOD), peroxidase (POX), glutathione reductase (GR), catalase (CAT), ascorbate peroxidase (APX), and guaiacol peroxidase (GPOD)) and nonenzymatic (glutathione, ascorbate, flavonoids, carotenoids, and tocopherols) antioxidant systems of plants inoculated with beneficial microbes can be optimized to remove ROS under drought stress conditions (Bárzana et al. 2012; Raheem et al. 2018). AMF symbiosis, endophytes, *Trichoderma* spp., or rhizobial inoculation stimulates the antioxidant system to preserve membrane integrity and protein stability and thus improve tolerance during oxidative stress (Qiang et al. 2019; Kaushal 2019). Under drought conditions, polyunsaturated fatty acids of membrane phospholipids are the main targets of ROS, which cause lipid peroxidation and fatty acid degradation generating various cytotoxic products such as malondialdehyde (MDA) (Nafady et al. 2019; Geng et al. 2015). Wheat plants inoculated with AMF showed lower MDA levels in leaves than control plants under water stress conditions (Wu et al. 2019). A similar decrease in MDA levels was recorded in maize plants colonized by *Glomus etunicatum* during drought stress (Zhu et al. 2011). Alterations in antioxidant enzyme levels in maize plants upon AMF inoculation constitute an effective mechanism of microbially induced systemic tolerance (MIST) against drought (Zhu et al. 2011). POX and CAT activity increased in AMF-treated wheat plants under drought stress (Boutasknit et al. 2021a). Similarly, higher CAT and APX activity was observed in AMF-treated rice plants, which reduces cell damage under drought conditions (Ruiz-Sánchez et al. 2010).

Recent studies have reported that AMF-inoculated plants significantly regulate the expression of root PIP aquaporin genes compared to untreated control plants (Xie et al. 2018). In fact, under drought stress, specific genes encoding AQPs were induced by AMF colonization, which could be a means to increase water flux in host plant tissues (Fig. 20.3).

20.4 Conclusions and Perspectives

Improving global food security is critical given that the growing population will remain food insecure and its association with conflict and civil unrest. Globally, weather variability accounts for one-third of the observed crop yield variability and much more in well-managed high-input systems. Drought is a major cause of yield and quality loss in cereal crops throughout many of the world's cereal growing areas. The year-to-year cereal yield variability is sensitive to water shortage, and this is projected to increase even after accounting for accelerated crop development. To sustain cereal production, several approaches are adopted/in adoption to maximize yields and profitability and minimize the impact on the unfavorable environment. Alleviation of drought in the field may be achieved in several ways, including adequately managing inputs by applying biostimulants.

Biostimulants—natural compounds and microbial inoculants—are a promising sustainable solution to stimulate nutrient uptake and efficiency, abiotic stress tolerance, and general cereal quality. This chapter provides a general overview of the extensive literature suggesting that biostimulants decrease the effects of drought stress in cereal and knowledge regarding cereal defense mechanisms. Nevertheless, the definition and concept of plant biostimulants and the physiological mechanisms of action are still limited and still evolving. The literature showed a strong role for a diverse range of biostimulants that have beneficial effects against abiotic stress. The literature herein shows the prominent roles of diverse biostimulants that have protective effects against drought stress and the potential to improve plant resilience to environmental perturbations. Although input-producing companies are investing in the development of new biostimulants, more research is needed to address several unanswered questions related to (i) molecular mechanism(s) responsible for the stimulatory effects (ii) the practical approach, timing, application rates, and phenological stages to boost productivity under normal and stressful conditions and (iii) holistically understand the complexity of the plants-biostimulants-abiotic stresses interaction, and (iv) the selection of the appropriate biostimulant as the effects can vary markedly between species.

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Heat Stress in Cereals and Its Amelioration by Biostimulants

21

Vinay Shankar and Heikham Evelin

Abstract

Human population is dependent on cereals for half of their calorie requirements. Likewise, cereals occupy 50% of the world's cultivated area. Pseudocereals, the superfoods, also contribute to the nutritional requirement of the world population. On the other hand, the global human population is escalating at a rapid pace, likely to reach 10.9 billion by 2050. At the same time, the mean annual temperature is rising across the globe. Simulation studies project a huge decline in cereal production owing to the increasing global temperatures. Of much concern is ensuring food security of the world population as high temperature stress impedes the growth and productivity of cereal crops. This calls for a sustainable approach to increase crop production even under high temperature stress. Plant biostimulants (PBs) are extremely dynamic and can improve the growth, flowering, productivity, and nutrient use efficiency of plants. They are also known to impart tolerance to extreme environmental conditions. Thus, PBs can be a suitable candidate for increasing crop production even under temperature stress.

Keywords

Biostimulants · Cereals · Heat stress · Food security · Pseudocereals

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21.1 Introduction

Cereals are the dry grains harvested from the plants belonging to the family, Poaceae. Cereals include wheat, rice, maize, barley, oat, millets, sorghum, and triticale, a hybrid of wheat and rye (FAOSTAT 2021). Crops such as fonio, buckwheat, and quinoa, also known as pseudocereals, are used to supplement cereals in different parts of the world. Cereals are responsible for providing 50% of the world's calorie requirements (Awika 2011). As such, cereals are grown in half of the world's cultivated area (FAOSTAT 2021). Of all the cereals, wheat, maize, and rice paddy are stapled foods to most of the world population and are regarded as primary crops (Wang et al. 2018). Of much concern is ensuring food security for the rapidly growing global population. By 2050, the number of individuals on earth is projected to clock 10.9 billion (Bekkering and Tian 2019). Hence, a 70–100% rise in cereal productivity has become a global necessity (Goldfray et al. 2010). So far, the demand-supply balance of cereals could be achieved owing to the outstanding research and breeding programs (Jagadish 2020). The top ten cereal-producing countries in the world are China, USA, India, Russia, Indonesia, Brazil, Argentina, Ukraine, Bangladesh, and Canada (Fatima et al. 2020). According to FAOSTAT (2021), cereal production in the world showed an increasing trend from 2000 to 2019. This has been attributed to their cultivation in a large area and employing better farming practices such as cultivating high-yielding varieties supplemented with improved irrigation, fertilization, and use of pesticides. Cereals were the most produced crops in 2019. However, it is discouraging to learn that the rate of increase in grain yield in cereals is plateauing (Lizumi et al. 2017; Zhao et al. 2017). One of the major reasons that can be attributed is the increasing occurrence of unfavorable environmental factors such as temperature, water, and salinity stresses (Zampieri et al. 2017; Pfleiderer et al. 2019). Among these, stress caused by extreme temperatures is considered to cause the biggest damage to the plants (Ortiz-Bobea et al. 2019). High temperature increases respiration rates in plants and reduces the net carbon gain, subsequently causing a decline in crop yield. In this regard, sustainable approaches such as the application of plant biostimulants (PB) may be explored as PBs have been known to improve the growth, development and productivity of plants.

Hence, this chapter is aimed at summarizing the recent knowledge on the effects of temperature stress on cereal crops and exploring the potential of biostimulants as a sustainable agronomic method to enhance crop productivity.

21.2 Temperature Stress

Many environmental factors such as temperature, sunlight, precipitation, soil pH, etc. determine the growth and productivity of cereal crops. Temperature is considered the most important environmental factor (Fatima et al. 2020); hence, abiotic stress due to extreme temperature is one of the key environmental setbacks that hinder crop yield. Plants, being sessile, are bound to endure the prevailing climatic conditions during their growth period. According to FAOSTAT (2021), both summers and winters have increasingly become hotter than the 1951–1980 average. In the 2000s, the average change in temperature was 0.96 °C, while in the 2010s, the value stands at 1.26 °C. In 2020, there was an increase of 1.7 °C in global mean annual temperature, and it was declared the warmest year. The Americas and Africa recorded 1.3 °C change in annual mean temperature. Europe observed the greatest change with 3.4 °C. The values in Asia and Oceania were 1.6 °C and 1.4 °C, respectively. The annual mean temperature is expected to further increase by 2.5–4.5 °C owing to the escalating level of greenhouse gases in the environment (Solomon 2007; Bernstein et al. 2008).

Temperature stress can be categorized as heat, cold, or frosting. Temperature stress negatively affects the rate of germination, growth, photosynthesis, metabolism, protein stability, membrane integrity, and oxidative balance in plants. (Kai and Iba 2014). Heat stress can negatively affect all vegetative and reproductive stages (Barnabás et al. 2008; Sakata and Higashitani 2008). However, the reproductive phase of the plant, especially pollen grain development, bears the maximum damage caused by temperature stress. Heat stress occurs when the temperature is above a critical threshold and can vary across crop growth and developmental stages (Djanaguiraman et al. 2018). High temperature strongly reduces photosynthetic efficiency by inducing stomatal closure, resulting in decreased CO_2 concentration with respect to O_2 in the chloroplast. This changes the attraction of rubisco toward O_2 thereby encouraging photorespiration, consuming up to 25% of the fixed carbon. The temperature rise also reduces water and nitrogen use efficiency due to the loss of more crop water and nutrients (Fatima et al. 2020). These negative impacts are often associated with low fruit set, yield quality, and death of the plants (Bita and Gerats 2013). Cold stress slows down plant metabolism resulting in decreased photosynthetic efficiency, foliar growth, and early senescence. On the other hand, frost can cause dehydration of plant tissues, increase osmolyte concentrations in the cytoplasm, and disrupt plasma membranes.

21.3 Effect of Heat Stress on Major Cereals

Cereal crops require an optimum range of temperature for maximum growth and development. Beyond the upper limit of the optimum temperature range, cereal crops start showing signs of distress due to heat stress. The effect of heat stress on major cereal crops is discussed below. Table 21.1 shows the optimum range of temperature of different types of cereals.

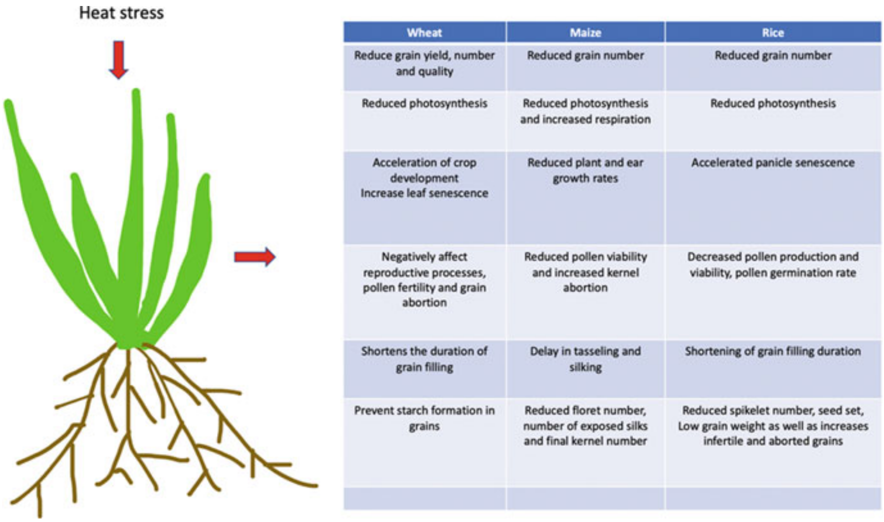
21.3.1 Wheat

Wheat (*Triticum* spp.) is consumed in many parts of the world. In fact, among cereals, it is the most widely cultivated crop. Wheat can be grown in two seasons, winter and spring; hence it can be classified as either winter wheat or spring wheat

Table 21.1 Cardinal (base (T_b), optimum (T_{opt}), and maximum (T_{max})) and extreme temperature thresholds (ceiling vegetative temperature (T_{C1}) and ceiling reproductive temperature (T_{C2})) for cereal crops (reproduced with permission from Fatima et al. 2020)

Crops	T_b (°C)	T_{opt} (°C)	T_{max} (°C)	T_{C1} (°C)	T_{C2} (°C)
Barley	0.0–5.00.0–5.0	25.0–31.0	50.0	30.0	40.0
Maize	8.0	30.0	38.0	33.0	44.0
Millet	10.0	34.0	40.0	30.0	40.0
Oat	0.0–5.0	25.0–31.0	31.0–37.0	–	–
Rice	20.0	28.0	35.0	22.0	30.0
Rye	0.0–5.0	25.0–31.0	31.0–37.0	–	–
Sorghum	8.0	34.0	40.0	32.0	44.0
Wheat	0.0	13.2	35.0	34.0	40.0

T_{max} and T_{min} are daily maximum and minimum air temperature, respectively
T_b is the base temperature



Wheat	Maize	Rice
Reduce grain yield, number and quality	Reduced grain number	Reduced grain number
Reduced photosynthesis	Reduced photosynthesis and increased respiration	Reduced photosynthesis
Acceleration of crop development Increase leaf senescence	Reduced plant and ear growth rates	Accelerated panicle senescence
Negatively affect reproductive processes, pollen fertility and grain abortion	Reduced pollen viability and increased kernel abortion	Decreased pollen production and viability, pollen germination rate
Shortens the duration of grain filling	Delay in tasseling and silking	Shortening of grain filling duration
Prevent starch formation in grains	Reduced floret number, number of exposed silks and final kernel number	Reduced spikelet number, seed set, Low grain weight as well as increases infertile and aborted grains

Fig. 21.1 Effect of heat stress on wheat, rice, and maize

(Ngwako and Mashiqa, 2013). The winter wheat completes its life cycle from October to July with a period of vernalization to flower. On the other hand, the spring wheat is sown from March to May and harvested from July to September.

Wheat plants grow well in sandy loam soil, with pH ranging between 5.5 and 6.5. The optimum temperature is −3 to 23 °C along with 4 to 6 hours of sunshine per day. For optimal yields, wheat plants require an adequate supply of N (70–200 kg), P (20–40 kg), and K (80–100 kg) for every hectare of cultivated area (Wang et al. 2018).

Wheat plants, when subjected to heat stress, exhibit accelerated development, decreased photosynthesis, and disruption in reproductive processes (Fig. 21.1) (Blum et al. 2001; Salvucci and Crafts-Brandner 2004; Farooq et al. 2011). Anthesis is the most sensitive stage of wheat plants to heat stress (Prasad et al. 2017) and has been correlated with the heat-induced reduction in the number, yield, and quality of grains (Ferris et al. 1998; Spiertz et al. 2006; Semenov 2009). Heat stress nearing anthesis affects pollen fertility and causes grain abortion (Calderini et al. 1999; Mitchell et al. 1993). On the other hand, as temperature increases, the development rate of the crop accelerates, during which the appearance of double ridge, as well as anthesis, speed up causing a reduction in the yield and quality of grains (McMaster and Wilhelm 1997; Barnabas et al. 2008). Recent simulation studies predicted a decrease in the yield of wheat due to heat in various parts of the world. Wheat yield in France is expected to lower by 3.5–12.9% between 2037 and 2065 and by 14.6–17.2% by the end of the century (Gammans et al. 2017). In China, temperature increase of 1 °C is expected to reduce wheat yield by 3–10% (You et al. 2009). Vanli et al. (2019) conducted a CERES-wheat crop simulation model at Islahiye and Nurdagi in Turkey. According to the model, wheat yield at Islahiye will decrease by 16.3% and 16.8% in mid-century and at the end of the century, respectively. While at Nurdagi, the values stand at 13.0% in mid and 14.4% at the end of the century.

21.3.2 Rice

Oryza sativa or paddy rice is the staple crop in as many as 95 countries. Millions of people are dependent on rice for their calorie needs. It is normally grown in water-flooded fields (Coats 2003), with requirements of 500–600 mm rainfall, optimal soil pH ranging from 5–6.5, temperature range between 22 and 31 °C, and 5–6 h of sunshine every day (Guo et al. 2011; Yao et al. 2012). Rice requires a great number of fertilizers throughout its cultivation period. The per hectare requirements are 90–120 kg N, 30–40 kg P, and 40–60 kg K (Santos et al. 2017).

Rice plants are extremely sensitive to elevated temperatures (>35 °C), particularly during gametogenesis and flowering (Fig. 21.1) (Prasad et al. 2006a, b; Jagadish et al. 2015). High temperature disrupts flowering dynamics resulting in lesser seed set and lighter grain weight (Mohammad and Tarpley 2009). Rice exhibits different responses to elevated temperatures during day or night. Daytime heat stress decreases the anthesis period, induces early flowering, and decreases the production, viability, and germination rate of pollen grains, producing more of infertile and aborted grains (Jagadish et al. 2007; Tao et al. 2008; Mohammad and Tarpley 2009). Elevated nighttime temperatures cause early panicle emergence associated with reduced fertility, reduced pollen germination rate, lesser spikelet and seed set, and reduced grain weight (Mohammad and Tarpley 2009; Shi et al. 2013). Xiong et al. (2017) conducted a meta-analysis and reported a 39.6% reduction in grain yield under high temperatures.

21.3.3 Maize

Maize (*Zea mays* L.) is an important crop grown for food and feed. It stands third in production behind wheat and rice (Piperno and Rannery 2001; FAOSTAT 2021). It is a good source of carbohydrates (76–88%), fat (4–5.7%), protein (6–16%), and minerals (1.3%) (Woldesenbet and Haileyesus, 2016). Maize grows well in nutrient-rich, moist soil. The optimal growth conditions required are temperature at 11–30 °C, soil pH ranging between 5.8 and 7.0, and 200 to 450 mm precipitation along with 5–6 hours of sunshine per day (Yin et al. 2014).

Maize is more susceptible to heat stress as compared to wheat and rice (Zhao et al. 2017; Zhang et al. 2019). Maize plants, under high temperature stress, reduce their yield potential substantially. Heat affects anther dehiscence as well as the anthesis-silking interval. This results in low viability and germination of pollen grains (Dong et al. 2021; Wang et al. 2021), mistiming of pollen availability, and anther dehiscence resulting in kernel abortion. Subsequently, it reduces the yield (Fig. 21.1) (Bakhtavar et al. 2015; Hatfield and Prueger 2015; Li and Howell 2021; Wang et al. 2021). According to simulation studies, maize yield can be reduced by 10% with an increase in 1 °C global mean temperature (Zhang and Zhao 2017; Dong et al. 2021).

21.3.4 Barley

Barley (*Hordeum vulgare* L.) is an important nutrient-rich cereal crop grown for consumption by humans and animals. According to FAOSTAT, barley plants are cultivated over a large area (50 MHa) producing 140 Mt. of barley grains. It occupies fourth place in terms of production. It is fairly tolerant to extreme environmental conditions (Baum et al. 2007); however, heat stress can reduce its qualitative and quantitative yield potential (Savin and Nicholas 1999; Rollins et al. 2013). Ortiz et al. (2008) projected that if temperature increases by 3–4 °C, barley yields could show a decline in Asia and Africa by 15–35% and in the Middle East by 25–35%. This could be attributed to low chlorophyll content and reduced maximum quantum yield of photosystem II. The impact of heat stress on the plant is also dependent on its phenological stage and the timing of the stress. For example, if heat stress occurred before anthesis, grain number and weight decreased (Ugarte et al. 2007; Dwivedi et al. 2017); however, if barley plants are heat stressed during anthesis, starch content declines while protein content increases. Nonetheless, crop yield is reduced substantially (Reinhardt 2013; Klink et al. 2014; Bohačenko et al. 2021).

21.3.5 Oat

Oat (*Avena sativa*) is the world's fifth most cultivated crop for grain production. Oat seeds are a good source of amino acids, fat, and dietary fiber (Berg et al. 2003; Chen and Yen 2007). Oat grows well in an optimum temperature ranging between 31 and 37 °C. However, the extreme temperature can affect nutritional values, seed vigor, and grain yield (Peterson et al. 2005). Reduced grain yield may also be related to the altered phenology of oat due to heat stress. Estrella et al. (2007) reported that over five decades between 1951 and 2004, an increase in average temperature led to the advancement of different phases of oats development. Sowing of oats advanced by 1.5 days decade^{-1}. Similarly, emergence, flowering, and harvesting periods advanced by 1.2, 4.9, and 6.4 days decade^{-1}, respectively. On the other hand, the sowing-anthesis phase was shortened by 3.4 days in decade^{-1}. The duration for anthesis maturity shortened by 1.5 while that of sowing maturity 4.9 days decade^{-1}, respectively.

21.3.6 Pearl Millet

Pearl millet (*Pennisetum glaucum* L. (R.) Br.) is grown for human food, animal feed, and bioenergy materials. It is a valuable cereal owing to its high concentration of protein, Ca, K, Mg, P, Zn, vitamin B, fats, and dietary fiber (Shivakumar et al. 2003; Davaiah et al. 2009). It is the sixth-most produced cereal grown on about 31 million hectares worldwide (Sun et al. 2021). It is a source of income to 90 million people (ICRISAT). India is the largest producer of pearl millet with 9.5 million tons of grain grown in 9.3 million hectares area (Yadav et al. 2012).

Pearl millet is grown in warm and hot countries which have semiarid environments. They require different optimum temperatures at different stages of their life cycle. For example, the optimum temperature for its seedlings is 31 °C, the vegetative phase is 26 °C, and the reproductive phase is 22 °C (Ong 1983a, b, Ashraf and Hafeez 2004). Pearl millet is highly tolerant to various abiotic stresses and can survive well over 45 °C (James et al. 2015; Huang et al. 2021). Nonetheless, increasing global temperature is alarming for pearl millet production. Djanaguiraman et al. (2018) in an exhaustive study reported that increasing day/night growth temperature from 32/22 °C to 44/34 °C significantly altered the phenology and reduced the weight and yield of seed. As the temperature touched 40/30 °C, seed size decreased by half, percent pollen germination reduced by 97%, the number of seeds per panicle lowered by 97%, and seed yield per panicle decreased by 98%. Seed formation ceased when the day/night temperature reaches 42.3/33.2 °C. Leaf photosynthetic rates were least affected by the increase in temperature and showed a 10% decline at 44/34 °C when compared with 28/18 °C.

Projection studies revealed that in Mali, climate change can cause a decline of 6–12% in the yield of pearl millet (Butt et al. 2005). However, adopting heat-tolerant genotypes can minimize the decrease in grain production between 0.7% and 8%. In South Asia and Africa, Knox et al. (2011) reported that pearl millet production declined by 10%. In West Africa, the projected decline in millet yields due to heat stress are approximated between 0 and 40% in the twenty-first century (Sultan et al. 2013). In sub-Saharan Africa, climate models projected a yield decline of between 7% and 17% by 2050 (Nelson et al. 2009; Schlenker and Lobell 2010). However, the extent of yield loss due to heat stress will depend on the intensity, duration, and timing of heat stress during the reproductive phase.

21.3.7 Sorghum

Sorghum [*Sorghum bicolor* (L.) Moench] is an important cereal crop grown for human food, animal feed, and fuel. It is a dryland crop and grows best at temperatures ranging from 26 to34°C during the vegetative phase (Hammer et al. 1993) and 25–28 °C during the reproductive phase (Prasad et al. 2006a, b). Under heat stress, sorghum plants exhibited disruption in anther dehiscence, alteration in pollen morphology, and impairment of pollen tube growth leading to pollen sterility. Subsequently, it impedes fertilization thereby resulting in a lower seed set, hence lesser grains and grain yield (Prasad et al. 2006b; Jagadish et al. 2007, Djanaguiraman et al. 2014; Singh et al. 2015). Simulation studies projected that heat stress will induce a huge decline in sorghum grain yield in the near future. In Mali, sorghum yield is projected to be lower by 11–17% by 2030 (Butt et al. 2005). According to Srivastava et al. (2010), by 2020, India will have a lower (7–14%) sorghum grain production due to heat stress. Projected declines in sorghum yield are also reported in Africa (Chipanshi et al. 2003; Tingem et al. 2008; Sultan et al. 2013, 2014).

21.3.8 Rye

Rye (*Secale cereale* L.) is a nutrient-rich and stress-tolerant cereal crop. It contains a good amount of anthocyanins, alkylresorcinols, benzoxazinoids, flavonoids, and phenolic acids (Pihlava et al. 2018). It requires an optimum temperature of 31–37 °C and can easily grow on nutrient-deficient sandy soils with a low pH (Miedaner, and Laidig 2019). On the other hand, rye plants improve soil structure and fertility (Wang et al. 2003; Li et al. 2013). Its fibrous roots can grow up to a layer of 15–20 cm into the soil and improve soil water retention, reduce sandstorms, and restore the original grassland ecosystem (Wang et al. 2003; Li et al. 2013). Though fairly resistant to abiotic stresses (Miedaner, and Laidig 2019), rye plants can fall victim to heat stress. Blecharczyk et al. (2016) studied and analyzed the phenological changes of rye grown in Poland over 55 years (1957–2012). During this period, as Poland experienced an increase in average temperature by 2 °C, they observed that the sowing dates of rye were delayed while flowering initiation advanced by 4 days decade $^{-1}$ resulting in reduced yield.

21.4 Pseudocereals

Pseudocereals, such as *Chenopodium quinoa* Willd. (quinoa), *Fagopyrum esculentum* Moench (buckwheat), *Digitaria exilis* (Kippist) Stapf (fonio), etc., are dicotyledonous plants that have earned the term "superfoods." They have an impressive nutrient profile, with high caloric value owing to enriched protein and lipid. They are rich in amino acids and possess a balanced amino acid profile. They contain more arginine, lysine, methionine, tryptophan, and sulfur-containing amino acids as compared to cereals (Matuz et al. 2000; Gorinstein et al. 2002). Pseudocereals lack gluten and are a preferred food for patients with celiac disease (Pirzadah and Malik 2020). Despite UNESCO declaring them as important foods and their numerous benefits, pseudocereals are at a disadvantage due to diminishing cultivation and increased exploitation in the wild (Pirzadah and Malik 2020). This may be attributed to a lack of knowledge of their yield potential, lack of awareness, genetic factors, and marketing constraints (Pirzadah and Malik 2020). As such, the effect of heat stress on pseudocereals is also not known. Therefore, in view of its importance, it calls for immediate attention to assess as well as predict effect of climate change on them so that mitigation strategies can be developed.

21.5 Biostimulants

Increasing frequency of harsh climatic conditions coupled with the ever-growing world population necessitates a sufficient increase in crop yield to meet the demographic demands. This calls for augmenting the resources' use efficiency, without causing damage to the ecosystems and human health. In this regard, exploring the potential of environment-friendly agronomic methods are gaining prominence over the last few years. One such promising agronomic means is the use of plant biostimulants (PBs). PBs have shown to be extremely dynamic and can promote plant growth, flowering, productivity, nutrient use efficiency and provide tolerance to different types of abiotic stressors (Colla and Rouphael 2015).

Plant biostimulant is defined as "an EU fertilizing product, the function of which is to stimulate plant nutrition processes independently of the product's nutrient content with the sole aim of improving one or more of the following characteristics of the plant or the rhizosphere: (1) nutrient use efficiency, (2) tolerance to abiotic traits, (3) quality traits, or (4) availability of confined nutrients in the soil or rhizosphere" (EU 2019).

21.5.1 Classification of Biostimulants

PBs are classified into four categories according to their role:

(1) *Humic and fulvic acids*, which are organic matter present in the soil. These organic matters are formed by the metabolic activity of microbes and decomposition of plant, animal, and microbial residues.
(2) *Animal and vegetal protein hydrolysates*, which are hydrolyzed proteins obtained from both animal and plant sources. Amino acids, peptides, polypeptides, and denatured proteins constitute the hydrolyzed proteins.
(3) Macroalgae seaweed extracts, which are extracts obtained from seaweeds. They contain complex polysaccharides (alginates, fucoidan, laminarin) and plant hormones (auxin, cytokinins) that contribute to plant growth.

(4) Silicon and beneficial microbes such as arbuscular mycorrhizal fungi (AMF) and *Rhizobium*, *Azotobacter*, and *Azospirillum (*N-fixing bacteria).

