# **Chapter 10 Actions of Biological Trace Elements in Plant Abiotic Stress Tolerance**

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**Abstract** With the increase of global population, the demand for food crops, oil, fiber and other by-product yielding crops is increasing. In contrast to this increasing demand, abiotic stresses hinder the productivity of plants. Abiotic stresses sometimes reduce more than half of the crop yields. To attain global food security, understanding of plant responses to abiotic stresses is crucial because this is the prerequisite for developing approaches/tools for improving plant stress tolerance. Trace elements are nutrients required in small quantities to facilitate a range of physiological functions. These elements stimulate growth but are not essential. Some are essential only for certain plant species or required under a given condition. Trace elements not only improve plant physiological processes and growth but play roles in improving plant stress tolerance. However, the actual physiological functions of trace elements in conferring abiotic stress tolerance are still under study. This chapter focuses

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on the roles of trace elements emphasizing especially the recent advances on the actions of biological trace elements in plant abiotic stress tolerance.

**Keywords** Abiotic stress • Trace elements • Antioxidants • Phytoprotectants • Metabolites

### **10.1 Introduction**

With the increase of global population, the demand of food crops, oil, fiber, and other by-product yielding crops is increasing (Condon et al. 2004; Morison et al. 2008). In contrast to this increasing demand, abiotic stresses hinder the productivity of plants. Abiotic stresses sometimes reduce more than half of the crop yields (Wang et al. 2003). Climate prediction models demonstrate the frequency of occurrence of different abiotic stresses including salinity, drought, flooding, extreme temperature, UV radiation, ozone, and metal toxicity that have increased to a great extent, compared to the previous decades (IPCC 2008; Mittler and Blumwald 2010). Under stressful conditions, plants are subjected to various physiological and metabolic changes throughout their life cycles starting from germination to final harvest. These changes include inhibition of germination, decreased growth, less photosynthesis, lower dry matter assimilation, water imbalance, impaired nutrient uptake, and ultimate reduction of yield and quality (Hasanuzzaman et al. 2012a, b, 2013a, b, c, d, 2014a, b, 2015, 2016). To attain global food security, understanding of plant responses to abiotic stresses is crucial because this is the prerequisite for developing approaches/tools for improving plant stress tolerance (Condon et al. 2004; Morison et al. 2008). In response to abiotic stresses, antioxidants, hormones, osmoprotectants, and many other essential metabolites are altered which have major roles to defend abiotic stresses. Traditional crop improvement methods are time-consuming, costly, sometimes uncertain, or unsuccessful and sometimes cause crop loss due to

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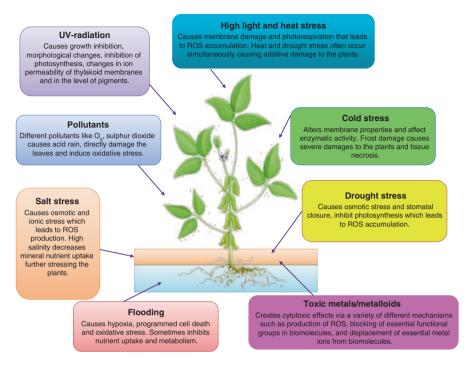
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evolution or genetic degradation. The use of exogenous phytoprotectants including micronutrient or trace elements is potent approaches to improve plant abiotic stress tolerance (Hasanuzzaman et al. 2011a, b, 2013a, b, c; Nahar et al. 2015a).