21.6 Biostimulants and Extreme Temperature Tolerance in Cereals

A detailed literature survey revealed the use of PBs as an ameliorator of different abiotic stresses in many plants. Surprisingly, the number of reports on the use of PBs in the amelioration of temperature stress in cereals is very limited.

Kauffman et al. (2007) reported that perennial rye grass (*Lolium perenne* L.) treated with amino acid-based PB (Macro-Sorb Foliar) showed 95% better mean photochemical efficiency and 65% better leaf membrane thermostability than non-PB plants. Ali et al. (2011) studied the effect of *Pseudomonas putida* (AKMP7), a thermotolerant strain on wheat (var. LOK-1) subjected to heat stress during the day (37–40 °C) and night (27–30 °C). They reported that the bacteria-inoculated wheat plants showed significantly better growth, higher biomass, more tillers, and more spikelet and grains than the non-inoculated plants. The inoculated plants showed less membrane injury, increased activity of antioxidant enzymes such as superoxide dismutase, ascorbate peroxidase, and catalase and higher concentrations of amino acids, chlorophyll, starch, sugars, proline, and proteins compared to non-inoculated plants. Similarly, El-Daim et al. (2014) reported beneficial effects of *Bacillus amyloliquefaciens* UCMB5113 and *Azospirillum brasilense* NO40 on two cultivars of wheat, Olivin and Sids1 given heat stress at 45 °C. The bacteria-inoculated plants showed lesser expression of stress-related genes and lower activity of enzymes of the ascorbate-glutathione redox cycle suggesting that these plants were more tolerant to heat stress as compared to non-PB plants. Mathur et al. (2018) reported that inoculation with arbuscular mycorrhizal fungi (AMF) can ameliorate maize plants from high temperature stress (44 °C) by expanding leaf width and increasing plant height, cob number, and photosynthetic efficiency. Quintero-Calderón et al. (2021) studied the effect of heat stress (40 °C for 15 days after 57 days of sowing) and PBs such as amino acids (AA), brassinosteroids (BR), nitrophenolates (NP), and botanical extract-based PB on two genotypes of commercial rice [‘Fedearroz 67’ and Fedearroz 60′]. They observed that PB-treated plants in both genotypes showed higher photosynthesis coupled with better stomatal conductance and improved transpiration than the plants without PB treatment. The PB-treated plants also showed less injury by preventing membrane peroxidation and accumulating low proline concentration. Mustafa et al. (2021) reported that foliar spray of Si can impart tolerance to wheat plants subjected to heat stress ((37 ± 2 °C). Application of 4 mM Si at the heading stage increased the concentration of pigments, chlorophyll a, b, and a + b, and carotenoids of flag leaf and the activity of antioxidant enzymes (superoxide dismutase, catalase, peroxidase) and osmolytes (soluble sugar protein and proline) as compared to control plants. Figure 21.2 shows the roles of biostimulants in counteracting heat stress in cereals.

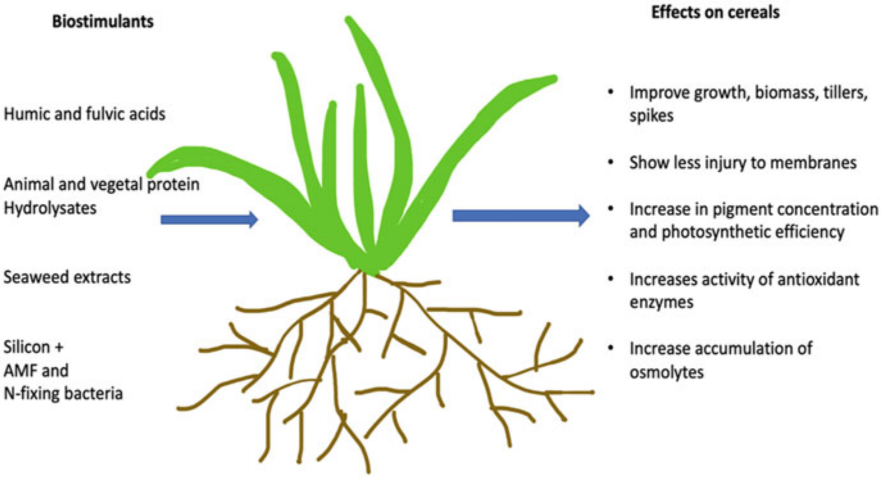


Fig. 21.2 Role of biostimulants in counteracting heat stress in cereals

21.7 Conclusion

Cereals are stapled crops for half of the world's population. The ever-increasing world population thus necessitates a parallel increase in cereal production. The current demand-supply of cereal crops is balanced; however, the increasing average global temperature is a threat to food security as it can disturb the growth, development, and yield of cereal crops. Simulation studies are an effective tool to equip us with the necessary information to combat the negative effects of heat stress. Pseudocereals are superfoods rich in micronutrients, amino acids, proteins, lipids, and dietary fibers, contributing to dietary requirements in different parts of the world. Thus, extensive simulation studies incorporating all the cereals and pseudocereals in different parts of the world can bridge the gap between heat stress and food security. In addition, alternative and innovative strategies must be explored for cereal production to meet the growing demands. In this regard, PBs are an efficient and sustainable agronomic tool to counteract the effects of temperature stress in plants. Considering that (1) cereals are responsible for more than half of the world's calorie intake and (2) temperature stress limits crop productivity, the potential of PBs in ameliorating temperature stress must be explored in cereals as well as pseudocereals. As the response of plants to heat stress varies with the genotypes and depends on the stage of plant development, in-depth studies must be carried out to determine the most suitable PB for different cereal crops. Additionally, it is known that PBs, by large, are a heterogeneous group, and thus, each component has a different mechanism of action. Unravelling the mechanism of action of PBs will provide a platform in understanding the role of PBs in amelioration of heat stress in cereals.

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Use of Biostimulants to Increase Heavy Metal Tolerance in Cereals

22

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Abstract

The world population is increasing rapidly, and this exponential growth not merely increased food contamination that is wreaking havoc on our food system and agricultural outputs. This chapter intendedly provides a detailed and thorough overview of biostimulants with regard to heavy metal tolerance in cereals production. Nowadays, cereals especially wheat, maize, rice, and barley plants supply most people's basic energy needs. Either because of the soil parent material or due to the chemicals used, those major plants grown across a vast region, hence, are more susceptible to metal(loid) (Cd, Cu, Cr, Fe, Ni, Pb, Zn, As, and Sb) accumulation. The toxicity effects through damaging various physiological (pigmentation, chlorophyll, and photosynthetic process), morphological (seed germination and crop growth), and metabolic processes (protein and

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enzymes degradation, reactive oxygen species (ROS), and lipid peroxidation). Also, toxic metals can lead to the extinction of species and varieties of biostimulant microorganisms in the soil. On the other hand, plants are fortified with antioxidants (catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), proline, phenolics phytochelatins (PC), and metallothioneins (MT)) to combat and segregate these aberrations that induced by heavy metals. Consequently, food safety from metal contamination by utilizing environmentally friendly goods or novel farming practices is among the primary goal of modern agriculture. Biostimulants are one of the unique inventions that have the potential to enhance crop tolerance in addition; they also possess many beneficial effects on both soil and crops, especially when faced with environmental constraints such as heavy metals. Biostimulants are compounds, one or more metabolites, or metabolic fusion and microbes that, when introduced to crops, improve plant defense abilities. Thus, the aim of this study is to better understand the metal toxicity and damage in cereals as well as how this phytotoxicity could be reduced by biostimulant integration. The insights presented here are indeed projected to support cereal producers and, as a result, enhance crop output effectively in a metal stressed environment.

Keywords

Biostimulants · Cereals · Commercial products · Heavy metal toxicity · Metal stress tolerance · Production technology

22.1 Introduction

To meet the food requirement of human population explosion, which is expected to hit 9.7 billion by 2050, has wreaked havoc on agricultural production and public health. In the last three decades, numerous technological breakthroughs have already been proposed to boost agricultural productivity operations via eliminating hazardous agrochemical compounds such as synthetic fertilizers and pesticides. However, the development of innovative biostimulants and their application is an evolving technique that is addressing such essential issues in a highly effective way (Rouphael and Colla 2018). It is noted from the literature that Prof. V.P. Filatov is credited with developing the idea of "biogenic stimulant," which began in the Soviet Union in 1933 (Filatov 1944), which later converted into the systematic discussion on biostimulants by (Basak 2008), while the present biostimulant science was conceptualized by du Jardin (2012). Generally, biostimulants are defined as natural miscellaneous materials including microorganisms that strengthen plant physiological processes, flowering, fruit and growth, nutrient efficiency, and crop yield. The biostimulants have a great potential to enhance tolerance against a wide range of biotic and abiotic stresses such as heavy metal (HM) tolerance (Yakhin et al. 2017). Under stress conditions, applying biostimulants can mitigate the negative impact of stress on plant growth.

Plant biostimulants are still being defined and conceptualized (Kirksey 2021), which is partially due to a wide range of inputs that might be called biostimulants. There are two scopes of the notion of biostimulants one in Europe and the other one in North America. The EBIC (The European Biostimulants Industry Council) defined biostimulants as plant biostimulants are molecules or microbes that, when given to plants or the soil, are to promote natural activities to improve nutrient absorption and efficiency, crop quality, and abiotic stress tolerance (Norrie et al. 2021). Because biostimulants have little or no significant impact on pests, hence they are not subject to the same regulations as pesticides (du Jardin 2012). As a conclusion, by focusing on benefits linked to better crop quality and production and stress tolerance, this definition distinguishes biostimulants from biocontrol agents and induced susceptibility to diseases. Hence, the products containing certain minerals are included in the EBIC definition of biostimulants, if the impact on plant development is not achieved by actual fertilization (Rouphael and Colla 2020; Youssef Rouphael 2020). However, the biostimulant alliance of North America described biostimulants as materials including microbes that are introduced to plants, seeds, rhizosphere, or any other growth medium that might also improve the plant's capacity to absorb provided nutrients or give advantages to plant growth. Biostimulants are not plant nutrients; hence, no nutrition promises can be made. In a comparable pattern as the EBIC biostimulants, coalition follows the definition of biostimulants, along with an explanation of their effects on plants as they originate from natural or biological sources and can be used in a variety of ways. For example, it assists to increase the efficiency of essential nutrients, as assessed whether by better nutrient absorption or decreased nutrient losses to the environment via leaching or evaporation, or maybe both, or operate as a soil application to improve overall soil structure, texture, and boost soil productivity and plant response when administered even in tiny quantities (Coalition 2013; Santini et al. 2021).

22.2 Classification

The authentic classification of biostimulants has been controversial; multiple researchers have reported the advancement of biostimulant categorizations at the various time that is listed in Table 22.1. However based on (Package 2016), biostimulants can generally classify into two main categories such as nonmicrobial biostimulants and microbial biostimulants that can further simplify according to biostimulant nature, mode of action, single or multicomponent formulations, composition, function, use, and type of activity and beneficial effects (Yakhin et al. 2017; Rouphael and Colla 2018).

22.3 Production Technology of Biostimulants

There are several biotechnologies and nanotechnologies employed in the manufacturing and production of biostimulants that are highly dependent on the type of raw material, whereas both the type and source of the raw ingredient as well

Table 22.1 Recommended classifications of biostimulants

Filatov (1951)	Karnak (2000)		Ikrina and Kolbin (2004)		du Jardin (2012)	Calvo et al. (2014), Kloepper (2014)	Halpern et al. (2015), Moshe Halpern (2015)	Du Jardin (2015)	La Torre et al. (2016)	Bulgari et al. (2019)	González-Morales et al. (2021)
Nonmicrobial biostimulants											
First proposed category	Based on plant growth promotion (hormones)		Based on natural resources	Based on available product (foliar)	Based on researchers, authorities, and consumer acceptance	Based on existing data	Based on plant root and growth promotion	Implied microbes to prevent contradiction with existing microbial categorization (biopesticides, plant hormones)	Based on composition and formulation	Based on raw material resources	Based on transcriptomics
Carboxylic fatty acids, for example, oxalic acid and succinic acid	Activated-nutrients Active humic-acid Antioxidants Carbohydrates Carbon-rich-organics Cellulose-fiber Complex-sugars Chelated-micronutrients Cytokinin Chelates Chemical-activators Enzymes Nutrient broth Lignin	Amino acids Amides Fermentation materials Gibberellic-acid Growth-simulators Hydrated-organic-proteins Humic-substances Kelp extract Manure-extract Intermediate-metabolites Natural-	Plant materials (land, freshwater, and marine)	Hormone containing products (seaweed extracts)	Humic substances	Humic acids	Humic substances	Humic and fulvic acids	Humic substances	Humic substances	Protein hydrolysates and other nitrogen-containing compounds
Carboxylic fatty hydroxy acids, for example, malic and tartaric acids			Sea shellfish, animals, bees	Humic substances	Complex organic materials	Fulvic acids	Protein hydrolysate and amino acid formulations	Protein hydrolysates and other N-containing compounds	Seaweed extracts	Seaweed extracts	Humic acid and fulvic acid
Unsaturated fatty acids, aromatic and phenolic acids, for example, cinnamic and hydroxycinnamic acids, coumarin			Humate- and humus-containing substances	Amino acid-containing products	Beneficial chemical elements	Protein hydrolysates and amino acids	Seaweed extract	Seaweed extract and botanicals	Hydrolyzed proteins and amino acids	Hydrolyzed proteins and amino acids contain	Chitosan and other biopolymers

Phenolic aromatic acids containing several benzene rings linked via carbon atoms, for example, humic acids	Organic-chelates Metabolites Minerals Plant extracts Yucca extract	wetting-agents Invert sugars Humic and fulvic acids Peptides Sea kelp Vitamins	Vegetable oils and natural minerals	Enzymatic hydrolysis	Inorganic salts (such as phosphite)	Seaweed extracts		Chitosan and other biopolymers	Inorganic salts	Agro-industrial waste	Inorganic compounds
	Monosaccharides Plant hormones Polysaccharides Plant nutrients Wetting agents Soil-conditioners Disaccharides Micronutrients	Non-ionic-wetting-agents Simple-sugars Seaweed Sugar acid-chelates Secondary-nutrients	Water (activated, degassed, thermal)	Available nutrient (N)	Seaweed extracts			Inorganic compounds		Nanoparticles and nanomaterials	
	Scientifically balanced formulation (no ingredients mentioned)		Resins	Peptides	Chitin and chitosan derivatives						
			Oil	Nucleotides	Antitranspirants						
				Fatty acids	Free amino acids and other N-containing substances						
Microbial biostimulants											
	Bacteria		Microorganisms (bacteria, fungi)			Microbial inoculants	Plant growth-promoting microorganisms (including mycorrhizal fungi)	Beneficial fungi	Microorganisms	Microorganisms (bacteria, yeast, filamentous fungi, and microalgae)	Beneficial fungi

(continued)

Table 22.1 (continued)

Filatov (1951)	Karnak (2000)	Ikrina and Kolbin (2004)		du Jardin (2012)	Calvo et al. (2014), Kloepper (2014)	Halpern et al. (2015), Moshe Halpern (2015)	Du Jardin (2015)	La Torre et al. (2016)	Bulgari et al. (2019)	González-Morales et al. (2021)
Nonmicrobial biostimulants										
First proposed category	Based on plant growth promotion (hormones)	Based on natural resources	Based on available product (foliar)	Based on researchers, authorities, and consumer acceptance	Based on existing data	Based on plant root and growth promotion	Implied microbes to prevent contradiction with existing microbial categorization (biopesticides, plant hormones)	Based on composition and formulation	Based on raw material resources	Based on transcriptomics
	Cyanobacteria	Microbial inoculants, petroleum fractions, shale substance					Beneficial bacteria			Beneficial bacteria
	Cultured living									Algae and botanical extract
	Microorganisms									
	Fungi									
	N-fixing bacteria									
	Mycorrhizae									
	PGRS									
	Yeast									

as the processing technique can influence the final constitution and potential functionality of commercialized biostimulant solutions. Some of the known methodologies are cultivation, lyophilization, extraction (acidic, alkaline), fermentation (controlled, independent), processing and filtration, hydrolysis (acid, enzymatic), and cell rupture by high-pressure treatment (Yakhin et al. 2017; Baltazar et al. 2021).

It is also reported that rather than to improve the commercial product's biological performance, numerous commodity-manufacturing procedures are dictated to satisfy operational and legal marketing needs (Kannan 2019). Beneficial microorganisms also can produce several biostimulants as well. Although production methods and product processing often certain compounds that aren't inherent in the primary material (raw material), for instance, numerous commercial seaweed extracts obtained from a certain taxon, which are seldom identical (El Boukhari et al. 2020). The commercial biostimulants made through identical supplies are generally sold as similar products, although their formulation and efficacy might vary significantly. Most commercial biostimulant producers don't divulge the secret of production technology because of business competition and rivalry (Traon et al. 2014; Lötze and Hoffman 2016; Bailey 2021). The following are some briefly described production methods of biostimulants on the basic raw material.

(1) Bacteria and fungi
The biostimulant made from plant growth-promoting bacteria and fungi has been successfully treated with various crops such as maize, tomato, leaf lettuce, and wheat. Generally, the production of living bacteria and fungi starts from the isolation of bacterial strains from samples and then culture on appropriate media (Traon et al. 2014; Pichereaux et al. 2019; Saia et al. 2019; Moncada et al. 2020). On the other hand, nonliving microbes and fungi and their metabolite-based solutions are derived from various techniques including lyophilization, fermentation, acid and alkali hydrolysis, cultivation, and enzymatic hydrolysis. The used bacterial strains found in literature include *Herbaspirillum seropedicae*, *Herbaspirillum rubrisubalbicans*, *Gluconacetobacter diazotrophicus*, *Arthrobacter* spp., *Enterobacter* spp., *Acinetobacter* spp., *Pseudomonas* spp., *Ochrobactrum* spp., *Bacillus* spp., *Rhodococcus* spp., *Bacillus licheniformis*, *Bacillus megatherium*, *Azotobacter* sp., *Azospirillum*, *Aeromonas rivuli*, *Agromyces fucosus*, *Bacillus pumilus*, *Bacillus safensis*, *Microbacterium* sp., *Nocardia globerula*, *Pseudomonas fluorescens*, *Pseudomonas fulva*, *Pseudoxanthomonas dajeonensis*, *Rhodococcus coprophilus*, *Sphingopyxis macrogoltabida*, *Streptomyces* spp., *Cytophagaceae*, *Phaselicystis* sp., *Verrucomicrobia*, *Bifidobacterium bifidus*, *Lactobacillus* spp., *Lactobacillus acidophilus*, *Lactobacillus buchneri*, *Lactobacillus delbrueckii*, *Lactobacillus johnsonii*, *Lactobacillus murinus*, *Lactobacillus paraplantarum*, *Lactobacillus pentosus*, *Lactobacillus plantarum*, *Lactococcus tactis*, *Leuconostoc oenos*, *Propionibacterium freudenreichii*, *Propionibacterium pelophilus*, *Propionibacterium shermanii*, *Propionibacterium* spp., *Propionivibrio limicola*, *Streptococcus* spp., and *Streptococcus thermophiles*, and fungi include *Ramicandelaber* sp., *Mortierella* sp., *Glomus intraradices*,

Trichoderma atroviride, *Candida* spp., *Hanseniaspora* spp., *Issatchenkia* spp., *Kloeckera* spp., *Kluyveromyces* spp., *Metschnikowia* spp., *Pichia* spp., *Saccharomyces bayanus*, *Saccharomyces boulardii*, *Saccharomyces cerevisiae*, *Saccharomyces exiguous*, *Saccharomyces pastorianus*, *Saccharomyces pombe*, and *Syncephalastrum racemosum* (Du Jardin 2015; Yakhin et al. 2017; Hellequin et al. 2018; Kopta et al. 2018; Khatoon et al. 2020).

(2) Mycorrhizae as a biostimulant
Beneficial rhizosphere microbial communities and their combined applications such as mycorrhizae, PGPR in agro-biotechnology, and biochemical engineering can bring different novel biological approaches that can provide opportunities for the soil and plant health (Rafique et al. 2017; Sarathambal et al. 2022). The application of beneficial microorganisms such as mycorrhizae and *Trichoderma* and their interactions have a biostimulant effect on plant growth and nutrient uptake. *Trichoderma* strains are capable to produce siderophores and auxin-like compounds under a wide range of substrate pH conditions (5.5–8.0) (Colla et al. 2015a, b). Mycorrhizal fungi are very efficient biostimulants to enhance mineral nutrients (Smith and Read 2010; Malik et al. 2021), also reinforcing the ability of the plant to resist abiotic and biotic stresses (Giovannini et al. 2020). In general, the application of biostimulants improves plant stress tolerance levels by increasing rhizosphere activity. Rhizosphere organisms such as bacteria and fungi activity levels are high against stress factors. Arbuscular mycorrhizal fungi (AMF) usually led to improved root growth parameters, and better root growth and root activity increase better soil development and better nutrient uptake (Rafique and Ortas 2018; Ortas and Yucel 2020). The AMF as a biostimulant enhances the salt tolerance of plants (Xu et al. 2017). Mycorrhizal fungi interfere with the phytohormone balance of host plants, influencing plant development as a bioregulator and inducing tolerance to soil and environmental stresses (bioprotector) (Rouphael et al. 2015). AMF produced their secondary metabolite such as the easily extractable glomalin-related soil protein which is acting as a biostimulant developed soil structure and makes better growth conditions (Ortas et al. 2021).

(3) Algae
Biostimulants such as seaweed extracts (SWE) or algal extracts including red, green, or brown account 10% of marine products and are becoming more widely available and active ingredients for commercial formulations to use as plant growth promoters and a means to increase tolerance (Van Oosten et al. 2017). The biostimulant production is usually carried out by numerous methods including fermentation, acidic extraction and processing, alkaline extraction, processing and hydrolysis, heated alkaline hydrolysis, aqueous extraction, cell rupture or cell burst via high pressure treatment, and cryo-processing. Besides this traditionally used methodology, some other newly developed extraction techniques are also are used to this purpose such as microwave-assisted extraction (MAE), pressurized liquid extraction (PLE) that is also described as (pressurized fluid extraction or enhanced solvent extraction or high-pressure solvent extraction, or accelerated solvent extraction techniques), supercritical fluid extraction (SFU), ultrasound-assisted extraction (UAE), enzyme-assisted

extraction (EAE), and neutral extraction (MAE) (El Boukhari et al. 2020; Yakhin et al. 2017). Most commercial products are derived from *Ascophyllum nodosum*, *Lithothamnium calcareum*, *Ascophyllum nodosum*, *Durvillaea potatorum*, *Caulerpa scalpelliformis*, *Chlorella ellipsoida*, *Durvillea antarctica*, *Ecklonia maxima*, *Enteromorpha flexuosa*, *Fucus serratus*, *Fucus vesiculosus*, *Gelidiella acerosa*, *Gracilaria corticata*, *Gracilaria salicornia*, *Himanthalia elongate*, *Hypnea musciformis*, *Kappaphycus alvarezii*, *Laminaria digitata*, *Laminaria hyperborean*, *Macrocystis integrifolia*, *Macrocystis pyrifera*, *Padina boergesenii*, *Padina gymnospora*, *Padina pavonica*, *Sargassum muticum*, *Sargassum tenerrimum*, *Sargassum wightii*, *Spirulina maxima*, and *Ulva lactuca* (Van Oosten et al. 2017; Yakhin et al. 2017).

(4) Higher plants and animals

Plant- and animal-based biostimulants have been shown to have beneficial impacts on growth and yield, as well as a variety of biophysical features in a range of horticultural and agronomic crops including tomato, lettuce, beans, pear, okra, pepper, pea corn, and maize (Moreno-Hernández et al. 2020; Zulfiqar et al. 2020; Malik et al. 2021).

The plant-derived biostimulants (PDBs) are generally obtained through various techniques such as controlled enzymatic hydrolysis or fermentation, conventional solid–liquid extraction or solid–liquid dynamic extraction, aqueous fully controlled or independent extraction, ethanol extraction, pressurized solvent extraction, microwave extraction, cool extraction, alkaline hydrolysis, and fully controlled enzymatic hydrolysis. The plant residues for PDB production include corn wet-milling, vegetable by-products, alfalfa hay, and legume seeds (Rouphael et al. 2015; Giuseppe Colla 2015a, b). The common species involve in PDBs are *Diplotaxis tenuifolia* L., *Agapanthus africanus*, *Saccharum officinarum*, *Allium sativum*, *Moringa oleifera*, *Brassica juncea*, *Zea mays*, *Brassicaceae*, *Musa acuminata*, *Digitalis* sp., *Fabaceae*, *Helianthus annuus*, *Castanea sativa*, *Lupinus albus*, *Vitis vinifera*, *Lupinus* sp., *Camellia sinensis*, *Lycopersicon esculentum*, *Ceratonia silique*, *Malus* sp., *Lycopersicon* sp., *Medicago sativa*, *Quercus sessiliflora*, *Nicotiana tabacum*, and *Vaccinium* sp., (Colla et al. 2017; Yakhin et al. 2017; Giordano et al. 2020; Zulfiqar et al. 2020).

However, the production technologies of animal-based biostimulants are slightly different from PDBs, for instance, thermal-hydrolytic processes, chemical-hydrolytic processes, acid hydrolysis, enzymatic hydrolysis, and controlled hydrolysis. The biomass of animal origin includes chicken feathers and casein, animal epithelial, or tissues such as by-products obtained through leather manufacturing or leather waste materials from enzymatic hydrolysis and secondary processing, blood meal, hemoglobin hydrolysate, fish by-products or chitin-containing waste from the seafood industry, hydrolysis of chrome-tanned waste, waste horns and bovine hooves, tannery wastes derived from the complex process of collagen protein hydrolysis, and meat flour (Colla et al. 2017; Yakhin et al. 2017; Mola et al. 2021).

(5) Organic acids or humate-containing raw materials

Humic substances (HS) are referred to a collection of several chemicals that are primarily categorized on the basis of their atomic weight and their solubility in humans, humic acids, or fulvic acids (Bhupenchandra et al. 2020). The sources to extract HS biostimulants are lignin; peat or volcanic soils (naturally humified organic matter); agro-industrial humic such as wastes, composts, vermicompost, and mineral deposits, for instance, leonhardite; and oxidation of lignite (Kannan 2019), while the most common technologies used to derive HS biostimulants include thermochemolytic and extraction (Yakhin et al. 2017).

22.4 Implication of Heavy Metal(s) in Cereals

Heavy metals are well-known for their natural perseverance as they are diversely found naturally in the earth's crust. HMs are revealed their lethal character in a variety of ways from minor symptoms to major diseases that have the potential to harm humans, disrupt significant ecological concentrations, and render the ecosystem unsuitable to both macro- and microorganisms (Sab-Udeh and Okerulu 2017). The HM accumulation in plants via air, soil, and water is among the most critical channels for these harmful pollutants to enter the human body that has direct effects on human health and food chain contamination (Din et al. 2020; Wei and Cen 2020). The contaminated irrigation water from rising industrialization and urbanization in agricultural regions and excessive use of fertilizers and pesticides are highly all contributing to HM contamination of crops (Kovač et al. 2021). According to US Environment Protection Agency (USEPA), As, Cd, Cr, and Pb have long been thought to be the most harmful in the environment and cereals are also a contributor to the HMs in the diet (Kemboi et al. 2018). Al, Sb, As, Cd, Mn, Hg, Cr, Pb, Zn, and Cu are some of the most well-known hazardous metals for many agricultural plants. However, Mn, Zn, Cr, Cu, Ni, and Fe are critical minerals required by plants as essential micronutrients and that can cause toxicity at high levels, while Hg, Cd, As, and Pb potentially cause damage to humans even in tiny quantities (Fakhar et al. 2022). The contact of cereal crops with HMs results in physiological, morphological, and metabolic alterations that are discussed below. The results of Nazir et al. (2021) showed the application of selected fungal biostimulants for increasing plant growth while improving the bioavailable fraction of the total metal contents.

22.4.1 Physiological Effects of Heavy Metals

The high levels of lead (Pb) adversely affect wheat and rice maize seedlings significantly. The seed showed delayed germination, thus resulting in decreased root length and shoot height and generating ROS stress. Along with this Pb enhances malondialdehyde (MDA) and H_2O_2 contents in wheat, rice, and maize by triggering their innate antioxidant system. On the other hand, Pb absorption by cereals is mostly determined either by the bioavailability of Pb in the rhizosphere, exposure duration, translocate capacity of crops, or most importantly genotypes (Muhammad Rizwan et al. 2018, 2019), while zinc (Zn) causes chlorophyll degradation in wheat leaves and decreased growth in rice (Muhammad Rizwan et al. 2019).

Cadmium (Cd) and arsenic (As) ions interfere with the physiological machinery of various cereal crops which lessens the plant strength and stunted growth. The common inverse effects of Cd toxicity in cereal crops include decreased seed germination rate, cell division, and plant growth, leaf chlorosis, water uptake, and nutrient restriction primarily phosphorus and nitrogen (Murtaza et al. 2017; Rafique et al. 2019; Kaya et al. 2020). Along with this high concentration of Cd uptake initiates oxidative stress and the generation of ROS including superoxide anion, hydrogen peroxide, and hydroperoxides. It is also reported that sometimes a cell dies as a result of acute plasmolysis, cytoplasm shrinkage, and decreased number of mitochondrial cristae and ribosomes (Ahmad et al. 2020). The results of Yazici et al. (2021) reported that mycorrhizal colonization significantly reduced Cd accumulation in wheat plants.

In the same manner, as other metals Cr and Selenium (Se) also generate ROS that causes specific damage to cells (Gill et al. 2016; Mostofa et al. 2017). High As and Se accumulation enhances hydrogen peroxide, lipid peroxidation, antioxidant enzyme peroxidase, and antioxidant activity in maize rice, wheat, and barley, respectively. It also lessens green chloroplasts concentration and breakdown of root cell organelles. Arsenic (As) causes cellular damage as well by creating ROS and via conversion of As (V) to As (III) in the cytoplasm (Ahmad et al. 2020; Kaya et al. 2020).

22.4.2 Morphological Effects of Heavy Metals

Kushwaha et al. (2018) reported that lead (Pb) accumulation via several ways such as Ca channels or ATPase/H+ pumps prevents seed germination and plant development by limiting the production of essential proteins and enzymes. Furthermore, it can also affect morphological characteristics, induce genotoxicity, and damage DNA in cereals. Along with this Pb toxicity severely affects trace nutrient uptake, water contents in leaf, and stomatal closure, seed germination, root/shoot length, and plant biomass of several cereal crops such as maize (Nawaz et al. 2017), wheat (Alamri et al. 2018), and rice (Alamri et al. 2018).

Cd high accumulation in cereals lessens chlorophyll content and photosynthesis rate, root and shoot length, and plant biomass (Ansarypour and Shahpiri 2017). Since zinc and Cd are chemically similar under heavy P fertilizer and Zn deficiency soils, Zn and Cd are competing for the same transporters during uptake. Cd toxicity also illustrates several phytotoxic symptoms, for instance, leaf epinasty, root browning, and leaf necrosis and chlorosis (Pramanik et al. 2018). Chromium (Cr) toxicity restricts seed germination and crop growth. High concentrations of Cr in cereal crops generate oxidative stress that interferes in various biochemical and morphological activities in plants which leads to a loss in yield (Handa et al. 2017; Ma et al. 2017). Besides induced metabolic system and photosynthetic impairment are among the significant complication of Cr toxicity in wheat (Mathur et al. 2016).

Ghosh and Biswas (2017) exposed that seed germination and growth of wheat seedling decreased because of toxicities of As. The As accumulation in resistant rice cultivar grains in a pot experiment has less sensitivity in contrast to that with nonresistant rice cultivars. It is also reported that flooding conditions significantly accelerate the promotion of As (Zhang et al. 2016). Apart from it rice is regarded as a higher As accumulator as compared with other cereal crops, hence becoming more susceptible to As toxicity in regard to crop development and productivity (Islam et al. 2016a, b). In other cereals such as maize, As toxicity affects root/shoot biomass and leaf area as identical to selenium (Se) observation in rice (Mostofa et al. 2017).

22.4.3 Metabolic Effects of Heavy Metals

The metabolic effects of Cd have been shown in literature, e.g., reduction of essential plant nutrient uptake, especially zinc, hindered or changes different enzyme activity specifically antioxidant defense system enzymes, ROS, and oxidative stress synthesis (Qin et al. 2018). Cd stress also affects nitrate transportation from roots to shoots inhibiting nitrate reductase functioning in the plant's shoots. It was observed during Cd treatments and the process of nitrogen fixation, and primary ammonia absorption in plants was also reduced (Marques et al. 2019). In another study, it is reported that Cd concentrations in sorghum have the potential to enhance or reduce the synthesis of numerous proteins involved in glucose metabolism and protein production. This leads to a reduction in the growth and biomass of sorghum (Roy et al. 2016).

An experiment on wheat seedlings in hydroponics illustrated the negative effects of lead (Pb) such as disturbance in nutrient uptake (Ca, Zn, Mg, and Cu), reduction in synthesis of metabolic products (proteins), and modifications in the activity of the enzymes, endoplasmic reticulum, dictyosomes, and mitochondrial cristae. Apart from this Pb stress, C_3 and C_4 oxidize numerous critical Calvin cycle substrates that result in a decrease in respiration rate (Ahmad et al. 2020). HMs such as Ni, Cd, Pb, and Zn disrupt the electron transportation mechanism and hinder the phosphorylation reaction, hence damaging DNA (Kumar and Prasad 2018). Exposure of Zn to wheat induces suppression of kinase and dehydrogenase enzymes (Yao et al. 2017), while copper (Cu) accumulation in wheat, maize, and rice induced different metabolic activites such as promotion of lipid peroxidation (Adrees et al. 2015).

Cr is usually transported by transporter channels of sulfate up to shoots and leaves in plants (Ali et al. 2021). The exposure to high levels of chromium (Cr) reduced nitrate-nitrogen (NO_3-N) and increased total N deposition in oats, sorghum, and barley (Wyszkowski and Radziemska 2013; Ahmad et al. 2020). Along with this, it also interferes with germination of seed, nitrate (NO^{3-}) and nitrite (NO^{2-}) reductases, and metabolism of carbohydrate and hydrolytic enzymes such as amylase (Singh et al. 2013; Christou et al. 2021). Se accumulation reduces the action of glyoxalases in rice plants resulting in methylglyoxal toxicity (Mostofa et al. 2017). The presence of Cr primarily causes harm to green pigments and photosystems of cereal crops (wheat), hence hindering carbon absorption, while it also adversely affects the process of enzymatic reactions and photosynthesis and chlorophyll content in maize (Islam et al. 2016a, b; Mathur et al. 2016).

Generally, As is absorbed by roots and translocated via plant shoot either by phosphate pathway (arsenate) or silicon pathway (arsenite), but proteins of silicon pathway are more sensitive to As, so consequently, they initiate structural changes in protein structure after coming into contact with As. Likewise, it is reported in research that As transformed from inorganic to organic form within the rice grains (Ahmad et al. 2020). Another study on rice showed phytochelatins to accumulate in roots and grains except leaves; on the contrary, glutathione levels increase in leaves (Heuschele et al. 2017).

22.5 Implication of Biostimulants in Heavy Metal Tolerance

A thorough review of the literature was carried out to present the role of biostimulants in HM tolerance in various cereal crops. Microbes, such as bacteria, yeasts, and fungus, are commonly employed in the manufacturing of biostimulants. In this concern Rizvi and Khan (2018) conducted a study on maize. The preparation of biostimulant was carried out from *Azotobacter chroococcum* by the process of lyophilization, and a significantly declined concentration of Cu and Pb through the high concentration production of indole acetic acid (IAA) and chelation was found. Another investigation on maize revealed the effective reduction of aluminum stress (Al) through utilizing *Pseudomonas fluorescens* biostimulant obtained via cultivation. This reduction is caused by the production of siderophores, ammonia, and 1-aminocyclopropane-1-carboxylate deaminase (ACCD) (Zerrouk et al. 2016).

The biostimulant derived by extraction process on maize grains showed excellent results on wheat with reduced contents of Cd^{2+} toxicity, lipid peroxidation (MDA), and hydrogen peroxide (H_2O_2) in contrast to the Cd^{2+} stressed control (Alzahrani and Rady 2019). In another similar study, a combination of different biostimulants used along with maize grains extracted biostimulants including silymarin and silymarin-enriched Meg. Through foliar spraying on maize, various progressive outcomes were observed such as hormonal homeostasis restoration, increased photosynthesis pigments, enhanced activities of numerous antioxidants, gene expression, and antioxidative enzymes (Alharby et al. 2021). Plant-based biostimulant extracted from *Orchis latifolia tuber* was used against Cd toxicity stress in maize. It accelerated seed germination, restricted translocation of Cd from root to shoot, ameliorated flow of photosynthetic electron, and enhanced non-photochemical quenching in Cd-treated plants (Seifikalhor et al. 2020).

A commercially available biostimulant (Fyto-fitness) was applied on wheat under a selenium-contaminated environment. It was observed that the biostimulant influenced the plant metabolism via enhancing the biomass by altering soil properties. The Se (IV) accumulated higher in root followed by shoot, and this indicates that this has the potential to protect the plant from Se stress (Xiao et al. 2020). Another commercial biostimulant (Glutacetine®) mixed with urea ammonium nitrate fertilizer showed declined Mg, Mn, Cu, and Ca concentration in wheat (Maignan et al. 2020). Moreover, a naturally derived biostimulant indole acetic acid (IAA) (Drobek et al. 2019) produced by AMF species (*Penicillium roqueforti*

Thom.,) depicted significant results on wheat to suppress Ni, Cd, Cu, Zn, and Pb that is grown in a heavy metal-rich environment (Ikram et al. 2018). Similarly, another AMF species (*Rhizophagus irregularis*) illustrated lower Mn, Co, and Ni levels in the AMF-inoculated grain in both wheat and barley (Watts-Williams and Gilbert 2020).

Several PGPR (such as *Azospirillum*, *Herbaspirillum*, *Rhizobium*, *Pantoea*, *Methylobacterium*, and *Burkholderia*) employ numerous traits including IAA, ACC deaminase, siderophore, and phosphate solubility that promote ROS production and modify the antioxidant system in rice and enhance tolerance of As (III), Cr (VI), and Pb (Mouhamad and Alabboud 2020). Likewise, it is revealed in a of meta-analysis that there are about 20 different bacterial genera which have the potential to act as biostimulants and mediate heavy metal tolerance of As, Pb, Cd, Hg, Cr, Al, and Br by enhancing the expression of stress response genes via activating numerous signaling pathways, including the reactive oxygen species (ROS) pathway and hormone signaling pathways (Franco-Franklin et al. 2021).

A yeast-derived and genetically engineered biostimulant through cultivation process demonstrated higher seedling growth (root, shoot panicle length) increased photosynthetic efficiency and declined As accumulation in root, shoot, and grains (Verma et al. 2019). Besides this there are several other studies that have been carried out to investigate different stresses that can either be elevated by HM accumulation or other adverse circumstances. Two different fusions of biostimulants were applied on wheat by foliar spray application including a mixture of amino acids and *Ascophyllum nodosum* extract and, secondly, extracted *Trichoderma* enzymes, sulfur, and manganese sulfate. It was observed that the proteins involved with stress and defense response showed positive results, and in the case of a stressful environment, they would assist in preventing protein denaturation. Along with this, they could use energy-dissipating mechanisms to regulate the production of ROS (Pichereaux et al. 2019), which are associated with Cd and Pb as well (Ahmad et al. 2020). Likewise, sugar beet extract was found highly beneficial as a biostimulant in reducing negative effects in wheat as it improved activities of antioxidants such as SOD and POD and increased photosynthetic pigments that generally got affected by high concentrations of Ni, Cd, Pb, Cu, and Zn (Kumar and Prasad 2018; Noman et al. 2018).

Furthermore, in maize, numerous stress conditions that emerge due to HMs such as reduction in antioxidant enzymes including guaiacol peroxidase (GPX) and CAT along with a significant increase in MDA can mitigate by commercially available biostimulant, namely Megafol (Panfili et al. 2019). Apart from this, a biostimulant extracted from *Moringa oleifera* was found highly rich with antioxidants namely salicylic acid, α-tocopherol, glutathione, and ascorbic acid together with different Osmo protectants and phytohormones, for instance, free amino acids, free proline, soluble sugars, cytokinin, auxins, and gibberellins. After spraying on sorghum plants in a stressed environment, it improved plant metabolism by phytohormones and enhanced tolerance through higher antioxidant activity (Desoky et al. 2018) (Fig. 22.1).

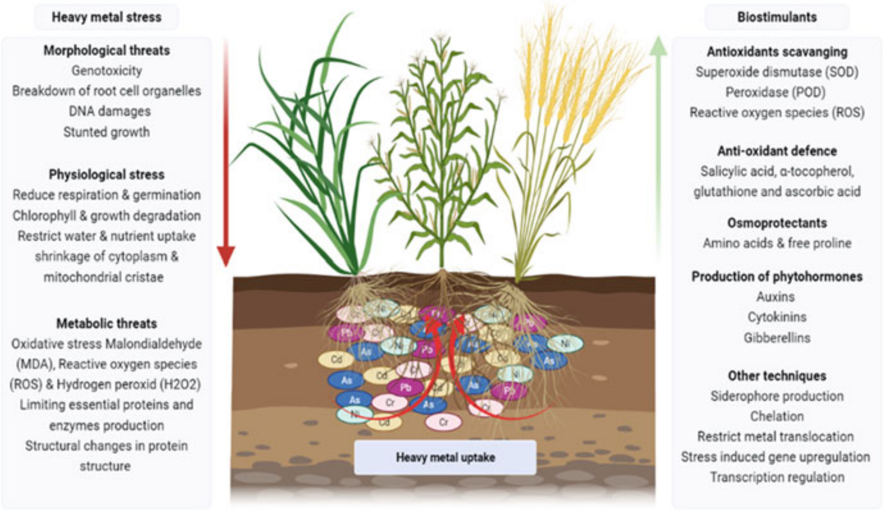

Fig. 22.1 Pictorial illustration of HM stress and biostimulant-induced tolerance techniques (Van Oosten et al. 2017; Yakhin et al. 2017)

22.6 Commercialized Biostimulant Products for Cereals (Yakhin et al. 2017; Kumar and Aloke 2020; Hamid et al. 2021)

Commercial products	Composition/raw material	Target crops	Target and possible functions	Manufacturer
Agrispon®	Natural plant extract	Barley, maize, rice, and wheat	Bioregulator	Agriculture Science, Inc. USA
Aminoplant®, Siapton®	Epithelial tissues (natural substances of animal origin)	Cereals	Inducing resistance to abiotic factors such as salinity, drought, low temperatures, transplant shock	Isagro Group, Italy
Asahi SL	Sodium Para-nitrophenolate, sodium ortho-nitrophenolate, sodium 5-nitroguaiacolate	Cereals	Bioregulator	Agrecol, Poland
BactoFil A10®	*Azospirillum brasilense*, *Azotobacter*	Monocotyledons (cereals)	Increased soil nutrient content that	Agro. Bio Hungary

(continued)

Commercial products	Composition/raw material	Target crops	Target and possible functions	Manufacturer
	vinelandii, *B. megaterium*, *B. polymyxa*, *P. fluorescens*		results in plant growth promotion and HM tolerance	Kft., Hungary
Bio-Gold	*Pseudomonas fluorescens* and *Azotobacter chroococcum*	Cereals	Growth promotion via nitrogen fixation, drought and HM tolerance, control of root rot and wilt diseases, phosphorus solubilization	Biopower, Sri Lanka
Cedomon®	*P. chlororaphis*	Barley and oats	Highly effective against various types of seed-borne diseases and HM tolerance	Lantmannen Bioagri AB, Sweden
Ceres®	*Pseudomonas fluorescens*	Cereals (field crops)	Biocontrol agent	Biovitis, France
FZB24®fl RhizoVital 42®	*B. Amyloliquefaciens* spp. *plantarum*, *B. amyloliquefaciens*	Cereals (field crops)	Phosphate availability and protection against pathogens	Abitep Gmbh, Germany
Gmax® PGPR	*Azotobacter,* *Phosphobacteria,* *P. fluorescens*	Cereals (field crops)	Nitrogen and phosphatic nutrition, disease prevention from HMs and helps in plant growth promotion	Greenmax Agrotech, India
Inomix® Biostimulant	*B. polymyxa (IAB/BP/01)*, *B. subtilis (IAB/BS/F1)*	Cereals	Plant growth promotion increases root and shoot weight, metal tolerance potential, strong root system	IAB (Iabiotec), Spain
Inomix® Biofertilisant	*B. megaterium*, *Saccharomyces cerevisiae*, *Azotobacter vinelandii*, *rhizobium leguminosarum*			

(continued)

Commercial products	Composition/raw material	Target crops	Target and possible functions	Manufacturer
Inomix® phosphore	*P. fluorescens*, *B. megaterium*, *Saccharomyces cerevisiae*			
Megafol	Organic nitrogen, potassium oxide, organic carbon and amino acids	Cereals	Promotes vegetal growth during environmental stress	Bulagro Ad, Bulgaria
Micosat F® Cereali	*B. subtilis BR 62*, *Paenibacillus durus PD 76*, *Streptomyces* spp. *ST 60*	Cereals	Increased nutrient and water absorption, increases stress tolerance, and enhances ISR	Ccs Aosta Srl, Italy
Nitroguard®	*Azospirillum brasilense NAB317*, *Azorhizobium caulinodans NAB38*, *Azoarcus indigens NAB04*, *bacillus* sp.	Cereals	Growth promotion via nitrogen fixation	Mapleton Agri Biotec Pty Ltd. Australia
Rhizocell® GC	*B. amyloliquefaciens souche IT45*	Cereals	Stimulates root growth by secreting growth metabolites and dissolving phosphorus by secreting phytases (enzymes)	Lallemand Plant Care, Canada
RhizoVital 42®	*B. amyloliquefaciens* sp. *plantarum*	Cereals	Phosphate availability and protection against pathogens	Abitep Gmbh, Germany

22.7 Conclusion

In modern times, feeding the growing population is among the most difficult challenge for food security, particularly when the agricultural sector is under fire for various complicated issues emerging through global climate change and anthropogenic activities such as HM contamination in plants and soils. Such environmental and human-induced issues contribute to the spread of pollution, weeds, phytopathogens, and crop-related diseases along with a significant reduction in the soil/plant favorable microorganisms that not only affects crop health, quality, and yield but also exposes crops vulnerable to various biotic stress. Additionally, for sake of plant protection and adequate production, farming became heavily dependent on synthetic agrochemicals that have undesirable consequences on the ecosystem. Consequently, in present days biostimulant usage piqued global attention to developing ecologically friendly substitutes to certain fertilizers and pesticides. Therefore, investigation and characterization of bioactive components of biostimulants and explanation of stimulation techniques at molecular and physiological levels are of great interest to the scientific and research world and commercial sector. It is also very important for the sustainability of ecosystem management. Owing to scientific research and technological developments over the last decades in several areas, we now have a greater understanding of cereal crop physiology than ever before. Although the toxicity of HMs effects on characteristics of numerous cereal plants generally, the introduction of biostimulants with contaminated cereals considerably reduces the negative impacts of HMs along with improved development and production. Thus, the market demand for biostimulants is growing quickly along with an exponential growth rate predicted in the coming years.

Several studies suggested a fusion of multiple biostimulants might produce more consistent results than treating each one alone. Since the actions of biostimulants are highly species and product-specific, it cannot generalize and transfer to another biostimulant or crop species. Contemporary biostimulants are complicated mixes obtained through numerous raw ingredients and manufactured by using various production procedures. Despite that limited research has been done so far, there is still a great room for further research to investigate the molecular processes of cereal crops underlying global reactions to HMs after treating with biostimulants to maximize their effectiveness and permitting tailored treatments, such as the development of novel compositions capable of increasing agricultural yields even in the metal-rich environment. In conclusion, to advance core fundamental and practical knowledge regarding the performance of biostimulants with respect to enhance HM tolerance in cereals and other agricultural plants, it is the need of the hour to conduct a wide range of studies on biostimulants via using a range of products and natural substances, treatments, and development stages. Also, it is important to use biostimulants against biotic and abiotic stress factors especially climate change stress factors. Biostimulants give the impression to be a unique and potentially useful class of agricultural inputs by supplementing synthetic agrochemicals and increasing HM tolerance and, as a result, improving the quality and yield of cereals.

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Use of Biostimulants to Improve UV Tolerance in Cereals

23

Mona F. A. Dawood and Arafat Abdel Hamed Abdel Latef

Abstract

The plant received sunlight radiation of different spectra, from which ultraviolet radiation (UV). The UV spectrum consists of UV rays with different wavelengths as UV-C (100–280 nm), UV-B (280–315 nm), and UV-A (315–400 nm). Despite UV radiation being a minor part of the sunlight radiation received by Earth, it induces considerable biological impacts on the plant ecosystem. UV has been found to differentially affect the growth, metabolism, and development of cereals. Thus, the first part of this chapter was conducted to study various responses of cereals to UV-A, UV-B, and UV-C on various plants' aspects. These stresses induce numerous adverse effects in cereals, impair biochemical/physiological and molecular processes, and eventually cause severe reductions in cereal growth, development, and overall productivity. The second part of chapter deals with the application of various biostimulants to ameliorate the damaging impacts of UV stress on cereals. Thus, the present chapter included various applicants such as phytohormones, nutrients, or organic compounds that may be aided in amelioration damage of UV stress.

Keywords

Biostimulants · Cereals · Defense mechanism · Ultraviolet radiation

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23.1 Introduction

Climate change along with increasing anthropogenic activity, plants in their ecosystems are compelled to continue in extreme conditions, with rapid changes in the ultraviolet (UV) radiation, ionizing radiation, temperature, humidity, and precipitation (Gateva et al. 2022). UV radiation participates in normal plant photosynthesis, growth, and development. The UV spectrum consists of UV rays with different wavelengths. UV-B (280–315 nm) is about 1% of the total spectrum of UV radiation, whereas about 95% of UV radiation is UV-A (315–400 nm). Although the exposure of plants to UV-A photons is 10–100 times more than to UV-B photons, the energy of UV-B radiation is high enough to induce numerous deleterious effects. In addition, UV-C (100–280 nm) is fully absorbed by the Earth's stratospheric ozone layer (Vanhaelewyn et al. 2020). Around 50% of global radiation is photosynthetically active radiation (PAR) which is in the range of 400–700 nm. PAR is defined as the electromagnetic radiation in the range of the light spectrum that phototrophic organisms mainly use in photosynthesis (Gateva et al. 2022). Life on Earth is exposed to the light spectrum ranging from ultraviolet-B (UV-B) to infrared wavelengths (295–2500 nm), hereafter referred to as natural radiation. The UV part of the electromagnetic spectrum comprises three classes, UV-C (200–280 nm), UV-B (280–315 nm), and UV-A (315–400 nm), with only UV-B and UV-A reaching the earth's surface. Radiation with wavelengths below 290 nm declines to undetectable levels (Vanhaelewyn et al. 2020).

Various wavelengths of the solar spectrum manage various photomorphogenesis and plant responses (Latef et al. 2020). Blue light affects stomata opening (Boccalandro et al. 2012), chlorophyll formation, chloroplast movement, and phototropism (de Carbonnel et al. 2010; Boccaccini et al. 2020). Greenlight can promote early stem elongation (Folta 2004) and prohibit stomatal opening triggered by blue light (Smith et al. 2017). The red light was found to manage shade-avoidance syndrome and plant phototropism (Demotes-Mainard et al. 2016), regulating plant vegetative development and architecture. On the other hand, UV perception influences leaf thickness, leaf curling, and auxiliary branching, while decreasing stem extension and leaf expansion (Qian et al. 2020; Dawood et al. 2021a, b). Despite various impacts of light on plant physiology and metabolism, the responses of plants to radiation are species- or even variety-specific (Yan et al. 2019). In response to UV and other types of radiation, plants accumulate multiple metabolites that aid them to adapt to UV-B, UV-C, and other environmental stressors (Zhao et al. 2020; Dawood et al. 2020). Light plays an important role in different types of biotic and abiotic stimulation, triggering the synthesis of many phytochemicals (Loconsole and Santamaria 2021a, b). Light-mediated alterations in antioxidants, such as ascorbic acid, glutathione, and phenolic compounds, were recommended in plants in response to various wavebands of the electromagnetic spectrum (Li and Kubota 2009; Siipola et al. 2015; Zhao et al. 2020). Phenolics play important roles as sunscreens and antioxidants, protecting plants from potential UV damage (Dawood et al. 2020, 2022). Low doses of UV radiation instigate the biosynthesis of phenolic compounds as flavonoid glycosides and hydroxycinnamic acids with strong

UV-absorbing characteristics, both under artificial and natural conditions (Morales et al. 2015; Rai et al. 2019). However, how UV mediates the production of individual phenolic compounds is dependent on their chemical structure (Neugart et al. 2014), UV spectral composition (Morales et al. 2010), and plant species and genetic variation between cultivars (Robson et al. 2019; Yan et al. 2019). The accumulation of flavonoids in plant cells is preceded by changes in the expression of CHALCONE SYNTHASE (CHS), the gene encoding the first enzyme in the flavonoid biosynthesis pathway (Jenkins 2009). Another key signaling gene that is transcriptionally regulated by UV and visible radiation is ELONGATED HYPOCOTYL5 (HY5). This transcription factor mediates the expression of hundreds of genes responding to UV radiation, including those involved in the flavonoid biosynthesis pathway (Binkert et al. 2014). In recent years, we have gained a substantial understanding of transcriptional responses regulated by UV in plants grown under different levels of photosynthetically active radiation (PAR, 400–700 nm) (Rai et al. 2019; Tissot and Ulm 2020). Plant responses to UV radiation are highly dependent on UV dose, general light environment (natural sunlight vs. artificial lighting), previous acclimation to UV, and other abiotic factors (Jenkins 2017; Rai et al. 2019). Most plant responses to UV radiation have been assessed using different UV: PAR ratios (Jenkins 2017).

Despite UV radiation being a minor part of the sunlight radiation received by Earth, it induces considerable biological impacts on living organisms which can impact plant interactions, with most studies performed on UV-B (Robson et al. 2015; Carvalho and Castillo 2018; Vanhaelewyn et al. 2020). UV radiation influences plant growth and quality, depending on wavelength, intensity, and exposure time. Studies have shown that high UV-A doses negatively impact PSII elaboration, decreasing maximum quantum efficiency, electron transport rate, and photosynthesis due to a reduction in ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) (C3 species) or PEP carboxylase (C4 species) and an increase in stomatal resistance and reactive oxygen species (ROS) production (Vass et al. 2002; Prado et al. 2012; Takahashi and Badger 2011; Kosobryukhov et al. 2015). UV-B can induce abiotic stress and photomorphogenic changes. High UV-B exposure induces physiological stress, including ROS production, DNA deterioration and damage, and impairment of cell processes (Heijde and Ulm 2012). Low UV-B exposure promotes photomorphogenic changes, such as cotyledon expansion, biosynthesis of anthocyanins and flavonoids, inhibition of hypocotyl growth, and stomatal opening (Ulm and Nagy 2005; Jenkins 2009). Interaction between plants and UV light is regulated by photoreceptors, such as UV resistance locus 8 (UVR8), which allows acclimation to UV-B stress (Ulm and Nagy 2005; Jenkins 2009; Rizzini et al. 2011). UVR8 is associated with the chromatin of UV-B-responsive genes, such as the promoter region of *elongated hypocotyl 5* (*HY5*). UVR8 activity is also associated with the E3 ubiquitin ligase, known as constitutively photomorphogenic 1 (COP1). UVR8 interacts with COP1, and both are associated with photomorphogenic responses (Favory et al. 2009; Loconsole and Santamaria 2021a, b). Like UV-B, UV-C induces stress responses in plants and may damage DNA and modify the functioning of chloroplasts and mitochondria (Balestrazzi et al. 2010; Saxena et al.

2011; Urban et al. 2018). Stressed plants may react by producing ROS. ROS signaling modifies physiological processes and produces secondary metabolites (Suzuki and Mittler 2006; Urban et al. 2016, 2018). UV-induced effects are dependent on the radiation intensity and developmental stages (Moreira-Rodriguez et al. 2017). UV irradiation has the potency to redirect the carbon flux resulting in changes in several classes of primary and secondary metabolites such as carotenoids, phenolics, glucosinolates, and even chlorophylls, with associate effects in the phyllosphere (Heinze et al. 2018; Vandenbussche et al. 2018; Vanhaelewyn et al. 2020).

23.2 Effect of UV-A, UV-B, and UV-C on Cereals

23.2.1 Effect of UV-A on Cereals

The sun is primarily a UVA source, as UVA amounts to over 90% of the UV radiation reaching the earth's surface. UVA radiation is further subdivided into UVA1 (340–400 nm) and UVA2 (315–340 nm). Although UV light is known to damage quality and production parameters, some studies show stimulatory effects of UV-A on biomass accumulation (roots and shoots) in certain species. The response of plants to UV radiation may be species-specific, ranging from stimulation to inhibition (Tezuka et al. 1993; Cooley et al. 2001; Kataria et al. 2014). This was ascribed to the enhancement of water use efficiency and improved the rate of photosynthesis. Changes in biomass allocation have also been linked to different allocations of resources (Verdaguer et al. 2017). On the other hand, UVA exposure attenuated adversely shoot system without affecting the root of *Triticum sativum* (Häder 1996). Negative effects of UV-A on shoot biomass were attributed to direct exposure of aerial parts to sunlight, and it was argued that promotion of root growth was associated with UV-A photoreceptors in shoots, implicated in the transmission of long-distance signals that regulate root growth. Rozema et al. (2002) stated that flavonoids as the main group of phenols associated with UV responses, and have a main antioxidant function. It has been denoted that flavonoids have UV-A and UV-B-absorbing characteristics. Most flavonoids absorb in the 315–400 nm UV-A range (Cerovic et al. 2002), playing an important role as antioxidants and protective compounds (Kotilainen et al. 2008, 2009). Thus, the potentiality of UVA depends on the dose, exposure period, intensity of UVA, crop species, growth stage, and plant organs. Yield losses of barley plants in response to UVA radiation have been reported by Tsygvintsev et al. (2019). During the vegetation, barley is the most sensitive to the influence of ultraviolet at the II–V stages of organogenesis (in the transition from the vegetative to the generative stage of development) and was the most sensitive stage to UVA radiation.

23.2.2 Effect of UV-B on Plants

UV-B radiation is essential for plant growth and metabolism. However, high UV-B exposure can cause damage to plant cells, which is then reflected in the physiological processes of the whole plant. Generally, dicotyledons are more sensitive to UV-B radiation than monocotyledons (Kataria et al. 2014). UV-B radiation, having higher photon energy, has a greater negative effect compared to UV-A radiation at the same dose of irradiation on the grain yield of barley (Tsygvintsev et al. 2019). The impact of UV-B exposure on plants is directly influenced by different factors like dose, fluence rate, wavelength, duration of UVB exposure, etc. (Escobar-Bravo et al. 2019). Various studies have explained that based on these factors UV-B radiation-caused impacts on plants system can be beneficial or deleterious (Schreiner et al. 2012; Parihar et al. 2015). It has been reported that applying UV-B to plants for a long time can accelerate reactive oxygen species (ROS) production, macromolecule destruction, and photosynthetic machinery damage, while low-dose and short-term UV-B radiation can work as a regulatory environmental cue that modulates morphology, biochemistry, and physiology of plants to ameliorate the UV-B toxicity and activate defensive strategies (Yadav et al. 2020; Tripathi et al. 2021). UV-B has also been found to differentiate the growth, metabolism, and development of crop plants. It has been reported that the efficiency of PSII (Fv/Fm), rate of photosynthesis, and stomatal conductance are significantly enhanced, along with a remarkable increase in carbonic anhydrase, PEP carboxylase, and total soluble proteins (Kataria and Guruprasad, 2014). A work by Liu et al. (2017a, b) reported that UV-B at the low level of 3.33 μmol m^{-2} s^{-1} induced an increment of stem diameter growth, soluble sugar content, total ascorbic acid, and superoxide dismutase, peroxidase, and catalase activities in cucumber leaves without compromising net photosynthesis rate. On the other hand, UVB induced inhibition of hypocotyl elongation and decrement in the net photosynthesis at a high intensity (5.54 or 6.67 μmol m^{-2} s^{-1}).

Solar UV radiations are known to reduce photosynthetic efficiency by impairing some important processes of photochemical reactions in thylakoid membranes, enzymatic processes in the Calvin cycle and stomatal limitations to CO_2 diffusion (Allen et al. 1998; Keiller et al. 2003) of the plants by causing structural and functional changes in the chloroplast. Exposure to UV-B results in the inhibition of photosynthesis in pea (Nogues and Baker 1995), cotton (Zhao et al. 2004), and oilseed rape (Allen et al. 1997). UV-B radiation causes the inactivation of light-harvesting complex II and alters gene expression for the synthesis of PSII reaction center proteins. Also, the Mn cluster of the water oxidation complex is the most important primary target of UV-B stress, while D1 and D2 proteins, quinone molecules, and cytochrome b6/f are the subsequent targets of UV-B (Kataria et al. 2014). In addition, UV-B induces expansion of thylakoid membranes and damage the chloroplast envelope (He et al. 1994), degradation of photosynthetic enzymes (Teramura and Sullivan 1994), reduction of electron transport rate (Pfündel et al. 1991), and damage to PSII (Caldwell 1981), photosynthetic pigment concentrations, and leaf anatomy (Feng et al. 2003). UV-B exposure results in a reduction in net carbon assimilation capacity (photosynthesis) which, in turn, affects biomass allocation and growth (Musil 1996). Anatomically, UV-B changes leaf structure in terms of increment of leaf thickness (Nagel et al. 1998), trichomes on the abaxial leaf surface (Barnes et al.1996), decrease in the number and diameter of xylem vessels, reduced stomatal frequency, and distorted leaf area (Lingakumar and Kulandaivelu 1993). UV-B stress can induce fluctuations in carbohydrate metabolism, thereby affecting CO_2 assimilation and partitioning of sugars from source to sink (Shahzad et al. 2021) in rice. UV-B can destroy pigments in the photosynthetic apparatus, such as chlorophylls and carotenoids, and consequently lower the fluorescence of photosystem (PS)II (Marwood and Greenberg 1996; Correia et al. 2005; Kataria et al. 2014). A decrease in the activity of Rubisco (an enzyme essential for carbon fixation) of UV-B-exposed plants leads to lower carbon dioxide fixation and oxygen formation, as was reported by Kataria et al. (2013). UV-B-treated barley, wheat, cotton, sorghum, and amaranth contain less chlorophyll than the untreated plants (Kataria et al. 2013; Klem et al. 2015). UV-B radiation can result in smaller specific leaf weights. UV-B can affect the photosynthesis rate also indirectly by reducing stomatal conductance, changing leaf anatomy (Bornman et al. 1983), and increasing leaf thickness (Bornman and Vogelmann 1991), which can change the light penetration into the leaf and thus change the morphology of the canopy (Hollósy 2002). UV-B also degrades amino acids, which leads to the inactivation of proteins and enzymes (Grossweiner 1984). Damage to lipids in plant cell membranes is also caused by UV-B radiation in the presence of oxygen, which is known as lipid peroxidation (Kramer et al. 1991). Lipid peroxidation can be defined by measuring the malondialdehyde content, which is formed through oxidation and degradation of polyunsaturated fatty acids (Dawood and Azooz 2020; Bashandy et al. 2021; Mourad et al. 2021).

The lighting dose may be modulated to maximize plant performance and accumulation of secondary metabolites (Schreiner et al. 2014). Phenol compound biosynthesis in plants is regulated by UV-A (Verdaguer et al. 2017) and UV-B (Trivellini et al. 2016) radiation. Several studies have shown that phenol production increased in sweet basil plants exposed to UV-B light (Bertoli et al. 2013, Ghasemzadeh et al. 2016). UV-B exposure triggered the accumulation of vitamin C, phenols, and flavonoids in different crops such as mung bean sprouts, and buckwheat (*Fagopyrum esculentum*) sprouts (Tsurunaga et al. 2013), tomato (Castagna et al. 2013), and *Hypericum* spp. (Namlı et al. 2014). Su et al. (2016) showed that UV-B at 5 W m^{-2} induced anthocyanin biosynthesis, with a time-dependent increase. Similar responses were recorded in apple (*Malus domestica*) skin (Solovchenko 2003), turnip (*Brassica rapa*) seedlings (Wang et al. 2012), and *Triticum* sprouts (Tsurunaga et al. 2013). Phenylalanine ammonia lyase (PAL) is the key enzyme of phenylpropanoid metabolism, triggering the biosynthesis of phenol compounds; several studies have shown that UV-B stress modulates an increase in PAL (Escobar et al. 2017). Mosadegh et al. (2018) displayed that plants exposed to UV-B have enhanced production of phenols relative to controls, reaching the highest values at 102 kJ m^{-2} day^{-1} revealing a dose-dependent behavior. Several studies have shown that PAL plays an important role in anthocyanin accumulation under UV-B irradiation (Park et al. 2013, Su et al. 2014). Based on the work of Murthy et al. (2014), UV-B stimulation of phenol compounds may be exploited in two steps: (1) plants are cultivated under optimal conditions until a determined growth stage; (2) secondary metabolism is stimulated by UV-B to enhance phenol production (Loconsole and Santamaria 2021a, b).

To adapt against the hazardous responses of UV-B, plants develop a variety of regulatory mechanisms, like enhanced protective mechanisms and activated repair mechanisms (Piccini et al. 2020). On UV-B exposure, enhanced or upregulated activities of antioxidative defense (enzymatic and nonenzymatic) systems in plants are known to cope with the excess accumulation of ROS and lipid peroxidation (Jaiswal et al. 2020). Antioxidant enzymes are affected differentially by UV-B-induced oxidative stress (Zlatev et al. 2012). UV-B irradiation stimulated superoxide dismutase (SOD), ascorbate peroxidases (APX), and glutathione reductase (GR) activities in wheat (Sharma et al. 1998). It has been shown that UV-B degrades IAA and can downregulate genes associated with IAA activity (Pontin et al. 2010; Ros and Tevini 1995). Also, the stimulation of the biosynthesis of the secondary metabolite suggests its protective role against UV-B stress (Yadav et al. 2020).

Ultraviolet-B is very potent to cause chemical modifications and DNA damage in natural conditions (Douki et al. 2003; Rastogi et al. 2010). UV-B can induce DNA damage and mutations in DNA replication (Jiang and Taylor 1993; Schmitz-Hoerner and Weissenböck 2003). Staxén et al. (1993) reported that UV-B radiation affects the plant cell cytoskeleton by causing breaks in cortical microtubules, and in some cases, this can inhibit cell division. UV-B radiation generates several distinct alterations in DNA, named photoproducts. The most likely photoproduct-inducing mutations are two different lesions that unite adjacent pyrimidine residues in the same strand. The major lesions are CPDs, accounting for about 75% of UV-B mediated DNA damage and 6-4PPs. Minor DNA damage includes hydrated bases, oxidized bases, and single-strand breaks (Takahashi et al. 2011). Interestingly, CPDs and especially 6-4PPs cause DNA bending, with unwinding reported for 6-4PPs, causing growth retardation, lethality, or mutagenesis (Tuteja et al. 2009). These types of DNA damage are usually not observed under low UVB rates (<1 mmol m^{-2} s^{-1}), which are sufficient to stimulate photomorphogenic and protective responses (Frohnmeyer et al. 1999). Given the unstable nature of DNA and the high occurrence of CPDs, plants developed sophisticated systems to deal with this type of DNA damage.

Blum et al. (2005) stated the effect of low and high levels of UV-B radiation on cereals (barley, oat, and winter wheat) was investigated and denoted significant changes in chlorophylls and carotenoids and phenolic substances and changes in peroxidase activity. It was shown that barley is the most sensitive and winter wheat is the most tolerant to UV-B. High doses of radiation caused high growth retardation during the vegetation period and biomass loss. Significant reduction of photosynthetic pigments (chlorophylls a and b) as well as carotenoids by UV-B irradiation. An increase of carotenoids content in winter wheat at UV-B irradiation can be considered an adaptive and protective reaction preventing from photodestruction of chlorophylls. But the reduction of carotenoids was reported barley revealing the absence of protective and the adaptive reaction of UVB irradiation. The content of phenolic compounds has been enhanced by UV-B radiation. The reduction of peroxidase activity after exposure to excessively high dose UV-B radiation (225.2 kal/cm^2) during 48 h is the evidence of already non-irreversible damages in cereal plants (Blum et al. 2005).

23.2.3 Effect of UV-C on Cereals

The morphological and biochemical changes of dicotyledon and monocotyledon plants exposed to pre-and postharvest UV-C illumination. But major studies especially on the effect of UV-C on postharvest fruits have been studied on dicot dicotyledon. In this regard, Darras et al. (2020) study evaluated the effects of UV-C on plant growth and photosynthesis. A positive effect of UV-C was found on tomato plants where a 25% increase in total fruit number and a 36% increase in fruit weight exposed to UV-C at 1.0 kJ m^{-2} compared to nonirradiated controls, while UV-C was found to decrease plant height and net CO_2 assimilation. This higher yield of tomatoes may be due to shared UV-B photoreceptors also absorbing UV-C light (Urban et al. 2018), as occurs in some photomorphogenic reactions, promoting an increase in biomass (Darras et al. 2020). Some experiments reported that pre-harvest UV-C irradiation triggered flowering in certain ornamental plants (Darras et al. 2012, 2015, 2019; Bridgen 2015). In most cases, there was no decrease in net CO_2 assimilation between UV-C-irradiated plants and controls, which means no damage to PSII. Similar results were found in other species: chlorophyll fluorescence (*Fv/Fm*) of lettuce (*Lactuca sativa*) plants exposed to UV-C light was not reduced by doses up to 1.70 kJ m^{-2}, indicating no damage to PSII (Vàsquez et al. 2017). On the contrary, there was a significant decrease in net CO_2 assimilation, stomatal conductance, *Fv/Fm*, and yield in strawberry plants exposed to 1.5 kJ m^{-2} every 4 days (de Oliveira et al. 2016).

Also, the major effects of UVC on plant metabolism have been reported on dicotyledons and rarely reported for cereals. In general, the chloroplast is the first organelle to show injury response to UV radiation and reduction in the chlorophyll contents may be due to inhibition of biosynthesis or due to degradation of chlorophyll and their precursors (Dawood et al. 2022). Photosynthetic pigments such as chlorophyll *a* and *b* as well as total chlorophyll contents were considerably reduced in UV-C treated crops (Reshmi and Rajalakshmi 2011; Soriano-Melgar et al. 2014). In these studies, chlorophyll *a* and chlorophyll *b* were more sensitive to UV-C radiation. The reduction of chlorophyll content is thought to hurt plant photosynthetic efficiency due to UV-C radiation being too severe. The inhibitory impact of UV-C on chlorophyll breakdown and the activities of Mg-dechelatase, chlorophyllase, and chlorophyll degrading peroxidase were recorded (Costa et al. 2006; Maharaj et al. 2010; Chairat et al. 2013). Carotenoids (β-carotene or pro-vitamin A) are scavenging molecules that induce the return of singlet oxygen to its ground state (Gomaa and Dawood 2021; Moursi et al. 2021; Dawood 2022). β-Carotene attenuated in *Turnera diffusa* as a result of UV-C treatment (0.38 mW cm^{-2}; 5 min day^{-1}, 10 min day^{-1}, and 20 min day^{-1} exposure and storage for 10 days) which could be due to photobleaching (Soriano-Melgar et al. 2014) and in fresh-cut mango when exposed to UVC for periods 1, 3, 5, and 10 min day^{-1} and storage at 5°C for 15 days. In light vine-ripe red tomatoes, using 1, 3, and 12.2 kJ m^{-2} levels of UV-C reduced β-carotene, while UV-C doses at 1 and 12.2 kJ m^{-2} enhanced the total lycopene (E + Z isomers), relative to control (Bravo et al. 2012). UV-C doses caused a decrease in β-carotene in mature green (breaker stage) tomato, while UV-C doses at the doses of 1.0 and 3.0 kJ m^{-2} over the control plants stimulated the total lycopene contents, and a decrement of *E*-lycopene was recorded at 12.2 kJ m^{-2} dose (Bravo et al. 2013). On the other hand, carotenoid levels increased in response to UVC in medicinal plant *Spilanthes acmella* (toothache plant) (Reshmi and Rajalakshmi 2011) and yellow bell pepper (Promyou and Supapvanich 2012). The increase in total carotenoids may be part of the antioxidant system where carotenes are involved in the protection of the chloroplast against photooxidation. In a study of Alegria et al. (2012), fresh-cut of carrots exposed to 0.78–0.36 kJ m^{-2} and storage at 5 °C for 10 days caused a consistent increase in carotenoid content at day 7 compared to A 64% loss in carotenoids level in UV-C-treated samples compared to controls was just after UVC exposure. Application of UVC at the doses of 3.7 and 24.4 at 16 °C for 28–35 days caused a general increase in carotenoids content, while a significant decline in lycopene accumulation was reported on mature green tomato (Maharaj et al. 2010). Illumination of mature green (breaker stage) tomato to 13.7 kJ m^{-2} UVC and storage at 12–14 °C for 21 days did not affect β-carotene content but enhancing lycopene level (Liu et al. 2009). In a study by (Jagadeesh et al. 2011), UVC exposure (3.7 kJ m^{-2}) and storage at 13 °C for 30 days reduced the lycopene content of mature green tomato (Jagadeesh et al. 2011). A recent study of Dawood et al. (2021a, b) reported that application of UVC on tomato seedlings adversely affected seedlings' fresh and dry weight, photosynthetic pigments, and antioxidant enzymes (CAT, SOD, APX, GPX), while triggering reactive oxygen species (superoxide anion, hydrogen peroxide, and hydroxyl radical), membrane damage traits (lipid peroxidation, lipoxygenase, and methylglyoxal), and nitric oxide. Subsequent study of Dawood et al. (2022) recommended the negative impacts of UVC in terms of oxidative membrane deteriorations and attenuation of the antioxidant system as major targets of UVC radiation.

Thus, the damaging impacts of UV radiation have been managed by various strategies. A number of efforts have been made to create transgenics having enhanced potential to activate the defense response against the UV-B stress through a change in the expression level of one or more genes. Even though success has been obtained in some cases (Jayaraj and Punja 2008; Al Khateeb and Schroeder 2009), there are no transgenic crop plants shown to perform successfully at the field level (Pandey et al. 2012). The use of improving substances is one of the major strategies that have been applied widely to improve the plant tolerance against UV stress as phytohormones, plant regulators, nanoparticles, minerals, etc. In the present study, we will focus on the ameliorative effects of various biostimulants on different forms of UV radiation.

23.3 Biostimulants Used for Improving the Plant Tolerance to UV Stress

Several researchers demonstrate that microbial and nonmicrobial biostimulants (PBs) are capable of inducing an array of morpho-anatomical, biochemical, physiological, and molecular plant responses such as boosting crop productivity, nutrient use efficiency, and increasing tolerance against abiotic stresses (Nardi et al. 2016; De Pascale et al. 2017; Rouphael et al. 2018; Rouphael and Colla 2020). The use of natural biostimulants to improve soil characteristics and nutrient availability for crops can allow a reduction in the use of chemical fertilizers, which in intensive application causes a serious problem in soil health (Randeep et al. 2021). Biostimulants have been defined as materials that, in small amounts, promote plant growth (Zhang and Schmidt 1999). They have also been described as any substance or microorganism applied to soils to improve plant nutritional efficiency and tolerance to abiotic stress (Du Jardin 2012). Biostimulants also increase root biomass, nutrient translocation, and soil enzyme activity (Halpern et al. 2015). There are many groups and forms of biostimulants, including enzymes, proteins, amino acids, micronutrients, and other compounds (Drobek et al. 2019). Natural stimulants, such as phenols, salicylic acid, humic and fulvic acids, and protein hydrolases, are often included under the term biostimulants (Du Jardin 2015; Chiaiese et al. 2018). Moreover, fungi and bacteria are also an important group of plant biostimulants that can alter the community of soil microorganisms (Drobek et al. 2019).

There is emerging evidence of biostimulants as plant priming agents, as demonstrated by theobserved effectiveness of these formulations in promoting and sensitizing plant defenses and resistance against different environmental stresses (Fleming et al. 2019). In the last decade, the field of plant biostimulants has been steadily growing in the agricultural industry and has positioned itself as one of the key emerging strategies for enhancing crop production and resilience to the changing climate. Plant biostimulants have received considerable attention lately and are increasingly being integrated into agriculture and production systems as plant growth and yield regulators/promoters as well as prestress conditioners (Yakhin et al. 2017). However, the limited fundamental research into the modes of action of many biostimulant products is among the knowledge gaps that require scientific attention. Elucidation of the biological basis of biostimulant function, and a broad mechanism of action at cellular and molecular levels, is a prerequisite for the development of a scientifically based biostimulant industry, leading to an effective exploration and application of formulations in agriculture (Yakhin et al. 2017; Fleming et al. 2019). We will focus our studies on the major studies that included using various substances that improve the cereals' tolerance to UV stress.

23.3.1 Silicon

Not many studies on the relationships between UV-B stress and mitigation of stress effects by Si supplementation can be found in the literature. Studies regarding the addition of Si or Si nanoparticles have been reported for cereals which shown that Si can reduce the negative effects of UV radiation through increased antioxidant capacity (Yao et al. 2011) and lower concentrations of ROS (Mihaličová Malčovská et al. 2014). It has been shown that addition of Si in the form of potassium silicate (K_2SiO_3) mitigates UV-B damage to wheat seedlings (*Triticum aestivum* L.) through an increase in plant antioxidant compounds and Si levels in leaves (Yao et al. 2011). Si treatment increased total plant biomass and contents of chlorophylls (a + b), soluble sugars, anthocyanins, and flavonoids, and reduced superoxide radical production and malondialdehyde content (which indicates lipid peroxidation) in the wheat seedlings (Yao et al. 2011). Mihaličová Malčovská et al. (2014) exposed maize seedlings to short-term UV-B radiation. The seedlings were grown hydroponically and treated with Si or left untreated, as the control. In control plants, after UV-B exposure, the content of ROS and thiobarbituric acid reactive substances increased, along with a small increase in the content of total phenols and flavonoids. After UV-B exposure, the maize treated with Si showed only a small increase in flavonoid content, which indicated stress mitigation by Si. In UV-B-exposed wheat, high levels of superoxide radical and H_2O_2 have been reported; therefore, lipid peroxidation and electrolyte leakage in wheat were increased (Tripathi et al. 2017). Tripathi et al. (2017) also showed differences in the anatomical properties of the wheat leaves. UV-B radiation reduced leaf thickness, size of mesophyll cells, and lignification in the metaxylem vessels. UV-B-exposed wheat showed damage to chloroplasts. The addition of Si and Si nanoparticles diminished the damaging impact of UV-B on the leaves. Moreover, the addition of Si and Si nanoparticles improved the lignification and suberization of bundle sheath cells and metaxylem vessels (Shen et al. 2010a, b). Shen et al. (2009) simulated UV-B radiation at 30% stratospheric ozone depletion and showed that UV-B–treated plants gain less biomass than the controls. UV-B–treated plants also contained more leaf N and P and less leaf Mg and Ca. UV-B increased the allocation of P, K, and Ca to the roots. The addition of Si increased the uptake of P and Mg and favored the allocation of P and Ca to the roots.

23.3.2 5-Aminolevulinic Acid (ALA)

Priming with ALA was reported to significantly reduce plant damage from UV-B radiation by promoting photosynthesis, enhancing antioxidant capacity, and improving nitrogen metabolism. As a key precursor of chlorophyll biosynthesis, ALA alleviated the deficiency of chlorophyll biosynthesis during UV-B stress; ALA pretreatment upregulates the expression of genes involved in chlorophyll biosyntheses such as glutamyl-tRNA reductase (HEMA1), Mg-chelatase (CHLH), and protochlorophyllide oxidoreductase (POR) in pigeon pea (*Cajanus cajan*), thus promoting plant photosynthesis during UV-B stress (Divya and Sheo Mohan 2021; Gupta and Prasad 2021). In addition, ALA priming-increased activities of antioxidant enzymes are essential for lettuce (*Lactuca sativa*) resistance to UV-B stress (Ozkan et al. 2017). In addition to enzymatic antioxidants, ALA also increases the content of nonenzymatic antioxidants such as flavonoids and phenolics (Gupta and Prasad 2021). Under UV-B stress conditions, ALA priming significantly improves the activities of nitrate reductase (NR), nitrite reductase (NiR), glutamine synthetase (GS), and glutamate synthase (GOGAT), and then increases the levels of NO_3^- and NO_2^- in the seedlings of pigeon pea (Divya and Sheo Mohan 2021). Foliar application of 10 and 25 ppm ALA to UVB (3.3 W m^{-2})-stressed plants resulted in a substantial increase in phenylalanine ammonia lyase (PAL) and γ-tocopherol, methyltransferase (γ-TMT) gene expression, antioxidant enzyme activity, and chlorophyll a and b concentrations. ALA priming contributes to UV-B tolerance by regulating photosynthesis, antioxidant, and nitrogen metabolism in plants. Seed soaking of 25 and 100 μM induced reduction in germination time and increased germination index and upregulated photosynthesis, antioxidant enzymes (CAT, SOD, and POD), total phenolic content, and total flavonoid content to balance ROS and reduce UV-B damage to plant productivity. In addition, it increased plant growth and growth regulating parameters and increased enzyme activity and nonenzymatic antioxidant content in the plant defense system and reduced oxidative stress (Gupta and Prasad 2021).

23.3.3 Polyamines (PAs)

Polyamines (PAs) are implicated in a variety of regulatory processes ranging from regulationof growth and cell division, regulating the activity of ribonucleotides and proteinase toinhibition of ethylene (C_2H_4) production and senescence. The anti-senescent activity of PAsmay also be related to their ability to be effective free radical scavengers, as well as stabilizingDNA and membranes by their positively charged cations associated with negative chargeson nucleic acids and phospholipids (Maharaj and Mohammed 2012). Changes in plant PA metabolism occur in response to a variety of abiotic stresses and have been shown to enhance the ability of plants to resist environmental stresses. Some studies reported accumulation of PA (free Putrescine) in fruits after exposure to UVC (Maharaj et al. 1999; Tiecher et al. 2013). Furthermore, exogenous application of 2 mM putrescine on UV-C stressed (72 kJ m^{-2} and storage at 4 °C) strawberry plants induced maintenance of firmness, reduction of weight loss, and protection of total antioxidant capacity and vitamin C content against degradation (Mortazavi et al. 2014). UV-C irradiation (0.1 and 0.3 kJ m^{-2}) triggered the accumulation of endogenous free, conjugated, and bound PAs (Spm, Spd, and Put) in leaves of young pea plants, while reduced membrane damage as a result of (Katerova and Todorova 2009).

23.3.4 Cytokinesis

Cytokinins, a class of plant growth regulators, are known to regulate several plant developmental processes and may play a significant role in protecting them against abiotic stresses. Singh et al. (2019) reported that UV-B exposure caused a substantial increase in reactive oxygen species contents (superoxide radical and hydrogen peroxide) and oxidative damage biomarkers (lipid peroxidation and electrolyte leakage), while the antioxidant potential was increased as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and glutathione-*S*-transferase (GST) activity, and radical scavenging capacity (DPPH activity), PAL activity, total phenolics, flavonoids, and anthocyanins contents. The seedlings pre-treated with kinetin (10mM) and subsequently exposed to UV-B exhibited a substantial increase in the antioxidant system (SOD, POD, CAT and GST activity, and DPPH activity), secondary metabolism way (PAL activity, total phenolics, UV-B screening pigments (flavonoids) and anthocyanins and hence, significant lowering in oxidative stress biomarkers was also reported. The possible reason for the diminished growth in test seedlings under UV-B stress was the depletion of endogenous cytokinin levels (zeatin riboside) in tomato cultivars under similar conditions (Yang et al. 2004). Thus, Singh et al. (2019) also demonstrated that in comparison to UV-B2, UV-B1 exposure in Kinetin-treated ameliorates the damage of UVB to tissues could be due to (i) substantial screening of UV-B radiation as a result of enhanced levels of flavonoids in the epidermal layer and mesophyll cells and (ii) accelerated activity of SOD, POD, and CAT which have ultimately kept the levels of ROS under limits. More recently, the mitigation effect of kinetin on the damaging impacts of UVC was investigated by Dawood et al. (2022). The kinetin spraying pre- or postexposure to UVC treatment enhanced photosynthetic pigments (chlorophyll *a*, *b*, and carotenoids), primary metabolites (amino acids, proteins, and sugars), secondary metabolism (PAL, phenolics, anthocyanins, and flavonoids), the chelating mechanism (reduced glutathione and phytochelatins), nonenzymatic antioxidants (ascorbic acid and α-tocopherol), and antioxidant enzymes (SOD, CAT, APX, GST, and GPX). Furthermore, kinetin caused the lowering of reactive oxygen species of UVC-stressed plants as hydrogen peroxide, superoxide anion, and hydroxyl anion as well as membrane damaging criteria (lipid peroxidation and lipoxygenase).

23.3.5 Nitric Oxide

Nitric oxide (NO) is an extremely diffusible bioactive signaling molecule. It is recognized to regulate a broad variety of physiological development like seed germination, mitochondrial functionality, iron homeostasis, floral regulation, and fruit ripening in plants. Furthermore, NO concentration also regulates the plant performance under different biotic and abiotic stresses like high and low temperature, UV-B, heavy metal, drought, and salinity (Desikan et al. 2002; Song et al. 2008; Tossi et al. 2011; He et al. 2012; Rahimian Boogar et al. 2014; Kataria et al. 2020a, b). In particular to UV-B stress, various mechanisms have been proposed for NO-mediated plant adaptation. For instance, UV-B exposure increases the abscisic acid (ABA) concentration which consequently activates the H_2O_2 and NO accumulation to recover the UV-B incited cell damage in maize leaves (Tossi et al. 2009). Similarly, UV-B exposure leads to increased H_2O_2 content which further upregulates the expression of NOS gene to enhance NO content (Zhang and Zhao 2008, Zhang et al. 2009). Also, NO provides a shield from oxidative injury caused by UV-B radiation (Santa-Cruz et al. 2014; Esringu et al. 2016).

23.3.6 Sitosterol

Shahzad et al. (2021) reported that the application of β-sitosterol improved numerous physiological parameters under UV-B stress associated with growth in terms of shoot and root length, RWC, whole plant biomass, chlorophyll pigments, and photosynthetic-related parameters (Pn, Gs, Tr, WUEi, Fv/Fm, and NPQ) compared to the stressed plants. Moreover, β-sitosterol enhanced oxidative stress tolerance via lowering ROS of the treated UVB-stressed plants and substantial trigger in activities of antioxidant enzymes (SOD, POD, CAT, and APX) in rice plants.

23.3.7 Magnetic Field

Raipuria et al. indicated that the seedlings obtained from SMF-primed seeds exhibited a significant stimulating effect on seed germination and early growth parameters of seedlings after UV-B (2.9 mW/cm^2/s, 1 h) exposure where higher expression of α-amylase gene and activity of total amylase in SMF-primed seeds even after UV-B exposure which resulted in the enhanced seed germination and seedlings vigor. Based on the observed increased total-amylase, NOS, and NR activities in SMF-primed seedlings after UV-B exposure, the expression of their corresponding encoding genes was also evaluated in the present study. Further, the increased expression of *GmAMY1*, *GmAMY2*, *GmNOS2*, and *GmNR2* genes in seedlings were obtained from SMF-primed seeds of UV-B treatment over seedlings of unprimed seeds. It indicated that SMF-priming enhanced the expression of these genes which helps the soybean seedlings to overcome the detrimental effects caused by UV-B exposure. The study declared that SMF-priming stimulates the *GmNOS2* and *GmNR2* expression to produce NO from L-arginine and nitrite reduction. Other studies showed increased growth, nitrogen and carbon fixation, and yield of soybean plants emerged after SMF-priming under ambient UV-B stress in field conditions (Kataria et al. 2017, 2020a, b). The study of Raipuria et al. stated that the supply of NO donor, SNP, further improved all the seedlings parameters in un-primed and SMF-primed seeds after UV-B exposure. The gene expression study also showed significant upregulation of α-amylase (*GmAMY1*, *GmAMY2*), nitric oxide synthase (*GmNOS2*), and nitrate reductase (*GmNR2*) encoding genes in UV-B exposed SMF-primed seedlings over un-primed seedlings. In particular, SNP+UV-B treatment enhanced the *GmNOS2* expression in both unprimed (31.9-fold) and SMF primed (93.2-fold) seedlings in comparison to their respective UV-B stressed plants only.

23.3.8 Salicylic Acid

Salicylic acid (SA) is a phenolic compound involved in the regulation of the growth and development of plants and their responses to biotic and abiotic stress factors (Dawood et al. 2021a, b). Significant induction in SA accumulation was evidenced in UV radiation-exposed maize plants (Horváth et al. 2002). Increased photosynthetic rate, pollen viability, leaf phenolic concentration, and yield in UV-B stressed rice were also reported (Mohammed and Tarpley 2013). SA can decrease UV-B caused chromosome aberration levels in the meristematic root tip cells (Ranceliene and Vyšniauskienė 2012). Exogenously applied SA was reported to promote photosynthetic function and its related variables in UV-B exposed plants (Karioti et al. 2008; Li et al. 2014). Earlier, UV-C radiation was also reported to upregulate the transcription of the *SA induction-deficient 2* gene coding for the SA biosynthetic isochorismate synthase 1 enzyme (Martinez et al. 2004).

23.3.9 Allantoin

Allantoin (a purine metabolite), in plants, purines' catabolism is a part of the nitrogenmetabolism could function in stress tolerance. A study by Dawood et al. (2021a, b) revealed that these toxic impacts of UVC were triggered by the greater oxidative damage and disruption of osmolyte homeostasis. However, pre-treatment of AT noticeably alleviated the stress-induced damages by enhanced chlorophyll, soluble protein, and soluble carbohydrate contents in AT-pretreated UVC-stressed plants relative to only stressed plants leading to the improvement of the plant growth and biomass. Moreover, AT pre-treatment enhanced endogenous AT and allantoate content, phenylalanine ammonia-lyase, nonenzymatic antioxidants, and the enzymatic antioxidants leading to reduced oxidative stress markers compared with only stressed plants, indicating the protective effect of AT against oxidative damage. The study recommended that the protective roles of AT are strongly associated with the improved antioxidants. On the other hand, posttreatment of AT showed less efficacy in UVC stress mitigation relative to pre-treatment of AT.

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Use of Biostimulants to Improve Ozone Tolerance in Cereals

24

Sercan Pazarlar

Abstract

Ozone (O_3) formed in the troposphere, one of the major threats to plant health, critically affects the various phases of the physiological processes of plants, resulting in a loss of plant productivity. Cereals as major contributors to the feeding of the human population are considered sensitive or moderate sensitive to O_3 stress. O_3 damage caused by the increasingly emerging impacts of climate change is among the main global problems that are expected to affect crop production more severely in the near future, and therefore, many researchers have focused on innovative strategies to reduce the negative impacts of O_3 stress. Plant biostimulants (PBs), relatively newly classified compounds, have been utilized for modifying/regulating the physiological process of plants to alleviate stress-driven limitations or promote growth. There are well-known synthetics and natural compounds that biostimulate plants for better performance and improved O_3 tolerance. PBs or compounds that act as PBs offer great potential to achieve the yield targets in cereals under the stress of O_3 in a much more efficient and relatively sustainable way; the types and properties of which have been tested in cereals so far are discussed in this chapter.

Keywords

Biostimulants · Ozone tolerance · Cereals · Plant stress

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24.1 Introduction

Ozone formed by complex photochemical reactions of nitrogen oxides (NO_x) with carbon monoxide (CO), volatile organic compounds (VOCs), and methane (CH_4) under solar radiation in the troposphere is considered one of the main environmental-polluting gases (Simpson et al. 2014; Liu and Kai 2021). Tropospheric O_3 (also called ground-level O_3) concentration has dramatically increased in many parts of the world as a consequence of a rapid increase in the O_3 precursors emitted by fossil fuel-based anthropogenic activities since the mid-nineteenth century (Parrish et al. 2012; Ciais et al. 2013; Cooper et al. 2014; Monks et al. 2015). Some evidence shows that ground-level O_3 concentrations are projected to decrease in some regions of the world, such as western Europe and North America, where emissions of O_3 precursors have been more tightly controlled (Schnell et al. 2016; Gaudel et al. 2018). Inversely, it has been projected to increase further, particularly in developing economies (Wild et al. 2012; Cooper et al. 2014; Sicard et al. 2017). More than ~50% increase in the average level of O_3 on a global scale in 2100 has been predicted based on modal simulations (Meehl et al. 2007).

Ozone is a colorless or pale blue, unstable gas, highly toxic to biological organisms and destructive to nonliving materials (Oyama 2000; Iriti and Faoro 2008). A wide range of health disorders such as cancer and respiratory and cardiovascular diseases may result from exposure to O_3 (Anenberg et al. 2010; WHO 2013; Nuvolone 2018). Tropospheric O_3, which is among the major threats to plant health, critically affects the various phases of the physiological processes of plants, resulting in plant productivity loss. Crops can be affected by exposures to a high concentration of O_3 over a short time (acute stress) as well as chronic exposures, which refer to continuous contact with high background O_3 concentrations throughout the growing seasons (Kangasjärvi et al. 2005).

Damage attributed to O_3 as a phytotoxic gas in crops was first reported in the 1950s (Middleton et al. 1956), and in the following years, an increasing number of reports have been published regarding O_3 damage in various plant species. Different research groups have conducted various studies based on several models that support the conclusion that tropospheric O_3 is responsible for serious losses in cereal production in different parts of the world. Cereals such as wheat, barley, maize, rice, sorghum, oat, and millet are grown in ~12.5% of the world's agricultural land area and are very crucial food sources for humans and livestock (FAO 2018). Tropospheric O_3 has gained considerable attention from researchers and policymakers due to the increasing reports of cereal damage related to O_3. O_3 is estimated to be responsible for more than 85 million tons of wheat loss in Europe, North America, and Asia (Pleijel et al. 2018). The harvest losses of wheat caused by O_3 range from 0 to 39% depending on the cultivar and region (Schauberger et al. 2019). The annual average losses in southern China for double-early rice, double-late rice, and single rice due to tropospheric O_3 pollution during the 2015 growing season were estimated to reach 108.1 million USD, 190.2 million USD, and 486.4 million USD, respectively (Cao et al. 2020). Wheat rhizosphere microbial communities that regulate many critical functions of plant growth and health were also reported to be adversely affected by elevated O_3 (Changey et al. 2018). The O_3-driven losses in the world are expected to increase by 2–6% for wheat and by 1–2% for rice based on the 2030 legislation scenario (Van Dingenen et al. 2009).

Developing stress-tolerant cereal cultivars that can have stable yields and quality under stress conditions of O_3 is an important research goal to ensure future food security (Fleury et al. 2010; Dwivedi et al. 2017; Hossain et al. 2021). Owing to the dynamic nature of O_3 and the time and effort required for developing O_3 tolerant cultivars, other strategies to improve plant tolerance against O_3 stress must be prioritized. Plant biostimulants (PBs) are substance(s) or microorganism(s) that can modify the several physiological processes of plants to improve productivity and enhance tolerance to stress factors. Several types of compounds, most of which have a biological origin, have been identified as PBs so far and have been demonstrated to mitigate the negative effects of abiotic stress in different crops. PBs or compounds that act as PBs offer great potential to achieve yield targets in cereals under abiotic stress conditions, including O_3. The exogenous application of PBs to improve tolerance to O_3 in crops has not been fully adopted despite its potential to mitigate the negative impacts of stress in a much more sustainable and affordable way. In this chapter, I intend to review the available publications on the negative impacts of O_3 stress and provide an overview of the potential of PBs and compounds acting as PBs to improve O_3 tolerance in cereals.

24.2 Ozone as an Important Abiotic Stress Factor Limiting the Production of Cereals

Ozone damages plants after entering leaves through stomatal pores and reacting with double bonds and sulfhydryl groups of organic molecules (Iriti and Faoro 2008; Grulke and Heath 2020). The gaseous O_3 in the extracellular space (apoplast) is degraded into reactive oxygen species (ROS) including hydrogen peroxide (H_2O_2), superoxide ($O_2^{\bullet -}$), and hydroxyl radical ($^{\bullet}OH$) which impair the integrity of lipids and amino acids of the plasma membrane, apoplastic enzymes, and several other organic molecules located in the cell wall (Vainonen and Kangasjärvi 2015; Ainsworth 2017). A plant-derived oxidative burst mediated mainly by plasma membrane-localized NADPH oxidases (Wohlgemuth et al. 2002) and by type III cell wall peroxidases (Wohlgemuth et al. 2002) is also known to occur by the interaction of acute O_3 and plants. Signals generated by oxidative damage of plasma membranes and an increase in the level of ROS activate intracellular signaling pathways, leading to various changes in primary and secondary metabolism (Kangasjärvi et al. 2005). Both acute and chronic O_3 stress are responsible for the impairment of the physiological and biochemical reactions of the plants, resulting in productivity and quality loss at varying levels depending on several factors, including genotype, growth stage, and physiological status of plants. Ozone has been shown to cause drastic photosynthesis impairment due to several reactions; for example, stomatal closure (Vahisalu et al. 2008, 2010) and non-stomatal reactions such as loss of assimilation which is attributed primarily to decreased Rubisco activity (Eckardt and Pell 1994) and decline in function of photosynthetic electron transport (Fiscus et al. 2005). It was also demonstrated that carbohydrate transformation and allocation are affected by the elevated level of O_3 (Asensi-Fabado et al. 2010). Early senescence and abscission of leaves due to probable alterations in ethylene metabolism are also among the symptoms observed in O_3-stressed plants (Conklin and Barth 2004).

Ozone stress negatively interferes with the physiological processes of crops, resulting in a significant reduction in crop yield and quality. The negative impacts of O_3 on the yield of cereals mainly depend upon the amount and duration of O_3 exposure, cultivar sensitivity, and the plant growth stage (Vainonen and Kangasjärvi 2015; Grulke and Heath 2020). A wide range of modelling approaches (exposure indices) has been used to assess the impact of O_3 exposure on vegetation injury, growth, and/or yield in cereals. Some of these exposure indices include AOT40 (accumulated O_3 exposure over an hourly threshold of 40 ppb) (Fuhrer et al. 1997), W126 (hourly concentrations weighed by a sigmoidal weighting function) (Tai et al. 2021), SUM06 (Sum of hourly O_3 concentrations above 60 ppb), and M7 (the seasonal means of daytime 7 h O_3 concentrations) (Heck et al. 1983) are based on quantification of O_3 concentration in ambient air during the crop growing season, while others such as POD_Y (phytotoxic O_3 dose above a threshold flux of Y nmol O_3 m^{-2} s^{-1} during a specified period) (Peng et al. 2019) integrates O_3 taken up into the leaves through the stomatal pores over a growing season.

Wheat, the most extensively cultivated cereal in the world, has been reported to be one of the plant species sensitive to O_3 stress (Mills et al. 2007; Avnery et al. 2011). The current surface O_3 concentration (34.6 ± 9.7 ppb) had significant negative effects compared to charcoal-filtered (13.7 ± 8.8 ppb) air treatment on grain yield, harvest index, and starch and protein concentration in wheat (Pleijel et al. 2018). Mauzerall and Wang (2001) estimated a yield loss of 5% for wheat in the European Union in the early 1990s based on the AOT40 metric. Under the O_3 level in 2000, the relative wheat losses estimated with AOT40 were 26.7–27.6%, 4.1–12.1%, 4.1–11%, and 12.3–15.4% in India, North America, Europe, and, World, respectively (Van Dingenen et al. 2009). A comprehensive study considering losses due to increased O_3 levels in the North China Plain revealed that the total wheat production losses for 2014, 2015, 2016, and 2017 accounted for 18.5%, 22.7%, 26.2%, and 30.8%, while economic losses valued at 6.292, 8.524, 10.068, and 12.404 million USD, respectively (Hu et al. 2020). Furthermore, various studies from different research groups have elevated wheat yield loss caused by O_3 stress using the AOT40-related response functions (Mills et al. 2007; Van Dingenen et al. 2009; Avnery et al. 2011; Debaje 2014; Sinha et al. 2015; Tao et al. 2017; Singh et al. 2018; Feng et al. 2019; Hu et al. 2019; Pleijel et al. 2019; Ghosh et al. 2020, 2021; Ren et al. 2020; Zhao et al. 2020). M7 is another model highly used to assess the impacts of O_3 exposure in wheat. Feng et al. (2008) showed that M7 mean values ranged from 31 to 59 ppb and O_3 was responsible for an around 18% reduction in winter wheat yield. Feng and Kobayashi (2009) estimated a 9.7% yield loss for wheat using the M7 model.

Rice, one of the most economically important cereals grown mainly in Asian countries, is known to be less sensitive to O_3 exposure than wheat (Mills et al. 2007). In (semi)urban sites of countries such as China and India, which account for almost 28% and 24% of total rice production in 2019, respectively, high O_3 episodes are becoming an increasing problem limiting production and productivity (Gao et al. 2020). Several studies estimated rice yield and quality losses based on different metrics (Ainsworth 2008; Van Dingenen et al. 2009; Akhtar et al. 2010; Lal et al. 2017; Ren et al. 2020; Zhao et al. 2020). Ozone has been reported to cause a reduction in grain size (Frei et al. 2012), starch content (Sawada et al. 2016), carbohydrate and nitrogen level (Zheng et al. 2013), and an increase in the number of chalky grains (Jing et al. 2016). Annual average losses in Southern China due to O_3 exposure estimated with AOT40 were 6.8% and 10.2% for double-early rice and double-late rice, respectively (Cao et al. 2020). Tropospheric O_3 caused rice yield loss of ~6% for India in the years 2014–2015 (Sharma et al. 2019) and 3.9–15% for China in 2014 (Lin et al. 2018). Decreased dry mass in the whole plant and grain yield per plant due to the O_3 exposure (100 nL L^{-1} during 10:00–17:00) for 4 months was also reported in Bangladesh, which is another Asian country responsible for 7.2% of total rice production (Akhtar et al. 2010).

The effects of O_3 exposure on C4 plants such as maize, sorghum, and pearl millet have been relatively less studied than on C3 plants. Maize is classified as moderately sensitive to O_3 (Mills et al. 2018). Based on the observations from 1980 to 2011, ambient O_3 caused ~10% yield reduction, amounting to ~$9 billion annually in rain-fed fields (McGrath et al. 2015). Peng et al. (2019) applied a flux-based approach, which takes into account several factors affecting stomatal conductance to estimate the influences of O_3 on maize yield and reported that 8.7 ppm h and 1.17 mmol m^{-2} projected leaf area (PLA) are critical levels of POD_6 for a reduction of approximately 5% of maize yield. Exposure to 30 ppb of O_3 caused a reduction in 1000-kernel weight and the content of starch in grains. It was also observed that oil extracted from O_3-treated maize seeds became more unsaturated (Singh et al. 2019). Total maize yield losses due to O_3 concentrations in the North Chain Plain for 2014–2017 accounted for 8.2%, 9.2%, 10.4%, and 13.4%, while economic losses amounted to 2343 million USD, 2672 million USD, 1887 million USD, and 2404 million USD, respectively (Feng et al. 2020).

24.3 Improving Ozone Stress Tolerance Through Biostimulants in Cereals

Plants are exposed to a complex set of abiotic stresses, including O_3, in the natural environment. According to future projections by recent research, O_3 damage caused by the increasingly emerging impacts of climate change is among the main global problems that are expected to affect crop production more severely in the coming years, therefore, many researchers have focused on innovative strategies in an attempt to mitigate the adverse effects of O_3 stress. The use of PBs is a promising strategy to alleviate abiotic stress in plants without any adverse effects on human and environmental health or with fewer adverse effects compared to alternatives (Yakhin et al. 2017; Rouphael and Colla 2018; Drobek et al. 2019; Ricci et al. 2019; Bulgari et al. 2019; Caradonia et al. 2019; Barros-Rodríguez et al. 2020; García-García et al. 2020; Nephali et al. 2020; Zulfiqar et al. 2020; del Buono 2021).

There had been ongoing confusion in defining what the PBs are, and the well-established definition of PBs was recently made by the EU regulation: "A product that stimulates plant nutrition processes independently of the product's nutrient content, with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: (a) nutrient use efficiency; (b) tolerance to abiotic stress; (c) quality traits; or (d) availability of confined nutrients in the soil or rhizosphere" (EU 2019). One of the definitions of PBS proposed in the 2019 USDA Report to Congress on Plant Biostimulants, which is still under draft review, is as follows: "A plant biostimulant is a naturally-occurring substance, its synthetically derived equivalent, or a microbe that is used for the purpose of stimulating natural processes in plants or the soil in order to, among other things: improve nutrient and/or water use efficiency by plants, help plants tolerate abiotic stress, or improve characteristics of the soil as a medium for plant growth" (EPA 2019). A biostimulant, whether it is made up of a single substance or a mixture of substances of biological, chemical, or physical origin, including microorganisms, modifies physiological, biochemical, and molecular processes that improve plant performance and tolerance to stress without providing any nutritional benefit to plants or any toxic effect directly to pathogenic microorganisms or pests. It should be noted that there is still conflict on the definition of PBs globally; therefore, there are difficulties in licensing the products. Different classes of compounds, such as naturally occurring humic substances, chitosan and other polymers, amino acids and other N-containing compounds, seaweed extracts, inorganic compounds, and microorganisms as well, are among the well-known PBs (Bulgari et al. 2019; García-García et al. 2020). Research and development of PBs have become one of the hot topics in agriculture in many parts of the world, and an increasing number of natural compounds and microorganisms have been successfully marketed as PBs. According to the Mordor Intelligence Report, the global PBs market that grew faster than expected was valued at approximately $ 2.6 million in 2020 and is projected to grow at a compound annual growth rate of 11.7% from 2021 to 2026 (Mordor Intelligence 2020).

The first line of defense in the extracellular space against O_3 is considered the production of antioxidant metabolites and enzymes functioning in the detoxification of ROS derived from O_3 (Kangasjärvi et al. 2005; Castagna and Ranieri 2009). Intracellular redox status during O_3 stress is also tightly controlled by antioxidant molecules depending on the capacity of the plant genotype (Luwe et al. 1993). Many studies using forward and reverse genetic approaches in different plant species have shown that the capacity and activity of the antioxidant system in plants determine the level of sensitivity to O_3 (Conklin et al. 1996, 1997; Eltayeb et al. 2007; Di Baccio et al. 2008; Yendrek et al. 2015). Therefore, researchers have attempted to improve antioxidant levels through the exogenous application of natural and synthetic compounds that can act as PBs to improve O_3 tolerance in plants. In this chapter, the compounds demonstrated to improve O_3 tolerance in cereals are categorized into two groups: (a) natural and (b) synthetic compounds.

24.3.1 Natural Compounds

Vitamins are among the natural compounds that are the most commonly used as PBs. Ascorbic acid (AsA, vitamin C) is one of the key nonenzymatic antioxidants of the scavenging system that maintain cellular homeostasis during stress conditions (Xiao et al. 2021). AsA, biosynthesized mainly through the D-mannose/L-galactose pathway, regulates various physiological processes of plants such as cell division and expansion as a cell signaling modulator (Kerk and Feldman 1995), as well as resistance to (a)biotic stress (Xiao et al. 2021). Apoplastic AsA protects cells from O_3-derived damage by reacting with ROS directly or by acting as a substrate in ROS detoxifying enzymatic reactions (Ye et al. 2012) Turcsányi et al. (2000) revealed that 30–40% and ~ 50% of O_3 entering the leaves could be detoxified by apoplastic and cell wall-bound AsA, respectively. Several reports showed a direct relationship between high AsA content and increased tolerance to O_3 in different plants (Mächler et al. 1995; Maddison et al. 2002). Furthermore, it has been pointed out that the tolerance level is not always correlated with Asa content (Loiacono and de Tullio 2012; Bellini and de Tullio 2019). A considerable number of studies have been done to explore the effects of exogenous AsA in alleviating O_3 stress (Freebairn 1957; Menser 1964; Siegel 1962; Yoshida et al. 1994; Wenzel et al. 1995; Mächler et al. 1995; Zheng et al. 2000; Agrawal et al. 2004; Daripa et al. 2016; Kobayakawa and Imai 2017). L-Ascorbic acid at a final concentration of 5 mM alleviated lipid peroxidation in rice protoplasts during O_3 treatment (Yoshida et al. 1994). Mächler et al. (1995) showed that treatment with AsA of barley plants fumigated with 0.8 μl L^{-1} O_3 for 4 h was effective in increasing the tolerance to O_3, by protecting the plasma membrane permeability. The regulation of Rubisco activity was also suggested to be involved in this protection. AsA application at 0.5 and 10 mM concentrations (for 5 days) to the roots 5 h before O_3 treatment protected the rice plants from O_3 injury (Kobayakawa and Imai 2017). The authors also found that treatment increased the endogenous AsA content and the redox state level of the rice leaves. Foliar application of 1% AsA to wheat plants improved the level of tolerance to O_3 and it was suggested that the protective role of AsA is due to an increase in the amount of endogenous AsA (Daripa et al. 2016). Furthermore, the application of AsA under O_3 stress in field conditions increased the yield by 23–26% and improved the Cu, Fe, Zn, and Mn content of the grains.

Chitosan, a natural linear polymer, has been widely shown to act as a powerful PB to alleviate biotic and abiotic stress in plants (Malerba and Cerana 2018, 2020; Shahrajabian et al. 2021). It also exerts antimicrobial activity on diverse groups of plant pathogens such as fungi and oomycetes (Torres-Rodriguez et al. 2021). Chitosan has attracted increasing attention as a potential alternative to synthetic chemicals in crop production due to its special properties, including biodegradability, simple producibility, nontoxicity, and availability (Rinaudo 2006). Chitosan as a

PB has been reported to increase the tolerance to O_3 in rice (Phothi and Theerakarunwong 2017) and wheat (Picchi et al. 2021). Phothi and Theerakarunwong (2017) conducted a field experiment to test the effects of chitosan on alleviating O_3 toxicity in rice. It has been reported that chitosan applied as a spray or leaf dip (0.05% w/v) reduces the negative effects of O_3 damage in plants exposed to ozone concentrations of 40 and 70 ppb for 21 days. In recent years, chitosan nanoparticles are increasingly becoming an important tool to deliver agrochemicals and boost innate immunity in plants against (a)biotic stress factors (Chandra et al. 2015; Bandara et al. 2020; Maluin and Hussein 2020). Recently, it was demonstrated that unloaded or loaded chitosan nanoparticles with N-acetyl cysteine, a well-known antioxidant compound, act as effective PBs in improving O_3 tolerance in wheat plants; this effect is believed to be achieved by enhancing the content of ascorbic acid (Picchi et al. 2021). The authors also showed that both treatments induced a significant increase in the 1000 grain weight, which is an indicator of a positive impact on grain quality.

Catechin, a natural polyphenolic compound that belongs to the flavonoid family, is found in many plant species and is known to have beneficial effects in mitigating oxidative stress by directly stabilizing free radicals and indirectly inducing antioxidant enzymes (Bernatoniene and Kopustinskiene 2018). The antioxidant potential and role of catechin in stress response in plants have been investigated for different types of abiotic stress including O_3 (Kittipornkul et al. 2020; Pheomphun et al. 2019). Salicylic acid (SA) and its derivatives, also well-known phenolic compounds, have been recognized as one of the key regulators of plant defense responses to biotic and environmental stress factors. SA and other phenolic compounds such as catechin are often considered natural PBs (Drobek et al. 2019). Treating rice plants at the vegetative stage with 5 mM of catechin before exposure to O_3 in the range of 100–150 ppb increased the stress tolerance by maintaining the chlorophyll contents and stomatal conductance (Kittipornkul et al. 2020). Up-regulation of genes encoding ascorbate peroxidase and catalase and reduction of the MDA level in catechin-treated plants led the authors to suggest that antioxidant enzymes are involved in alleviating O_3 stress by scavenging ROS causing peroxidation of lipids. It was also reported that SA at 100 μM concentration does not exhibit protective activity against O_3 in rice.

Plant-derived extracts as PBs to overcome abiotic stress factors and improve plant growth have gained considerable interest in recent years to ensure sustainable plant production (Abdel Latef et al. 2017, 2019, 2021; Elzaawely et al. 2017; Hayat et al. 2018; Rouphael et al. 2018; Rady et al. 2019; Zulfiqar et al. 2020; Osman et al. 2021). Phytohormones, secondary metabolites, and other compounds such as antioxidants in the PBs could be involved in increasing the tolerance to several abiotic stress factors by functioning either as a regulator of growth or an inducer of plant defense (Zulfiqar et al. 2020). Although plant-derived biostimulants are effective in decreasing the negative consequences of several abiotic stress conditions, there are only a few studies that have investigated the use of PBs to improve tolerance to O_3. The application of water extracts obtained from the leaves of several plant species such as *Ocimum basilicum*, *Tagetes patula*, and *Salvia sclarea* that are known to contain a high level of secondary metabolites and antioxidants were shown to be effective in protecting plants against O_3, and this effect was less stable and weaker than synthetic antioxidants such as EDU and Topaz in protecting plants against O_3 (Blum and Didyk 2007). Microbial-derived PBs mainly developed with arbuscular fungi, mycorrhizal fungi, and beneficial bacteria that modify plant productivity and resistance to a wide range of abiotic stress conditions. However, to the best of my knowledge, there is no study reporting that microbial-derived PBs improve O_3 tolerance in plants so far.

24.3.2 Synthetic Compounds

Studies showing synthetic molecules can be used to increase O_3 tolerance in plants are very limited. Tomlinson and Rich (1973) reported for the first time that phenylurea applied as a foliar spray protected bean leaves against O_3 injury. The phenylurea-based synthetic antiozonant, ethylenediurea (N-[2-(2-oxo-1-imidazolidinyl) ethyl]-N′-phenyl-urea) (EDU), was first identified by Carnahan et al. (1978) at Du Pont de Nemours and Company in Wilmington, Delaware. The exogenous application of EDU has been shown to improve plant tolerance to O_3 stress in various crops, including cereals. EDU is not included in the PBs list based on the EU regulation (2019/1009), and no product containing EDU as an active compound is available in the current PBs market. However, based on the research with solid experimental designs demonstrating that EDU covers one of the four characteristics of PBs defined by EU regulation, which is abiotic stress tolerance, it is possible to claim that EDU acts as a PBs. EDU is effective in protecting plants from O_3 injury whether applied by foliar spray (Manning et al. 2011; Paoletti et al. 2014), soil drench (Agathokleous et al. 2016; Pasqualini et al. 2016), or stem injection (Ainsworth et al. 1996; Paoletti et al. 2007). EDU has also been widely used as a tool for assessing the responses of plants, cultivars, and genotypes to O_3 damage in chamber and field studies (Tiwari et al. 2005; Wang et al. 2007; Singh et al. 2009; Manning et al. 2011; Tiwari 2017; Ashrafuzzaman et al. 2017; Feng et al. 2018).

The positive effects of EDU on wheat under different levels of O_3 stress have been documented (Agrawal et al. 2004; Tiwari et al. 2005; Wang et al. 2007; Singh et al. 2009; Singh and Agrawal 2010; Fatima et al. 2019; Gupta et al. 2021). Tiwari et al. (2005) demonstrated that wheat plants treated with different concentrations of EDU (150, 300, 450 ppm) as a soil drench at 10-day intervals yielded more grain than non-treated plants under O_3 concentrations frequently exceeding 40 ppb during the experimental period at a suburban site of India, Varanasi. At the same site in India, wheat cultivars treated with EDU showing different levels of susceptibility to O_3 exhibited enhanced growth (plant total biomass and number of tillers) under O_3 stress conditions (AOT40: ~9.17 ppm during the experimental period) (Fatima et al. 2019). Similarly, it was demonstrated that 400 ppm of EDU application as a soil drench at 12-day intervals restored the loss of wheat grain yield driven by O_3 concentrations varied between 34.2 and 54.2 ppb during the production (Singh et al. 2009). Another study on the impact of the application of foliar EDU on the tolerance capacity of wheat subjected to high ambient O_3 stress (average O_3 concentration of 60 ppb) (Gupta et al. 2021). EDU treatment alleviated the destructive effects of high O_3 stress and increased the number of spikelets and 1000 grain weight. Mitigating the O_3 stress through EDU may show variation among the cultivars because of the various physiological or genetic factors involved in EDU uptake and processing (Feng et al. 2018).

Some studies demonstrate that EDU is a useful molecule to improve O_3 tolerance in rice (Pandey et al. 2015; Ashrafuzzaman et al. 2017, 2018) and maize (Gupta et al. 2020). The foliar application of EDU at a concentration of 300 ppm in weekly intervals significantly mitigated the formation of O_3-induced symptoms and lipid peroxidation in O_3-sensitive rice cultivars (Ashrafuzzaman et al. 2017). Sensitive rice genotypes exhibited fewer symptoms of O_3 damage when treated with 300 ppm of EDU once a week while under the stress of ~110 ppb of O_3 for 8 days (Ashrafuzzaman et al. 2018). Contrary to these findings, Wang et al. (2007) observed no significant effect on O_3 tolerance regarding the foliar application of EDU in rice, and they have suggested that this may be due to the fact that rice is a more tolerant species to O_3.

The mode of action of EDU in alleviating O_3 toxicity remains relatively unknown, although decades have passed since the first evidence of antiozonant properties of EDU was produced by Carnahan et al. (1978). The view that the mechanism behind the EDU-mediated tolerance to O_3 in plants is based on the enhanced activity of the enzymes involved in the scavenging of ROS is still widely accepted among plant scientists (Gupta et al. 2021). When applied to the soil, EDU is taken up by the roots through the symplastic pathway and then transported to the leaves via the xylem. In the case of foliar application, it enters the leaves through the stomata and reaches the apoplast where the O_3-induced ROS are primarily formed. Some views support the theory that EDU-triggered hormesis can explain the mode of action of EDU (Agathokleous and Kitao 2018). Although its success in increasing tolerance to O_3 in different plant species has been demonstrated with many micro- and macroscale studies, it is not used in practice due to reasons such as the effects on human and environmental health are not known enough and the production costs are high due to the complexity of the molecule (Saitanis and Agathokleus 2020).

24.4 Conclusions and Future Prospects

Chronic and acute ozone stress affects plant physiology and biochemistry during crop production resulting in serious yield losses and reduced quality. Cereals are one of the most important groups of crops worldwide in terms of feeding the increasing population and providing feedstock for industry. Some members of cereals such as wheat and rice are known to be sensitive or moderate sensitive to O_3 stress. The use of PBs to control (a)biotic stress and improve nutrient use efficiency has drawn great interest in recent years, and many natural compounds have already been commercialized as PBs so far.

In this chapter, I intended to paint an overall picture of the attempts in the literature on the use of PBs to improve O_3 tolerance in cereals. I also addressed the possible mechanisms by which these compounds contribute to the protection of the plants. The number of studies showing that PBs or compounds that act as PBs can be used to improve O_3 tolerance in plants is relatively lower than those that are used for disease control or growth promotion. Based on the review of the literature, AsA and EDU are the most studied and the most effective compounds to mitigate the negative effects of O_3 in cereals. It is possible to conclude that the mechanism of reaction behind the control activity of AsA and EDU proceeds through the enhanced amount and/or activity of endogenous antioxidant enzymes and their level of redox state, which leads to the homeostasis of O_3-derived ROS. It should be noted that PBs mentioned are currently not applied in practice in fields to cope with O_3 stress; thus, there is a great knowledge gap in the real evaluation of their efficacy and the environmental risks of these compounds.

Observations and research based on the models have demonstrated that the tropospheric O_3-driven damages in cereals are expected to increase in fields where O_3 precursors and frequent heat waves have been increased. Managing O_3 stress with agricultural practices has therefore been required to ensure the sustainability of future cereal production. To implement the use of PBs in improving the O_3 tolerance in practice, there is an immense need to screen different compounds showing the properties of PBs and more basic and practical studies on how PBs can be applied in crop production. The use of natural compounds that biostimulate plants to improve O_3 tolerance in crop production may offer advantages, e.g., nontoxicity and biodegradability.

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Part V

Application of Gene Editing Approaches and Nanotechnology for Induction of Abiotic Stress Tolerance

Genome Editing and miRNA-Based Approaches in Cereals under Abiotic Stress

25

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Abstract

The unpredictable climate change and alarming rise in the world's population warrant technological advancements in crop breeding to achieve a sustainable increase in crop productivity. Several efforts have been conducted in recent decades to improve cereal crops using classical or molecular breeding methodologies. The changing environment warrants a better understanding of molecular biology by focusing on certain genes to produce desirable plants. The creation of high-yielding stress-tolerant crops is required to ensure food security for the world's growing population, particularly under susceptible climatic conditions. The readily available genome sequence information of major cereal crops enables the development of genomics-assisted breeding approaches aimed at assembling trait-specific genes using innovative mating designs. In recent times, CRISPR/Cas9 is being considered a technology that revolutionized fundamental as well as applied research in plant breeding. Using CRISPR/Cas9-mediated targeted mutagenesis, further developments in genome engineering permitted quicker phenotypic improvement. One of the possible uses of genome

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engineering is the creation and selection of superior alleles using genome editing techniques. Traditional CRISPR/Cas9 advancements such as identifying and modifying Cas9 variants, base editing, and multiplex editing would pave way for precision genome engineering. Progressive research in this direction may result in the production of enhanced crop varieties that can withstand multiple abiotic stresses. The applications of CRISPR/Cas9 technology for abiotic stress tolerance in cereal crops are discussed in this chapter.

Keywords

Genome editing · CRISPR/Cas 9 · Abiotic stress tolerance · Cereals

25.1 Introduction

The global population is predicted to reach more than 10 billion by 2050, necessitating a 70% increase in food supply/production (Tilman et al. 2011). To attain this goal, crop breeding techniques must be innovated in order to produce sustainable growth in agricultural productivity. The current rate of increase in production in major crops will not satisfy the expected demand (Ray et al. 2013). Furthermore, climatic changes or global warming events, such as drought, salinity, submergence, temperature extremes, and other natural disasters, increase the frequency of recurrence posing a new threat to agriculture (Wani et al. 2021). Crop response to adverse effects of abiotic stresses is mainly dependent on tissue, organ, genotype, ploidy levels, and crop type (Cramer et al. 2011). Abiotic stresses lead to the overproduction of reactive oxygen species (ROS) (Ramadoss et al. 2021), which is a signaling molecule, depending on its concentration, can be toxic to plants, causing damage to cell membranes, protein structure, lipids, carbohydrates, and DNA, damage that ultimately inhibits physiological and metabolic processes in crop plants (Le Gall et al. 2015; Gangola and Ramadoss 2018). To adjust to unfavorable abiotic stress conditions, plants tend to activate their physiological and molecular response systems which include stress-resistant genes (Hu et al. 2018; Duan and Cai 2012), transcription factors (Guo et al. 2016; Ramadoss et al. 2020; Gangola and Ramadoss 2020), secondary metabolites (Selmar and Kleinwachter 2013), antioxidant enzymes (Pandey et al. 2017), and phytohormones (Sah et al. 2016) for better growth and survival.

Hybridization and mutation breeding are the two approaches that come to mind while discussing breeding tools for crop improvement in modern agriculture. It takes several years to introduce desirable alleles and to increase the number of desirable alleles through conventional breeding approaches. The current availability of genome editing tools has avoided the limitations of conventional genetically modified or traditional breeding methods and is developing a new age of crop improvement in the field of abiotic stress-tolerant crops (Waltz 2018; Mishra et al. 2018). In recent times, genome editing has become an alternative to improve crop plants through plant breeding and maintain sustainable food production (Belhaj et al.

2013). Modification of the target region in plant genome using genome editing technology has advantages over the traditional method of genetic modification, generally done by random insertion events, which most of the time affects the expression level of the transgene (Forsyth et al. 2016). Genome editing is preferably alteration of the target genome to illuminate and control gene functions in plant research (Li et al. 2014). In genome editing technology, the genome of an organism itself is modified by knocking out or replacing the targeted gene for desired and selected traits, whereas in transgenic approaches biologically nonexistent foreign genes are introduced to the original genome to develop new characters in the existing species (Mushtaq et al. 2018). To date, several genome editing techniques like zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9 (CRISPR/Cas9) systems have been implemented in plant molecular biology. Compared with ZFNs and TALENs, CRISPR/Cas9 has more advantages including higher targeting efficiency, multiplex genome editing, and simpler to design and implement and less expensive. CRISPR/Cas9-based genome editing can be used for plant functional studies and plant improvement for tolerance to environmental stress, which overcomes the problems of time consumption, the requirement of a large area for growing encountered by traditional breeding techniques (Demirci et al. 2018).

25.2 Genome Editing

Crop production must be improved to fulfill the demands of a growing population as well as adverse climatic circumstances. As a result, we want a targeted, quick, and low-cost strategy for increasing agricultural output and developing multi-stress-resistant crop varieties (Xu et al. 2014). Genome editing has recently emerged as a viable option for improving plant breeding, agricultural plants, and cost-effective food production (Belhaj et al. 2013). In plant research, genome editing is described as the change of the target genome to illuminate and control gene processes. The use of genome editing technology to modify the target region of the genome has potential advantages over the traditional approach of genetic alteration, which is usually done by random insertion events and frequently impacts the transgene's expression level (Forsyth et al. 2016).

The genome of an organism is modified by knocking out or replacing the targeted gene for desired and selected traits in genome editing technology, whereas, in transgenic approaches, biologically nonexistent foreign genes are introduced to the original genome to develop new characters in existing species (Mushtaq et al. 2018). Unlike the transgenic approach, which results in random insertions and, in many cases, unpredictable phenotypes, genome editing approaches yield specified mutants, making them a powerful tool in functional genomics and crop breeding. Genome-edited crops have an advantage over transgenic plants in that they "carry" the desired trait's modified DNA (Malzahn et al. 2017). In plant molecular biology, various genome editing approaches have been used to date. Researchers have been able to build DNA sequence-specific target areas of genes using these strategies. To change the targeted plant genome, researchers used zinc finger nucleases (ZFN), transcription activator-like nuclease (TALEN), and clustered regularly interspaced short palindromic repeats (CRISPR)/Cas9 (Yin et al. 2017). These genome editing technologies typically cause double-strand breaks (DSB) or single-strand breaks (SSB), which result in mutation of the target genome regions. Nonhomologous end-joining (NHEJ) or homologous recombination (HR) methods are then used to repair the broken ends. Thus, by using a gene knockout, knockin, or replacement strategy, site-directed mutagenesis-based genome editing is induced at the target regions of the genome, resulting in changes to several morphological, physiological, and enhancement tolerance/resistance characters, as well as crop plant growth and development (Wood et al. 2011). Modification of plant genetic information in an accurate and particular manner would not only aid in the research of gene function and biological systems but will also aid in the creation of numerous novel phenotypes such as higher yield and stress-tolerant crops. When compared to conventional genetically modified (GM) crops, such improved crops can be employed in breeding programs, and the resulting varieties can be used immediately with less acceptability/consumption concerns and fewer regulatory procedures (Waltz 2018). In this sense, genome editing technology has emerged as a cutting-edge method for improving agricultural yield under abiotic stress (Osakabe and Osakabe 2017).

25.2.1 Engineered Nucleases

Genome editing using engineered nucleases (“GEEN”) is a powerful genetic engineering technique that employs “molecular scissors” or chemically created nucleases, to target and degrade DNA at particular sites throughout the genome. The designed nucleases cause a double-stranded DNA break (DSB) at the target spot, which is subsequently repaired naturally through the processes of homologous recombination (HR) or NHEJ (Osakabe and Osakabe 2015). A sequence-specific DNA binding domain is fused to a nonspecific nuclease domain in engineered nucleases. The targeted gene can be accurately cleaved by such fused nucleases, and the breaks can be repaired using NHEJ or HR, thus the phrase “genome editing.” First-generation genome editing tools are engineered nucleases including meganucleases, ZFNs, and TALENs which require labor-intensive and time-consuming processes to attain target specificity. On the other hand, second-generation genome editing techniques like CRISPR/Cas9 use simpler design and execution processes that are robust and cost-effective.

25.2.1.1 Meganucleases

Meganucleases (MgNs), also referred to as homing endonucleases, are extremely active enzymes found in a variety of microorganisms. They have lengthy recognition sequences ranging from 12 to 40 base pairs. I-SceI and I-CreI are the most often employed MgNs for genome editing (Weeks et al. 2016). Despite their high activity and specificity, MgNs are limited in their application due to the difficulties in tailoring their DNA binding domains for any desired target DNA besides their natural DNA binding sites (Surabhi et al. 2019).

25.2.1.2 Zinc Finger Nuclease

In general, zinc finger nuclease (ZFN) is employed to break a target DNA site, which is then exploited in error-prone NHEJ, resulting in mutagenesis of the specified site. Endogenous genes in a variety of cell types and organisms have been modified using ZFNs. ZFNs may introduce several types of genomic modifications such as deletions, insertions, mutations, duplications, inversions, and translocations, providing researchers with great instruments to execute genetic manipulations. Fusion of ZFNs consisting of zinc finger protein domains capable of sequence-specific DNA binding and a nuclease domain is commonly employed for protein domain identification, with each domain recognizing around 3 bp of DNA (Carroll 2011). Modular design, assembly, and development of zinc fingers targeting specific DNA sequences, followed by linking of single ZFs in the direction of targeting bigger sequences, are all part of the design and implementation of ZFNs. Zinc finger domains have been developed in recent years to recognize a large number of triplet nucleotides, allowing the selection and assembly of zinc fingers into a sequence that would allow recognition of the target sequence of interest (Kamburova et al. 2017). There are a number of internet applications that may be used to design the ZF array for a certain gene. This genome editing method is highly specific yet technically difficult to build, and its manipulation is limited to a small number of target sequences (Roy et al. 2021). ZFN has been successfully implemented in tobacco, *Arabidopsis*, soybean, and maize (Zhang and Voytas 2011; Shukla et al. 2009; Townsend et al. 2009; Curtin et al. 2013). However, the ZFN-based method has a number of drawbacks, including the difficulty and high cost of creating protein domains for each genomic region, as well as the risk of improper cleavage of target DNA due to single nucleotide changes or inappropriate interaction between domains (Nemudryi et al. 2014).

25.2.1.3 Transcription Activator-Like Effector Nucleases (TALENs)

The invention of TALENs was inspired by the research of microorganisms belonging to the genus *Xanthomonas*. These bacteria are pathogens that infect crop plants including rice, pepper, and tomato, inflicting significant economic loss in agriculture, prompting more research. These bacteria produce effector proteins (transcription activator-like effectors, TALEs) into the cytoplasm of plant cells, which change processes in the cell and make it more vulnerable to pathogens (Nemudryi et al. 2014). The DNA binding domain of TALENs is taken from bacterial TALE, and the DNA cleavage domain is derived from the FokI restriction enzyme (Christian et al. 2010). The type III secretion system secretes TALEs from the *Xanthomonas oryzae* bacterium into the host plant cells. TALEs attach to a specific sequence in the promoter of target plant genes and trigger transcription when they enter the host cells. TALENs take use of their ability to attach to a specific DNA sequence. TALENs, like ZFNs, have numerous TALE repeats as DNA binding domains.

TALENs are dimeric proteins. One TALEN monomer attaches to one strand of target DNA, while the other binds to the opposite strand. Between the two TALEN monomers, there is a spacer DNA that is roughly 20 base pairs long. The FokI cleavage domain attaches to the spacer DNA and causes a double-strand break (DSB). Except for two amino acids at positions 12 and 13, each TALE is made up of 13–28 repeats of 34 conserved amino acids (Deng et al. 2014). The binding specificity is determined by these two hypervariable amino acids, which recognize one nucleotide of the target DNA. NG, NI, HD, and NN are hypervariable amino acid pairs that recognize thymine, adenine, cytosine, and guanine/adenine, respectively, and changes in these amino acids can result in favored target binding for a site-specific DSB (Scholze and Boch 2010). By transcriptionally activating the particular rice disease susceptibility (S) gene, *Xanthomonas oryzae* TAL (transcription Activator-like) effectors serve to lessen the severity of the bacteria *Xanthomonas*. To combat the virulence strategy of the bacteria *Xanthomonas*, TALEN technology was used to alter the particular S gene in rice. This genetically modified genome confers resistance to bacterial blight, a devastating crop disease (Chu et al. 2006). TALEN had shown much interest with researchers than ZFN as they are rapid and easy to design. Both TALEN and ZFN require time for protein designing, synthesis and validation which made CRISPR/Cas9 system a better option than these tools due to its simplicity, efficiency, and design flexibility (Barrangou and Doudna 2016).

25.2.1.4 Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR/Cas9)

The CRISPR/Cas9 gene editing system was initially discovered in mammalian cells in 2012, and its utility in genome editing has transformed studies in animal and plant biology (Jinek et al. 2012). Unlike ZFNs and TALENs, CRISPR genome editing is simpler, requiring the creation of a guide RNA (gRNA) of around 20 nucleotides that is complementary to the target gene's DNA stretch. CRISPR stands for tandem repeats flanked by non-repetitive DNA stretches (Jansen et al. 2002), which were discovered in downstream of *Escherichia coli* IAP genes for the first time (Ishino et al. 1987). Foreign DNA sequences originating from plasmids and phages were shown to be homologous with these non-repetitive sequences in 2005. Following that, the mechanism of homology-dependent cleavage was investigated for genome editing, and CRISPR/Cas9 cleavage was "discovered" as a promising genome editing tool (Liu et al. 2017).

CRISPR activity is usually controlled by a collection of Cas genes present near the CRISPR. Proteins required for the immunological response are coded for by the Cas genes. There are three steps to the CRISPR-Cas-mediated defense mechanism. Adaptation is the initial stage, which involves inserting new spacers into the CRISPR locus. The system is then primed for action by expressing the cas genes and transcribing the CRISPR into a lengthy precursor CRISPR RNA, which is known as expression (pre-crRNA). After that, Cas proteins and ancillary factors arrange the precrRNA into mature crRNA. The target nucleic acid is detected and removed in the third step of CRISPR-mediated action, known as interference, by the interactions of crRNA and Cas proteins (Asmamaw and Zawdie 2021).

The creation of large off-target cleavage levels as a result of complexing of the gRNA with mismatch complementary target DNA within the genome is one of the key drawbacks of the CRISPR/Cas9 system, which was first developed from *Streptococcus pyogenes* (Rath et al. 2015). Approaches such as utilizing Cas9 nickase, Cas9n, and dCas9 (mutated version of Cas9), gRNAs truncated at the 5′-ends (trugRNAs) and careful design have been used to induce site-directed alterations in plants to improve specificity and limit off-target impacts of the CRISPR-Cas system (Mushtaq et al. 2018).

The use of genome editing technology, which offers a proficient technique to plant domestication and thus boosting agricultural production by elevating the diversity of crop species, has been expanding day by day. As a result, new domesticated crops featuring enhanced tolerance levels will emerge in the near future, which will aid in the resolution of agriculture-related issues such as feeding the world's growing population and promoting agricultural diversity (Rao and Wang 2021). Plant synthetic biology (plant editing reagents introduced in plant genome to change desired trait or change plant and cell behavior by synthetic DNA sequences, which include promoters, gene, transcriptional regulatory elements, and genome assemblies) is being pushed forward by the CRISPR/Cas9 system, which has the potential to improve plant biology and engineering. Plant synthetic biology also aims to build regulatory pathways that can control diverse plant features and develop novel functions that can ultimately improve crop yield.

The CRISPR/Cas system's precision, adaptability, robustness, accuracy, and simplicity have accelerated the field of genome editing, making it one of the most prevailing and powerful platforms for defined improvement in crops through point mutations, knockouts, substitutions, and other pertaining variations at any desired gene locus. CRISPR/Cas has been effectively employed for abiotic and biotic stress tolerance in various cereals (such as wheat, maize, rice, and others), as well as for high-throughput mutant library development for antiviral breeding. However, effectively transmitting technologies necessitates the rapid discovery of economically relevant features at the genome level, to increase the efficacy of the desired gene through replacement or insertion. It is critical to concentrate on CRISPR/Cas delivering materials that work successfully inside plant cells, as well as the accessibility of base editors with better frequency and targeting range, as well as the ability to regenerate plants using tissue culture or without it.

25.3 CRISPR for Crop Improvement

Sustainable food supply can be achieved by continuous innovation in crop breeding and genetics and recent developments in genome-editing technologies, particularly the CRISPR-Cas system, have made targeted and precise genetic manipulation of crops increasingly viable, hastening the move to precision breeding for crop enhancement. The availability of whole-genome sequencing data for a variety of

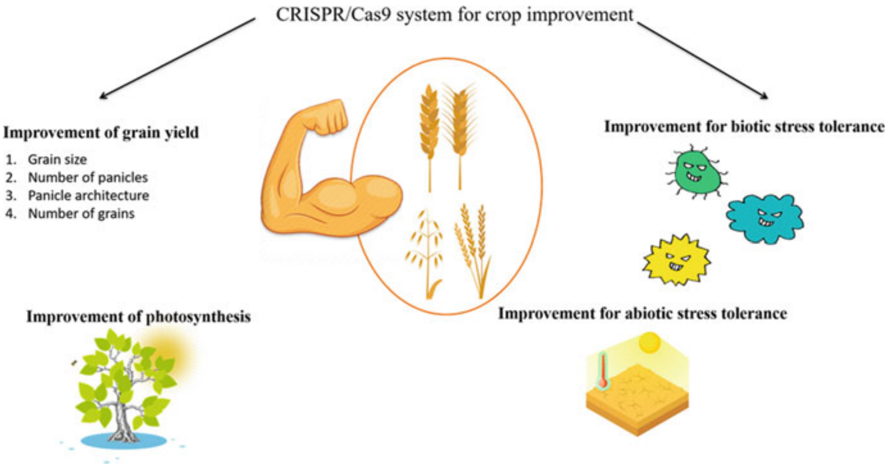

Fig. 25.1 Potential applications of CRISPR/Cas 9 technology for cereal crop improvement

crops, combined with advances in genome-editing tools, opens up a slew of possibilities for achieving desirable features. For high-yielding, climate-resilient, high-quality, and environmentally friendly agriculture, genome editing is essential. Many cereal crops, including rice, wheat, maize, and barley, have been successfully edited using the CRISPR/Cas9 system (Fig. 25.1). So far, the CRISPR/Cas9 gene-editing technology has been used in over 20 crop species for a variety of features such as yield improvement as well as biotic and abiotic stress management (Ricroch et al. 2017).

25.3.1 Improvement of Grain Yield

Rice grain size was improved by CRISPR-based editing of OsGS3 and OsGL3.1, which boosted the 1000-grain weight and overall yield per plant. In comparison to wild type, multiplex gene editing of GS3, GW2, and Gn1a boosted grain production in edited plants. Another study used CRISPR-Cas9 to knock out GS3, OsMYB30 (which regulates drought tolerance in rice) and OsPIN5b (which controls panicle length) all at the same time, resulting in high-yielding drought-resistant rice lines (Lacchini et al. 2020). By knocking out specific undesired genes or their transcription factor regulators, CRISPR-Cas has been utilized to enhance plant architecture. SLR1, which codes for the DELLA protein, has been edited to produce short-stature rice plants. Similarly, CRISPR/Cas9-based targeted disruption of carotenoid cleavage dioxygenase 7 (CCD7) resulted in a dramatic increase in tillering, as well as a reduction in height, which was restored by the synthetic strigolactone (SL) equivalent GR24 (Lu and Zhu 2017; Butt et al. 2018).

25.3.2 Improvement of Photosynthesis

Rubisco, a major CO2-fixing enzyme regulating the rate of photosynthesis in plants, is one of the key targets for improving photosynthesis. Under the current environmental conditions, however, the activity of Rubisco is limited due to its low catalytic rate (kcat), a poor affinity for CO_2 (Kc), and selectivity for CO_2 (Sc/o). It is made up of large (52 kDa) and tiny (14–15 kDa) subunits which are encoded by a single gene in the chloroplast genome (RbcL) and a multigene family in the nucleus (RbcS). Rubisco has a higher kcat in C4 plants than in C3 plants in general. Researchers recently used the CRISPR-Cas system to disrupt the RbcS multigene family in rice (a C3 plant) and replace its RbcS machinery with RbcS from the C4 sorghum. The rice plants that resulted had a photosynthetic rate that was comparable to that of C4 plants, as well as higher crop output. Homozygous mutant plants had higher kcat, Kc, and Sc/o than heterozygous mutant plants (Matsumura et al. 2020).

25.3.3 Improvement for Biotic Stress Tolerance

Introducing dominant resistance genes (R) into crops by breeding or transgenic technology is one of the most important crop protection strategies; nevertheless, R genes are usually pathogen-specific and nonessential avirulence genes. As a result, R-gene methods tend to encourage resistance development in the target pathogen but may not necessarily impart long-lasting, broad-spectrum resistance. Utilizing CRISPR-Cas to target susceptibility genes (Su) in a plant genome is an alternate technique. These genes are responsible for the pathogen's ability to support infection. Researchers use targeted mutagenesis to knock off Su genes, reducing disease vulnerability (Ahmad et al. 2020). Su genes in plants have also been altered to defend them from viral infections. A translation initiation factor 4 gamma gene (eIF4G) controls resistance to rice tungro disease caused by the Rice tungro spherical virus. CRISPR-Cas disruption of eIF4G resulted in rice tungro disease-resistant rice lines which are transgene-free (Macovei et al. 2018). In polyploid crops like wheat, knocking off Su loci becomes more difficult; however, CRISPR-Cas can be used to concurrently target numerous homologues. Wheat resilience to several diseases has been boosted by utilizing CRISPR/Cas to knock off Su genes. Wheat resistant to powdery mildew was created by targeting all three homologues of MLO at the same time (Wang et al. 2014).

Developing biotic stress tolerance has a lot of potential for improving disease resistance and lowering crop losses. CRISPR/Cas, for example, would give versatile and long-lasting resistance by directly targeting viral genomes. Strategies that target Su genes, on the other hand, necessitate the time-consuming discovery of Su genes for each individual crop-pathogen interaction; developments in genomics techniques may speed up this process. Furthermore, more studies will be required to restrict growth-defense trade-offs for disease resistance that is developed.

25.3.4 Improvement for Abiotic Stress Tolerance

In addition to biotic challenges, plants are subjected to a variety of abiotic stresses, such as temperature, salt, drought, and heat/cold stress all of which halt crop growth and result in considerable, if not disastrous, yield losses around the world. Sensitivity genes are plant genes that exacerbate the negative impacts of abiotic stressors (Se genes).

Tomato susceptibility to heat stress is increased by CRISPR editing of orthologues mitogen-activated protein kinase 3 (SlMAPK3) and agamous-like 6 (SlAGL6), whereas sensitivity to salinity shocks is increased by ADP-ribosylation factor 4 (SlARF4). These CRISPR-edited mutant plants displayed improved agronomic features and resilience to abiotic stressors (Bouzroud et al. 2020). Acetolactate synthase 1 (*ZmALS1*) and *ZmALS2* were edited using CRISPR/Cas9 base and prime editing systems, which increased herbicide tolerance in maize (Nuccio et al. 2021). The fusion of Cas9 endonuclease and VirD2 enhances the cleavage of the *OsALS* gene in rice, and simultaneous HDR-mediated repair of the *OsALS* gene resulted in herbicide resistance (Ali et al. 2020). Similarly, employing primary editing technology, precise nicking of the *OsALS* gene and HDR-mediated repair boosted herbicide resistance in rice (Butt et al. 2020). A list of genes responsible for abiotic stress tolerance using genome editing approaches has been listed in Table 25.1.

25.3.4.1 Drought Tolerance

During the past decade, many studies on CRISPR/Cas 9 for abiotic stress has been published, among which drought has been widely studied. The mechanism involves knock out of genes such as signaling pathway (ABA and ethylene responsive genes), genes for leaf rolling, stomatal responsive genes, and drought tolerance genes. These genes showed tolerance to drought by ROS activity, leaf rolling, hormonal signaling, and leaf rolling. Mutant alleles are created in several family genes such as *AREB*, *MAPK*, *SAPK*, *SRL*, *NPR*, and *SRL* genes. They were found to show promising results to drought responses in crops (Joshi et al. 2020).

Mutant alleles with knock off *OsSAPK2* rice gene showed high tolerance to drought by promoting ROS scavenging activity (Lou et al. 2017). Similarly, rice having mutant alleles of *SRL1* and *SRL2* showed semi-rolled leaf and good agronomic performance such as panicle number, length, and yield under drought (Liao et al. 2019). During germination and post-germination phases, *OsSAPK2* mutants revealed an ABA-insensitive phenotype. Drought stress and reactive oxygen species (ROS) were more severe in this mutant than in wild-type plants, suggesting that *OsSAPK2* is required for drought responses in rice (Lou et al. 2017). CRISPR/Cas9-mediated genome editing resulted in a homozygous 5 bp deletion in OsmiR5350s coding sequence, indicating that OsmiR535 might be a viable genetic editing target for drought and salinity tolerance (Yue et al. 2020). Using the CRISPR-Cas9 technology, the drought and salt tolerance (*DST*) gene in *indica* rice *cv.* MTU1010 was modified.

Table 25.1 List of genes targeted through genome editing for abiotic stress tolerance

S. No.	Crop	Target gene	Tool/system used	Transformation method	Trait	Reference
1	Rice	*OSPDS*, *OsMPK2*, *OsBADH2*	CRISPR/Cas9	Protoplast	Abiotic stress tolerance	Shan et al. (2013)
2	Rice	*OsMPK5*	CRISPR/Cas9	Protoplast	Abiotic stress tolerance	Xie and Yang (2013)
3	Rice	*OsDERF1*	CRISPR/Cas9	*Agrobacterium*	Drought tolerance	Zhang et al. (2014)
4	Rice	*OsPMS3*	CRISPR/Cas9	*Agrobacterium*	Photoperiod-sensitive male sterile	Zhang et al. (2014)
5	Rice	*BEL*	CRISPR/Cas9	*Agrobacterium*	Herbicide resistance	Xu et al. (2014)
6	Rice	*OsAOX1a*, *OsAOX1b*, *OsAOX1c*, *OsBEL*	CRISPR/Cas9	*Agrobacterium*	Abiotic stress tolerance	Xu et al. (2015)
7	Rice	*RAV2*	CRISPR/Cas9	*Agrobacterium*	Salinity stress	Duan et al. (2016)
8	Rice	*Csa*	CRISPR/Cas9	*Agrobacterium*	Photosensitive genic male-sterile	Li et al. (2016a, b)
9	Rice	*EPSPS*	CRISPR/Cas9	Protoplast/particle bombardment	Herbicide resistance	Li et al. (2016a, b)
10	Rice	*ALS*	Base editing by nCas9 and/or dCas9	*Agrobacterium*/ particle bombardment	Herbicide resistance	Sun et al. (2016), Shimatani et al. (2018)
11	Maize	*ALS2*	CRISPR/Cas9	Biolistic	Herbicide resistance	Svitashev et al. (2016)
12	Rice	*OsCSA*	TALEN	*Agrobacterium*	Photoperiod-sensitive male sterility	Zhang et al. (2016)
13	Rice	*OsDERF1*	TALEN	*Agrobacterium*	Drought tolerance	Zhang et al. (2016)
14	Rice	*TMS5*	CRISPR/Cas9	*Agrobacterium*	Thermo-sensitive genic male sterile	Zhou et al. (2016)
15	Rice	*OsSAPK2*	CRISPR/Cas9	*Agrobacterium*	Drought tolerance	Lou et al. (2017)
16	Rice	*OsHAK1*	CRISPR/Cas9	*Agrobacterium*	Low cesium accumulation	Nieves-Cordones et al. (2017)
17	Rice	*OsAnn3*	CRISPR/Cas9	*Agrobacterium*	Decreased cold tolerance	Shen et al. (2017)

(continued)

Table 25.1 (continued)

S. No.	Crop	Target gene	Tool/system used	Transformation method	Trait	Reference
18	Maize	*ARGOS8*	CRISPR/Cas9	Biolistic	Enhanced yield under drought stress	Shi et al. (2017)
19	Rice	*C287*	Base editing	*Agrobacterium*	Herbicide resistance	Shimatani et al. (2017)
20	Wheat	*TaDREB2*, *TaERF3* (transcription factor genes)	CRISPR/Cas9	Protoplast	Drought	Kim et al. (2018)
21	Rice	*OsPRX2*	CRISPR/Cas9	Protoplast	Potassium deficiency tolerance	Mao et al. (2018)
22	Rice	*ERECTA*	CRISPR/Cas9	*Agrobacterium*	Abiotic stress	Zhang et al. (2018a, b)
23	Rice	*OsNAC041*	CRISPR/Cas9	*Agrobacterium*	Salt stress (sensitivity)	Bo et al. (2019)
24	Rice	*SF3B1*	CRISPR/Cas9	*Agrobacterium*	Herbicide resistance	Butt et al. (2019)
25	Rice	*SRL1*, *SRL2*	CRISPR/Cas9	*Agrobacterium*	Drought tolerance	Liao et al. (2019)
26	Rice	*OsRR9*, *OsRR10*	CRISPR/Cas9	*Agrobacterium*	Salinity tolerance	Wang et al. (2019)
27	Rice	*OsEPFL9*	CRISPR/Cpf1	*Agrobacterium*	Improved stomatal patterning under stress	Yin et al. (2019)
28	Wheat	*ALS*	Base editing	Particle bombardment	Herbicide resistance	Zhang et al. (2019a, b, c)
29	Rice	*OsRR22*	CRISPR/Cas9	*Agrobacterium*	Salinity tolerance	Zhang et al. (2019a, b, c)
30	Rice	*OsOTS1*	CRISPR/Cas9	*Agrobacterium*	Salt tolerance	Zhang et al. (2019a, b, c)
31	Rice	*OsALS1*	Base editing	*Agrobacterium/* particle bombardment	Herbicide resistance	Kuang et al. (2020)
32	Rice	*OsDST*	CRISPR/Cas9	*Agrobacterium*	Drought and salt tolerance	Santosh Kumar et al. (2020)
33	Rice	*OsAAA-1*, *OsAAA-2*	CRISPR/Cas9	*Agrobacterium*	Drought tolerance	Lu et al. (2020)
34	Rice	*OsERA1*	CRISPR/Cas9	*Agrobacterium*	Drought tolerance	Ogata et al. (2020)

35	Rice	*OsPYL9*	CRISPR/Cas9	*Agrobacterium*	Drought tolerance	Usman et al. (2020)
36	Barley	*HvITPK1*	CRISPR/Cas9	*Agrobacterium*	Abiotic stress	Vlcko et al. (2020)
37	Rice	*OsNAC006* (transcription factor)	CRISPR/Cas9	*Agrobacterium*	Drought and heat sensitivity	Wang et al. 2020
38	Rice	*OsMYB30*	CRISPR/Cas9	*Agrobacterium*	Cold tolerance	Zeng et al. (2020)
39	Rice	*SUB1A*	CRISPR/Cas9	*Agrobacterium*, biolistic	Abiotic stress	Liang et al. (2021)
40	Rice	*OsTubA2* (ACCase)	Base editing	*Agrobacterium*	Herbicide resistance	Liu et al. (2021)

Researchers in maize used CRISPR-Cas9 to disrupt the auxin-regulated gene involved in organ size 8 (*ARGOS8*) gene, which increased drought tolerance (Shi et al. 2017). Downregulation of *ARGOS8*, an ethylene repressing gene in maize under drought stress, showed more yield compared to unedited plants. Based on the functional and its differential expressed genes in stress, several genes of drought stress were successfully knocked out and showed promising results. To clearly understand the function of one of the ABA receptors, *OsPYL9* was mutagenized in rice using CRISPR/Cas9. Under both drought and well-watering circumstances, the OsPYL9 mutants showed an increase in grain output. Overall, the results showed that CRISPR/Cas9 mutations of *OsPYL9* have the potential to improve rice drought tolerance and yield (Usman et al. 2020).

25.3.4.2 Salinity Tolerance

Several studies of CRISPR/Cas 9 for salinity tolerance have been successfully conducted so far. Site directed mutation of *OsRR22*, rice gene codes for 696–amino acid B-type response regulator transcription factor. This transcription factor was found to be involved in cytokinin metabolism. Bo et al. (2019) provided evidence that OsNAC041 has an important role in salt resistance in rice. Site-targeted OsNAC041 (NAC transcription factor) coding gene mutant using CRISPR/Cas 9 has superior plant height and resistance to saline conditions than wild-type in rice (Nazir et al. 2022). The expression patterns of five *OsRAV* genes were studied under salt stress situation. Only one gene, *OsRAV2*, was stably active when cells were exposed to extreme salt. The GT-1 element's regulatory involvement in *OsRAV2* salt induction has been demonstrated in situ in plants using CRISPR/Cas9-based targeted alterations (Duan et al. 2016). Due to a reduction in stomatal density and a widened leaf area for enhanced water retention and light-use efficiency, mutant lines with a 366-bp deletion in the coding sequence were resistant to drought, salinity, and osmotic stressors (Santosh Kumar et al. 2020).

25.3.4.3 Cold Tolerance

Cold stress has a negative impact on leaf photosynthesis and biomass buildup, both of which are important sources of grain output (Liu et al. 2019). Using CRISPR/Cas9 and RNAi technologies, Li et al. (2016a, b) found that two *Arabidopsis* glycotransferase genes, *UG79B2* and *UGT79B3*, are engaged in cold stress under the control of CBF1. Shen et al. (2017) suggested that knocking down the rice annexin gene *OsAnn3* in *japonica* rice variety, Taipei.309, by CRISPR/Cas9 driven genome editing imparted cold tolerance.

25.3.4.4 Heat Tolerance

Global warming has posed a significant threat to crop yield around the world. Heat stress (HS) has become a severe hazard to global food security as a result of a rapidly rising climate. Using the CRISPR/Cas9 technology, a heat-shock (HS) inducible mutant was produced in rice (Nandy et al. 2019). A soybean heat-shock protein gene and a rice U3 promoter were used to create Cas9 and sgRNA, respectively, to test the efficiency of the CRISPR/Cas9 system in targeted mutagenesis.

25.3.4.5 Submergence Tolerance

Techniques for *Agrobacterium*-mediated biolistic transformation and regeneration of *indica* rice have enabled CRISPR/Cas9 gene editing of the *SUBMERGENCE 1A-1* gene of the variety, Ciherang-Sub1. These methods pave way for employing CRISPR/Cas9 gene editing to quickly improve *indica*-resistant rice variants (Liang et al. 2021).

25.4 miRNA-Based Approaches

The study of nonprotein-coding short RNAs' post-transcriptional regulation, which involves inhibiting certain messenger RNAs (mRNAs) or altering epigenetic alterations at the transcriptional level, has gotten a lot of interest. The RNA species that constitute the family members of these short ribonucleotide sequences differ from one another in size, biogenesis, mechanism of action, and/or regulatory function. The micro RNAs (miRNAs) are small (20–24 nt) sized, noncoding, and single-stranded ribo-regulatory RNAs abundant in eukaryotes. miRNAs regulate gene expression by pairing with and cleaving their target mRNA or by blocking protein translation. The discovery of miRNA genes in *Caenorhabditis elegans* has been followed by a sharp increase in the identification of more and more plant miRNA families, making them a research hotspot (Chaudhary et al. 2021). In plants, endogenous miRNA coding genes encode primary miRNA (pri-miRNA), which is translated by RNA polymerase II (Pol II). Pri-miRNAs fold into a stem-loop secondary structure to generate mature miRNAs, which link with respective target mRNAs/transcripts to destabilize or inhibit protein translation after a series of enzymatic processes (Reis et al. 2015). miRNAs play a crucial role in plant growth and development, as well as plant responses to a variety of environmental stimuli. miRNAs have recently been discovered to be at the crossroads of complex gene regulatory networks. As a result, miRNAs have emerged as promising targets for improving plants' ability to adapt to and survive stress. Some of the studies on rice engineered with miRNA are successfully tolerant against abiotic stresses (Zhang et al. 2014).

25.4.1 Micro-RNA (miRNA) with Macro Functions

Plants have a lot of miRNAs, which are thought to play a major role in post-transcriptional regulation via base-pairing with complementary mRNA targets, especially transcription factors (TFs). miRNAs, which are created by Dicer-like1 (DCL1) from miRNA precursors transcribed from miRNA genes, have a role in post-transcriptional gene control in plants. Plant miRNAs and transcription factors (TFs) are two key groups of gene regulators, and both molecules are thought to have comparable regulatory logistics as well as cooperate in gene regulatory networks. miRNAs have a variety of vital functions in plant growth, development, and metabolism, as well as their participation in abiotic stress and pathogen responses

(Mangrauthia et al. 2013). They regulate various stages of growth and development through meristem boundary formation, auxin signaling, organ separation, leaf polarity, lateral root formation, and transition from the juvenile-to-adult vegetative phase to the flowering phase. They regulate biotic and abiotic stress tolerance, miRNA silencing genes for metabolic pathways. Stress-induced miRNAs have been studied in various crops under various abiotic and biotic stress conditions, including drought, cold, bacterial infection, salinity, mechanical stress, and UV radiation (Khariwesh et al. 2012).

25.4.1.1 Salinity and Drought

Studies with miRNAs in drought and salt stress of *Arabidopsis* have revealed that they play a general role for the above stresses. miRNA families such as miR168, miR171, and miR396 were proven to have high salinity responses in *Arabidopsis*, thus confirming the hypothesis of miRNAs role in abiotic stress adaptive responses (Khariwesh et al. 2012). *Arabidopsis* miRNA families, such as miR156, miR158, miR159, miR165, miR167, miR168, miR169, and miR171, miR319, miR393, miR394, and miR396, were shown to be highly drought-responsive in model plants. In rice, miR169g was highly upregulated during drought while miR393 was transiently expressed. Genome-wide profiling and analysis of miRNAs in rice were carried out in a wide range of developmental stages, from tillering to inflorescence formation under drought, using a microarray platform (Zhou et al. 2010).

25.4.1.2 Heat and Cold Stress

The expression analysis of *Arabidopsis*, *Brachypodium*, and *Populus* for miRNAs under cold stress showed up regulation of miR397, miR169 and miR172. Wheat miRNAs showed differential expression under heat stress. Small RNAs from wheat leaves treated by heat stress were cloned. Among the cloned 32 miRNA families detected in wheat, nine conserved miRNAs were putatively heated responsive (Xin et al. 2010).

25.4.1.3 Hypoxia and Oxidative Stress

Several studies suggested that miRNAs are found to be involved in plant oxidative stresses. Several miRNAs were differentially regulated when the seedlings were under submerged conditions; early during submergence induced, Zm-miR166, Zm-miR167, Zm-miR171, Os-miR396, and Zm-miR399 but Zm-miR159, At-miR395, Pt-miR474, and Os-miR528 were downregulated. Seven H_2O_2-responsive miRNA families such as miR169, miR397, miR528, miR827, miR1425, miR319a.2, and miR408-5p, i.e., miRNAs that were differentially expressed in rice under H_2O_2-treatment. Among these miR169, miR397, miR827, and miR1425 were highly upregulated, and miR528 was highly down regulated by H_2O_2-treatments (Khariwesh et al. 2012).

25.4.2 MiRNA-Micro-RNA with Macro Functions

Plants have a lot of miRNAs, which are thought to play a big role in post-transcriptional regulation via base-pairing with complementary mRNA targets, especially transcription factors (TFs). miRNAs, which are created by Dicer-like1 (DCL1) from miRNA precursors transcribed from miRNA genes, have a role in post-transcriptional gene control in plants. Plant miRNAs and transcription factors (TFs) are two key groups of gene regulators, and both molecules are thought to have comparable regulatory logistics as well as cooperate in gene regulatory networks. miRNAs have a variety of vital functions in plant growth, development, and metabolism, as well as their participation in abiotic stress and pathogen responses (Mangrauthia et al. 2013).

25.4.3 Computational Identification of miRNA

So far, both experimental and computational techniques have been utilized to find miRNAs in plants. Direct-cloning methods were used to identify miRNAs in plants in the early 2000s. Several miRNA families in various crops were identified and studied under developmental and stress conditions. In all major crops, several miRNAs have been identified and characterized (Tripathi et al. 2015). Apart from identifying the miRNA experimentally, the cheapest and simplest method is identification computationally. Several online tools and software are available for identification of these noncoding RNAs which are listed in Table 25.2.

25.4.4 miRNA Engineered Plants Against Abiotic Stresses

In crop improvement studies, a variety of transgenic techniques are used with the primary goal of increasing crop output and quality. The focus of these enhancement efforts has primarily been on abiotic stress genes. Since miRNA affects gene expression at the transcriptional or post-transcriptional stages, miRNA-based genetic alteration appears to be the most promising of all the techniques. Desired overexpression/repression of stress-responsive miRNAs and/or their target mRNAs, miRNA-resistant target genes, target-mimics, and artificial miRNAs are some of the approaches that may be used to manipulate miRNAs (Sriram et al. 2016).

miRNA engineered plants showed better results against various stress. Among which majority of crops include both monocot and dicot crops found to have better results in case of knockout of a particular gene for tolerance against multiple stress. Especially abiotic stress like drought, salinity, heavy metal toxicity, hypoxia, and waterlogging is overcome by developing transgenic plants of *Arabidopsis*, rice, and soybean engineered with miRNA (Agarwal and Grover 2006). Only very few studies for abiotic stresses have been published on cereals, especially in rice. Hence, this area remains unexplored till date and opens a scope for furthermore

Table 25.2 List of online tools and software for identification of noncoding RNAs

S. No.	Tool	Role	Link	Reference
1	miRBase	Online miRNA repository	http://www.mirbase.org	Kozomara and Griffiths-Jones (2014)
2	miRNEST	Provides sequence-related information and useful degradome support for plant miRNA	http://rhesus.amu.edu.pl/mirnest/copy/	Szczesniak and Makalowska (2014)
3	PNRD	Contains information of noncoding RNAs of 166 species	http://structuralbiology.cau.edu.cn/PNRD/index.php	Yi et al. (2015)
4	PMTED	Database to retrieve and analysis of expression profiling of miRnA targets	http://pmted.agrinome.org	Sun et al. (2013)
5	miRTour	Online tool for homology-based discovery of pant miRNAs	http://bio2server.bioinfo.uniplovdiv.bg/miRTour/	Milev et al. (2011)
6	PmiRExAt	Online resource focusing on plant miRNA expression levels at variable tissues	http://pmirexat.nabi.res.in/	Gurjar et al. (2016)
7	miRTarBase	Database contain experimentally validated miRNA targeted interactions	http://mirtarbase.mbc.nctu.edu.tw/php/index.php	Chou et al. (2018)
8	PlantCircNet	Database to visualize the regulatory network of miRNA-circRNAs	http://bis.zju.edu.cn/plantcircnet/index.php	Zhang et al. (2017)
9	TAPIR	miRNA target prediction tools with the help of FASTA	http://bioinformatics.psb.ugent.be/webtools/tapir/	Bonnet et al. (2010)
10	miRPlant	Tool to identify the miRNA from RNA sequencing data	http://www.australianprostatecentre.org/research/software/mirplant	An et al. (2014)
11	miRge	miRNA entropy determination and identification differential miRNA-isomers	http://atlas.pathology.jhu.edu/baras/miRge.html	Baras et al. (2015)
12	P-SAMS	Tool to study artificial miRNA, synthetic trans-acting small interfering RNAs	http://p-sams.carringtonlab.org	Fahlgren et al. (2016)

Table 25.3 miRNA-mediated genome engineering for abiotic stress tolerance

S. No.	miRNA	Expression strategy	Response	Reference
Crop: Rice				
1	miR319	RNAi	Enhanced tolerance to chilling stress	Yang et al. (2013)
2	miR156	Overexpression of *OsmiR156k*	Reduced cold tolerance	Cui et al. (2015)
3	miR390	Over expression of miR390	Reduced Cd tolerance/ enhanced Cd accumulation	Ding et al. (2016)
4	miR159	Overexpression of *MYB TF*	Increased drought resistance in down-regulated plants	Zhao et al. (2017)
5	*OsMIR528*	CRISPR/Cas9	Positive regulator of salt stress	Zhou et al. (2017)
6	miR166	Overexpression of *SPL TF*	Drought tolerance in knocked-down mutants	Zhang et al. (2018a, b)
7	*OsMIR535*	CRISPR/Cas9	Drought and salinity tolerance	Yue et al. (2020)
8	OsmiR818b	CRISPR/Cas9	Drought response	Chung et al. (2020)
9	*OsMIR168a*	CRISPR/Cas9	Environmental stress responses (pleiotropic gene)	Zhou et al. (2022)
10	miR393a and miR396c	CRISPR/Cas9	Salinity tolerance	Jaganathan et al. (unpublished data)

studies. A few success stories in cereal crops pertaining to rice are listed in Table 25.3.

25.5 Bottlenecks in the Application of Genome Editing Tools for Crop Improvement

1. *Lesser Transformation Efficiency*
   Although genome modification for genetic enhancement of essential crops is a rare revolutionary revolution, there are still significant obstacles to its implementation. The ability to use current advancements in plant genome editing techniques to improve any single crop species is primarily dependent on transformation efficiency. For stable transformation, the regeneration step is a common limitation compared to stable integration of the transgene. Extensive studies should be carried out to magnify the number of transformed plants and regeneration responses by targeting a wide range of tissues and genotypes. Several investigations are being carried out to optimize tissue culture protocol to apply genome editing techniques (Jia et al. 2019).

2. *Lack of Specific Targets*
   Although CRISPR-Cas9-based genome editing is a technological breakthrough in today's world, caution should be exercised when designing sgRNAs, as off-targets are a limitation and not every gene or region can be efficiently targeted due to a lack of highly specific sgRNAs in the desired location (Tang and Chu 2017; Zhou et al. 2017). Despite various attempts to limit off-target effects in gene-edited plants, such as the identification of cas9 orthologs and cas9 variations, specificity problems still exist. A novel approach to creating desirable SNPs mimicking allele replacement by base editing or prime editing will be beneficial for the precision and reducing the drawbacks of off-target editing.
3. *Polyploid Nature of Crop*
   Polyploidy genomes are complex and difficult to sequence due to excessive repetitive sequences and large genome size. Functional annotations are especially difficult for the larger number of gene copies and different functionalities of duplicated genes that have evolved through neofunctionalization. It is difficult to get the necessary mutations because of the intricacy. Due to the dosage effect of additional paralogous copies of genes, some mutations, notably knockdown or knockout of genes, may result in no phenotypic change. Such challenges arise when trying to modify the DNA of a polyploidy crop like wheat. The concurrent editing of multiple homeologs through CRISPR-Cas9 mutagenesis without any background mutations will provide a new possibility to use mutant genotypes in breeding (Ansari et al. 2020).
4. *Regulatory Problems*
   Although genome editing has gained in popularity among scientists and has been used in several crop systems for the development of superior lines, all of the research is still done in the lab. In many countries, regulatory mechanisms to establish whether gene-edited crops are transgene-free or genetically modified crops are still unclear, and there are no universally recognized frameworks available in the current situation (Mao et al. 2019). The key to future acceptance of genome editing goods is the facilitation of in-country product-based regulatory clearance frameworks, as well as the cost of authorization that is affordable for public sectors and its harmonization across several countries.

25.6 Conclusion and Future Prospects

The continuous increase in food demand and the exigencies of climate change call for great flexibility and innovations in crop resilience and production systems. Although genetic improvements through conventional breeding and tissue culture technologies are already available, these approaches have been reported to carry their limitations, viz., inefficient in genetic manipulation of complex traits, time-consuming, and linkage drag. CRISPR/Cas9 and related genome editing methods have ushered a revolution in crop improvement, which is critical for fulfilling the rising food demand and assuring the uninterrupted supply of cereals for future generations. Finally, gene-editing tools, especially the CRISPR/Cas9 system, have been increasingly important in defining plant research in recent years. Because of its ability to induce mutations at specified sites in the genome with increased accuracy, efficiency, and simplicity, it has emerged as the most effective tool for crop improvement. Despite the availability of genome editing techniques, there are still limitations in the use of CRISPR tools for agricultural crop enhancement due to global regulations. By overcoming the limitations of CRISPR approaches for gene editing, crop plants created using CRISPR/Cas9 genome editing could be used as food. Crop plants generated through CRISPR/Cas9 genome editing might be established as a nongenetically modified organism, for their fast acceptance at the field level. We can predict that the deployment of CRISPR/Cas9 technology in agriculture will revolutionize crop productivity and recreate a second green revolution that will ensure the world's ever-increasing population for their dietary and nutritional needs.

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Nanotechnology and Its Role in Cereal Crops under Abiotic Stress

26

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Abstract

Crops confront various types of abiotic stress such as extreme temperatures (freezing, cold, heat), water availability (drought, flooding), and ion toxicity (salinity, heavy metals) which adversely affect the plant growth and productivity worldwide. These abiotic stresses are interconnected to osmotic stress that results in the disruption of ion distribution and cell homeostasis. The use of nanoscale materials carries an immense scope in the mitigation of a multitude of biotic and abiotic stresses by acting on the common pathway or regulators. The characteristic structural dimensions provide nanoparticles (NPs) the properties of enzymes and cofactors that enable the NPs to participate in the metabolic pathway network. Penetration of NPs inside the extracellular or intracellular environment triggers enzymatic responses and influences the redox homeostasis that helps to augment the antioxidant pathway in plants. For instance, NPs based on Si, Zn, Fe, etc. boost the chlorophyll content, plant biomass, vigor, and biological yield. NPs help to enhance the activities of CAT, APX, GPX, and SOD and lower lipid

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peroxidation and H_2O_2 content that are vital for promoting drought stress tolerance in wheat and maize. Application of Fe NPs increased root dry weight, photosynthetic pigments, total soluble carbohydrate, membrane stability index, and relative water content of salinity-stressed rice plants. Gene expression controlling reduced metal uptake is favored manifolds by NPs like Si, Cd, etc. The systemic movement of NPs and their cellular compartmentalization is going to have a great bearing on interaction pathways linked to stress tolerance in plants.

Keywords

Cereals · Nanotechnology · Nanoparticles · Abiotic stress · Tolerance · Drought · Salinity · Metal

26.1 Introduction

The term nanotechnology was first coined and used in 1974 by Taniguchi of the Tokyo Science University. The prefix “nano” is a Greek word that means “dwarf” (Nikalje 2015). Nanotechnology refers to the manipulation of matter on an atomic and molecular scale. Nanotechnology deals with structures that are in the size range of 1–100 nm (Arivalagan et al. 2011). In this size range, the matter has properties that are far different from the macroscopic level. The change in properties is due to reduced molecular size and also due to changed interactions between molecules. The properties of nanoparticles are high reactivity, high mobility in their free state, large specific surface area, and exhibiting quantum effects and enhanced bioavailability and bioactivity (Gutierrez et al. 2011). Common types of nanomaterials include nanotubes (single-walled carbon nanotube, multi-walled carbon nanotube), dendrimers, quantum dots, fullerenes, and those based on metal (Ag, Si, Au, etc.) and metal oxides (TiO_2, SiO_2, ZnO, CuO, etc.). Nanomaterials can be formed by two main processes: (1) bottom-up process that involves the building of nanomaterials from the atomic scale and (2) top-down process of grating down of bulk materials. Nanomaterials can be nanoscale one dimension (e.g., surface films), two-dimension (e.g., strands or fibers), or three dimensions (e.g., particles). They can exist in single, fused, aggregated, or agglomerated forms with spherical, tubular, and irregular shapes (Das and Das 2019).

Globally, rice, wheat, and maize are the three most important cereal crops, which together comprise at least 75% of the world’s grain production. Major abiotic stresses which affect crops include heat, salinity, cold drought, flooding/submergence (anoxia), chemical toxicities, and excess light (Lavania et al. 2015). In the backdrop of a multitude of production constraints, meeting the food demands for the rapidly increasing world population is a challenge, especially when the global grain production has to be increased by 70% by 2050 (FAO 2009). The ability of cereal crops to tolerate abiotic stresses which comprise water deficit (drought), flood (anoxia), salinity, high/low temperature, and other osmotic stresses is an essential aspect of yield resilience, and its improvement has long been a target for plant breeders and researchers (Jeyasri et al. 2021). NPs have been investigated to improve plant growth, development, and productivity, thus proving their use to overcome various abiotic and biotic stress of crops. In the last decade, the science of nanotechnology has attained a promising position to mitigate the constraints associated with the amelioration of abiotic stresses (Tariq et al. 2021). Rice, maize, and wheat experience varied kind of abiotic stresses and prominently include drought/salinity, drought, and cold/drought, respectively, for the three major food crops. This chapter aims to bring an overview of the use and scope of nano-materials in combating these productivity constraints.

26.2 Applications of Nanotechnology in Agriculture

Nanotechnology is considered one of the potential technologies that can boost agriculture (Kuzma and Ver Hage 2006). The use of nanoparticles in agriculture has a multitude of applications in plant genetic modifications (Torney et al. 2007), fertilizer use efficiency, crop protection (Anjali et al. 2012), precision farming (Kalpana-Sastry et al. 2009), crop growth, soil enhancement (Anjali et al. 2012), stress management, smart systems for food packing and processing, smart fertilizer and pesticide delivery systems, and plant pathogen detection (Moraru et al. 2003; Chau et al. 2007). For instance, the area affected worldwide by drought, cold, and salinity is 64%, 57%, and 6%, respectively). The field of nanotechnology finds direct application to reverse the harmful impact of the stress environments on production and productivity.

26.3 Entry of Nanoparticles (NPs) into the Plant System

The size of NPs is one of the main criteria for penetration into plant tissues, and usually, 40–50 nm particle size is regarded as the exclusion limit (Taylor et al. 2014). Further, the chemical composition is another factor influencing the uptake (Ma et al. 2010). After the penetration into the plant, the NPs move through tissues in an apoplastic or symplastic manner. Apoplastic transport takes place outside the plasma membrane through the extracellular spaces, cell walls of adjacent cells, and xylem vessels (Sattelmacher 2001), whereas symplastic transport involves the movement of water and substances between the adjacent cells through plasmodesmata (Roberts and Oparka 2003) and sieve plates. Normally, NPs enter the plant root system through the lateral root junctions, move through the cortex and pericycle, and reach xylem vessels (Dietz and Herth 2011). The interaction of nanoparticles with plant systems generates reactive oxygen species (ROS) and are absorbed through active transport of ionic cell membrane and cause oxidative damage and lipid peroxidation. After entering plant cells, the NPs react with sulfhydryl and carboxyl groups of proteins and alter their activity. NPs can form complexes with membrane transporters or root exudates and are then transported to the plant (Kurepa et al. 2009; Watanabe et al. 2008). Nanomaterials move from leaves to developing roots, stems, and seeds. The xylem acts as an important channel for the uptake and transport of nanoparticles (Biebaum et al. 2010; Pola et al. 2012). Nanomaterials also can penetrate leaf cuticles and enter the cytoplasm of cells (Sharif et al. 2013). In the cytoplasm, NPs can bind to various organelles and interfere with the metabolism processes there (Zhang and Monteiro et al., 2009). Ag nanoparticles of 20 nm size can be transported inside the cell via plasmodesmata (Wuncheng 1986; Unrine et al. 2012). NPs show differential mobility based on the crops. Cifuentes et al. (2010) reported a higher accumulation of carbon-coated iron nanoparticles in the roots of wheat and faster translocation to the aerial parts in pea and wheat compared. On the other hand, Zhu et al. (2012) found that rice roots accumulated higher amounts of gold nanoparticles through comparably less than radish. Also, the positively charged gold nanoparticles were taken up faster by the roots and the negatively charged ones were more efficiently translocated to the aerial parts.

26.4 Enhancement of Defensive System by Nanoparticles: Abiotic Stress Tolerance

The world population by 2050 is expected to reach 9.1 billion, and agricultural production has to match the needs of the burgeoning population. In climate change scenarios, abiotic stresses are considered to be the major constraint for sustainable crop production. Approximately 70% of crop yield reduction is promoted by varied kinds of abiotic stresses (Acquaah 2007). Abiotic stress leads to a series of morphological, physiological, biochemical, and molecular changes that adversely affect plant growth and productivity. Drought, salinity, and extreme temperatures are the most prevalent stresses, besides the growth limitations caused by heavy metals, floods, cold, etc. (Gull et al. 2019).

During stress conditions, plant cells go through oxidative harm due to the exorbitant release of ROS, prompting fast lipid peroxidation and electrolyte spillage. Plants harbor an antioxidant pathway called ascorbate-glutathione cycle which serves to deliver both enzymatic and nonenzymatic antioxidants. Recent studies show that metal nanoparticles that act as cofactors in different enzymatic responses influence the redox homeostasis that in turn help in better administration of harmful ROS; therefore, augmenting antioxidant pathway in plants. To avoid oxidative damage and loss of water plants usually respond by the closure of stomata and increase in secondary metabolites (Serraj and Sinclair 2002).

26.4.1 Drought Stress

Drought stress is reported to have severe consequences at different crop growth stages. About 1.8 billion people will face absolute water shortage in the first quarter of the twenty-first century, and 65% of the human population will live in conditions of partial shortage of water taking into account modern forecasts (Nezhadahmadi et al. 2013). Overall, water deficit reduces nutrient availability in the root zone, absorption at root hair, translocation in xylem and phloem vessels leading to impaired metabolism of nutrients in cells and tissues, reduced growth, limited carboxylation, decreased water potential, and oxidative stress (Farooq et al. 2009; Kumari et al. 2018; Wang et al. 2012a, b). To mitigate these growth-limiting effects, nanotechnology has a promise to improve photosynthetic rate, stomatal conductance, and relative water content, increase plant biomass, lower the stress metabolite content and electrolyte leakage, increase osmolyte content and phenolic substances, and improve the activity of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POX). TiO_2 plays a significant role in increasing pigments *Zea mays*. TiO_2 was reported to stabilize the integrality of the chloroplast membrane and protect the chloroplasts from aging at flowering. The use of nano titanium dioxide at 0.03% concentration at the flowering stage increased total chlorophyll, Chla and Chlb, carotenoids, and anthocyanins (Morteza et al. 2013). Foliar application of chitosan NPs (0, 30, 60, and 90 ppm) in *Triticum aestivum* L. particularly at 90 ppm at tillering, stem elongation, and heading stages caused an increase in leaf area, crop yield, and biomass as compared to the control. Application of C NPs was found to increase the relative water content, chlorophyll content, photosynthetic rate, and CAT and SOD activities in comparison to the control in the case of wheat (Behboudi et al. 2019). Si NPs (0, 25, 50, and 100 mg/kg) application to drought-stressed plant of *Triticum aestivum* L grown in Cd contaminated soil showed maximum values of shoot, root, and grain dry biomass, i.e., 70%, 54%, and 75%, respectively (at 100 mg/kg). The application of Si NPs also significantly increased the contents of chlorophyll and ameliorated oxidative stress by lowering the content of malondialdehyde (MDA), H_2O_2, and electrolyte leakage (Khan et al. 2020). Fe (25, 50, and 100 mg/kg), when applied to *T. aestivum* L., resulted in increased plant height, spike length, and dry weight under drought stress as compared to control. Chlorophyll a content increased up to 66% in wheat plants and activated the antioxidative defence system against oxidative stress (Adrees et al. 2020). Under drought stress the delay in panicle initiation time was reduced, grain yield was significantly increased, and Zn uptake was increased on applying ZnO NP (1.0%) in *Triticum aestivum* L. (Dimkpa et al. 2020). Silicon in sorghum (*Sorghum. bicolar*) increases leaf area index (LAI), specific leaf weight (SLW), chlorophyll content (SPAD), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), and total dry weight (TDW). Application of silicon on two sorghum cultivars having different drought susceptibility showed improved drought tolerance irrespective of their drought susceptibility by lowering shoot to root (S/R) ratio, which perhaps suggested the improved root growth and the maintenance of the photosynthetic rate (Ahmed et al. 2011). ZnO NPs (0, 25, 50, and100 mg/L) application in *Triticum aestivum* L. resulted in improved growth and crop yield in wheat. Here the foliar spray of ZnO NPs increased chlorophyll content and SOD and POX activities (Adrees et al. 2021). Spraying of Se/SiO_2 increased drought tolerance by increasing the activities of CAT, APX, GPX, and SOD and lowered lipid peroxidation and H_2O_2 content. The antioxidative defence system in plants includes the enzymes catalase (CAT), ascorbate peroxidase (APOX), superoxide dismutase (SOD), glutathione reductase (GR), and dehydroascorbate reductase (DHAR). CAT

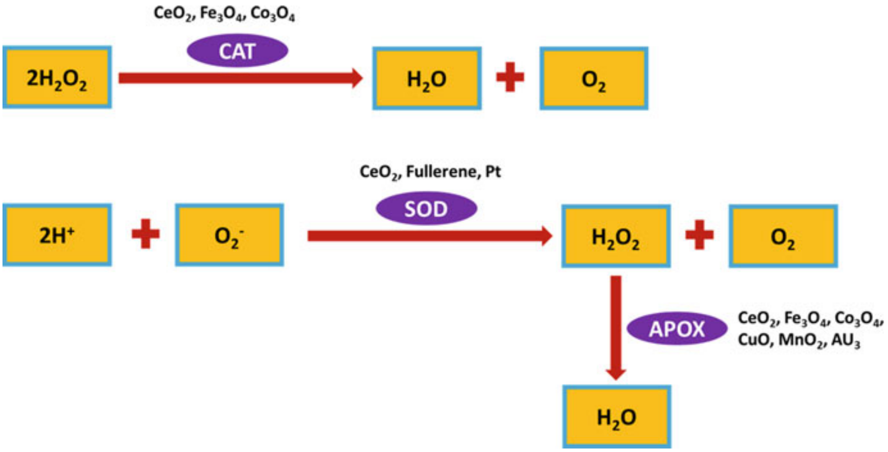

Fig. 26.1 NP role as enzymes in detoxification of stress factors

quenches both ROS and peroxy radicals while SOD catalyzes the dismutation of O^{-2} to H_2O_2. The APOX, DHAR, and GR are involved in a network of redox reactions that control ROS. The APOX directly reduces the H_2O_2 generated by SOD into H_2O. The DHAR regenerates ascorbate that is utilized by APOX for the reduction of H_2O_2. NPs play an important role in mimicking the activity of natural enzymes. Nanoparticles $nCeO_2$, nFe_3O_4, nCo_3O_4 mimic catalase, $nCeO_2$, nFe_3O_4, nCo_3O_4, $nMnO_2$, nCuO, and nAu exhibit peroxidase activity; $nCeO_2$, fullerene, and nPt, demonstrate superoxide dismutase property (Fig. 26.1).

Zerovalent copper NPs (3.333, 4.444, and 5.556 mg/L) in *Zea mays* improved the biomass of drought-stressed plants and increased the total seed number and grain yield of maize plants. Treatment of Cu NPs also increased the contents of anthocyanin, chlorophyll, and carotenoid and improved drought stress tolerance by decreasing oxidative stress via the enhancement of ROS scavenging antioxidative enzymes (Nguyen et al. 2021). Also, maize plants exposed to CeO_2 nanoparticles depicted excessive generation of H_2O_2 and upregulation of HSP70 (Zhao et al. 2012).

Taran et al. (2017) reported that Cu and Zn nanoparticles decreased the negative effect of drought action upon plants in wheat through the increased activity of antioxidative enzymes, increased relative water content in leaves, and reduced the level of accumulation of thiobarbituric acid reactive substances (TBARS). Iron oxide NP-treated rice plants increased biomass, antioxidant enzyme contents, photosynthesis efficiency, and nutrient acquisition together with the decrease in ROS under drought conditions (Temoor et al. 2021). Wheat seedlings (*Triticum aestivum* v. Dolores) exposed to CuO NPs (300 mg Cu/kg) exhibited increased lignification which corresponded with increased strength and toughness of the wheat shoots, measured with tensile testing. CuO NP-induced lignification has been related to preventing lodging in mature cereal crops and measures to reduce pathogen invasion (Potter 2020). Lignification of sclerenchyma is associated with higher resistance to lodging in plants. They further studied the interactions with the bacterium

Pseudomonas chlororaphis O6 (PcO6) in the presence of the NPs change plant metabolism which was shown to result in enhanced drought tolerance. The accumulation of nitric oxide (NO) at the root surface triggers elevated levels of gene expression at drought tolerance-related loci. Mahakham et al. (2017) discussed nanopriming of aged rice seeds with photosynthesized AgNPs at 5 and 10 ppm which significantly improved germination performance and seedling vigor compared to unprimed control and conventional hydropriming. Nano potassium in rice (*Oryza sativa*) improves mineral nutrients by enhancing total tillers and fertile tillers per hill (Lemraski et al. 2017). Nanopriming could enhance α-amylase activity resulting in higher soluble sugar content for supporting seedling growth. Furthermore, nanopriming stimulated the upregulation of aquaporin genes in germinating seeds and ROS production. We suppose that these approaches may be helpful even under moisture limiting conditions and, therefore, shall result in enhanced growth of plants.

26.4.2 Salinity Stress

Globally salinity stress alone decreases crop production by about 23%. The agricultural land affected by salinity is increasing worldwide which presents two primary concerns: osmotic stress, and ionic stress. Salinity affects different physiological and metabolic processes in plants like growth retardation, increase in cell senescence, and programmed cell death under severe conditions (Parida and Das 2005). Nanoparticles play a great role in mitigating these adverse effects by reducing Na^+ ion toxicity, elevation in K^+ uptake, regulating ionic balance, activation of antioxidative defence mechanism, and increased stomatal conductance (El-Sabar et al. 2021).

Potential of nanotechnology in salinity stress alleviation: seed priming with Ag NPs (0, 2, 5 and 10) in *Triticum aestivum* significantly augmented the fresh and dry biomass of salinity stressed wheat plants at all doses compared to the control. It also increased the activities of vital antioxidative enzymes while declining the contents of stress indicators, i.e., MDA and H_2O_2 in wheat leaves as compared to salt-stressed plants (Mohamed et al. 2017). It also increased leaf relative water content, leaf photosynthetic rate, leaf stomatal conductance, and chlorophyll content in comparison to the control; improved nutrients contents, leaf proline content, and leaf gibberellic acid level; and enhanced the contents of protein and carbohydrates and antioxidative enzymes' activities in wheat (Mahmoud et al. 2019). It was recorded that the interaction of NaCl and ZnO reverses the salinity-induced consequences (L-proline, protein, MDA, aldehydes, sugars, H_2O_2, and antioxidative enzymes) (Mahmoud et al. 2020). Seed priming with TiO_2 (40, 60, and 80 ppm) in *Zea mays* L. positively impacted the germination (germination percentage, germination energy and seedling vigor index) and seedling growth (lengths of root and shoot, fresh, and dry weight) and reduced the mean emergence time. They showed the enhancement in potassium ion concentration, relative water content, contents of total phenolic and proline contents; increased SOD, CAT, and PAL activities; and decreased sodium ion concentration, membrane electrolyte leakage, and MDA content (Shah et al. 2021). Nanomaterial MWCNTs (multi-walled carbon nanotubes) in Barley (*Hordeum vulgare*) improve drought and salinity tolerance by boosting seed water absorption and increasing seedling water content (Karami and Sepehri,2017). The effect of synthesized zinc NPs, characterized for size, shape, surface structure, crystalline nature, and elemental proportion, was studied in pearl millet (*Pennisetum americanum* L.) cv. HHB 67 (Tarafdar et al. 2014). The results indicated that synthesized NPs of 15–25 nm brought significant improvement in root and shoot growth, chlorophyll content, total soluble leaf protein, plant dry biomass, and enzyme activities of acid phosphatase, alkaline phosphatase, phytase, and dehydrogenase in 6-week-old plants. Moreover, grain yield was improved by 37.7% due to the application of zinc Nano-fertilizer (NF).

26.4.3 Heavy Metals

Heavy metal (HM) concentration is increasing at an alarming rate in our environment due to industries and human activities (Chaplygin et al. 2020; Ghazaryan et al. 2020). The heavy metal contamination in cultivated land and water bodies is of great concern (Ennaji et al. 2020; Zamora-Ledezma et al. 2021). The accumulation of these HHs result in genotoxic, carcinogenic, and mutational changes (Zamora-Ledezma et al. 2021; Galiti et al. 2021; Kontas and Bontasci 2020; Sall et al. 2020). Usually, heavy metals like Cu, Zn, Cf, Pb, As, and Hg are associated with our environment (Raja et al. 2021; Zhao et al. 2021). To level down the accumulation of these heavy metals, eco-friendly nanoparticles have gained much popularity (Wang et al. 2012a, b). Fe_3O_4 treatment in *Triticum aestivum* L. minimized the inhibitory action of HMs and improved the level of superoxide dismutase and peroxidase (Konate et al. 2017). Si (19, 48, and 202 nm), when used in *Oryza sativa* L., enhanced the number of cultured cells and decreased proportionally with the rise in NP size; the treatment maintained the cellular integrity in the presence of metals. Si NP amendment also caused altered expression of genes responsible for reduced metal uptake (Cui et al. 2017). ZnO (0, 50, 75, and100 mg/L) treatment in *Zea mays* L. caused a rise in plant length, leaf number, and biomass. Its application also enhanced chlorophyll content, gas exchange characteristics, and antioxidant enzymes; addition led to a reduced content of Cd in root and shoot (Rizwan et al. 2019a, b). ZnO (0, 25, 50, 75, and100 mg/L) and Fe NPs (0, 5, 10, 15, and 20 mg/L) when applied in *Triticum aestivum* L. induced plant growth, dry weight, and grains under Cd stress. The addition of NPs also decreased the loss of electrolytes and activity of superoxide dismutase and peroxidase along with diminished Cd accumulation (Rizwan et al. 2019a, b). The incorporation of Si NPs improved the chlorophyll content and reduced the Hg content in root and shoot (Li et al. 2020). Mel-Au (200 M) caused a reduction of Cd level in root and shoot, improved chlorophyll content, and raised the activity of antioxidant enzymes in *Oryza sativa* (Jiang et al. 2021). Fe NPs (25 and 50 mg/L) treatment in *Oryza sativa* L. improved plant length and dry weight, causing a rise in the level of proline, glutathione, and phytochelatins.

Fe NP addition led to improved defence enzymes and glyoxalase machinery (Bidi et al. 2021). ZnO NPs (10–100 mg/L) in *Oryza sativa* L. increased the growth of seedlings. Treatment also facilitated the reduced accumulation of arsenic in root and shoot together with the rise in phytochelatin levels (Yan et al. 2021). Cu (25, 50, and 100 mg kg^{-1} of soil), when treated in *Triticum aestivum* L., resulted in rising in plant height and shoot dry weight, an increase in N and P content, reduced Cd transport and rise in the level of vital ions and antioxidant pool (Noman et al. 2020a, b). Cu NPs (0, 25, 50, and 100 mg/kg of soil) in *Triticum aestivum* L., improved biomass and growth of the plant, reduced Cr availability, increased nutrient uptake, and increased antioxidant content (Noman et al. 2020a, b). Fe_2O_3 (0, 25, 50, and 100 mg/kg soil) improved fresh and dry biomass; increased height; augmented detoxifying enzymes, photosynthetic potential, and nutrient uptake attributes; reduced formation of ROS; lowered expression of genes supporting the transport of Cd; and restricted Cd mobilization in upper plant parts of *Oryza sativa* L. (Ahmad et al. 2021). Fe_2O_3 (25, 50, and 100 mg kg^{-1} soil) when used in *Triticum aestivum* L. resulted in an increase in plant fresh, dry biomass and plant length, Cd transport was reduced, and N, P, and K content enhanced and antioxidants and pigment content also increased (Manzoor et al. 2021). Au (200 M) NPs reduced the level of Cd in root and leaves of *Oryza sativa* L. by 33 and 46.2%, respectively, improving in antioxidant defence enzyme and restricting the expression of genes associated with metal transport (Jiang et al. 2021). Si (0, 25, 50, and 100 mg/kg soil) NPs in *Triticum aestivum* L. improved plant height, chlorophyll content, photosynthesis, and diminished Cd content in tissues (Khan et al. 2020).

26.5 Conclusions and Future Strategies

NPs are assuming vital applications in the field of agriculture particularly when it comes to augmenting stress mitigation strategies in cereal plants. Increased tolerance to drought on direct application of NPs on crop canopy or their planned entry through the root system is possible. NPs help plants evade oxidative stress. Besides, NPs help to confer salt and heavy metal tolerance by way of conditioning membrane permeability and ionic balance. The direct effect of NPs on the enhancement of chlorophyll content leads to increased biomass and yield. Nanomaterials find their use in seed priming and other pre-germination treatments that prepare the plant system to counter stresses like drought and low moisture.

The proteins and enzymes involved in redox-dependent processes trigger the cellular pathway which confers stability within the cell compartments. The compartmentalization of many proteins, including antioxidant and/or redox-associated enzymes, is a controlled phenomenon. The use of NPs in one compartment may be as such independent of their relocation in other compartments so that the net pathway requirement expected of the NPs may not be fulfilled. Future research demands deeper insight into the inter-compartmental movement and signal sharing between the NP-NP, NP-protein, and NP-metabolite counterparts.

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