Trace elements are nutrients required in small quantities to facilitate a range of physiological functions. These elements stimulate growth but are not essential. Some are essential only for certain plant species or required under a given condition. The micronutrients or trace elements may include iron (Fe), zinc (Zn), copper (Cu), manganese (Mn), molybdenum (Mo), chromium (Cr), cobalt (Co), nickel (Ni), selenium (Se), silicon (Si), etc. Trace elements not only improve plant physiological processes and growth but play roles in improving plant stress tolerance. For instance, Si has been proved to improve plants' tolerance against drought, salinity, high temperature, chilling, UV radiation, nutrient imbalance, and metal toxicity (Raven 2001; Liang et al. 2007; Ma and Yamaji 2008; Hasanuzzaman and Fujita 2011; Ahmed et al. 2012). Plant species supplemented with Se have shown enhanced resistance to salinity (Hawrylak-Nowak 2009; Hasanuzzaman et al. 2011a, b), drought (Hasanuzzaman et al. 2010; Hasanuzzaman and Fujita 2011), extreme temperature (Djanaguiraman et al. 2010; Hawrylak-Nowak et al. 2010), metal toxicity (Hasanuzzaman et al. 2012b), and UV radiation (Yao et al. 2010). Selenium enhances reactive oxygen species (ROS) and oxidative stress tolerance (Hasanuzzaman et al. 2010; Hasanuzzaman and Fujita 2011). Exogenous Zn improved cadmium (Cd) tolerance and increased biomass accumulation by reducing its uptake and Cd-induced membrane damage (Wu and Zhang 2002). Zinc application reduced sodium uptake, enhanced antioxidants, and reduced salt-induced lipid peroxidation and electrolyte leakage (Aktas et al. 2006; Tavallali et al. 2010). Zinc also increased seed yield and thousand kernels weight against drought stress (Monjezi et al. 2012). Exogenous application of boron (B) conferred drought tolerance (Moeinian et al. 2011; Abdel-Motagally and El-Zohri 2016), salt tolerance (Salim 2014), and aluminum (Al) tolerance (Zhou et al. 2015). Salt (Pandya et al. 2004), Cd (Pal'ove-Balang et al. 2006; Peng et al. 2008; Sebastian and Prasad 2015), and drought (Upadhyaya et al. 2012) stresses were alleviated by exogenous manganese (Mn) application. However, the actual physiological functions of trace elements in conferring abiotic stress tolerance are still under study. Considering their importance, this chapter focuses on the roles of trace elements emphasizing specially the recent advances on the actions of biological trace elements in plant abiotic stress tolerance.

#### **10.2** Abiotic Stress: The Worst Enemy for Plants

Unlike animals, plants are sessile organisms and thus are bound to grow in the same habitat fighting with various environmental factors termed as abiotic stress. In the era of climate change, plants are constantly suffering from various abiotic stresses like salinity, drought, extreme temperature, flooding, metal toxicity, air pollution, ozone, UV radiation, and so on. These episodes are becoming more common due to rapid changes in climate. These stressors, alone or in



**Fig. 10.1** Major abiotic stresses for plants and their general effects (Hasanuzzaman et al. 2016; With Permission from Elsevier)

combination, attack plants, and thus the consequence is often unpredictable and becomes more severe than we expect. These effects are also greatly varied with the type and duration/extent of stresses and also depend on the plant species and genotypes (Pandey 2015). Therefore, it is very difficult to generalize the common effect of abiotic stress in plants. However, the major effects of abiotic stress in plants includes loss of seed germination, growth inhibition, disruption of energy assimilation and photosynthesis, imbalance in metabolism, imbalance in nutrient homeostasis and nutrient uptake, reduction of crop yield, and deterioration in crop quality (Fig. 10.1). One of the most common effects of abiotic stress in plants is oxidative stress which is described separately in a section later in this chapter.

### **10.3** Plant Responses to Abiotic Stresses

## 10.3.1 Salinity

Among these abiotic stresses, salinity/salt stress is considered as one of the most destructive stresses which reduces the land area and production of crop (Yamaguchi and Blumwald 2005; Shahbaz and Ashraf 2013). Salinity has terrible effects on the germination, vigor, and yield of the crop (Munns and Tester 2008). Genotype, growth

stage, intensity, as well as duration of stress are some of the most important factors which are accountable for the response of the plant to salt stress. When plant exposed to high salinity, it suffers from osmotic stress, ionic specificity, nutritional and hormonal disorders, changing metabolic and physiological processes, and finally oxidative damage (Munns 2002; Zhu 2007). Cellular membrane disorder, photosynthesis reduction, different toxic metabolite synthesis, nutrient unavailability, and ultimate plant death are some common consequences of salt stress in plants (Mahajan and Tuteja 2005). Thus, there are three main ways of affecting plants through salt stress, e.g., by developing osmotic stress through the reduction of soil water potential, creating the ionic imbalance within the cell, lowering the concentration of some ions specially potassium (K<sup>+</sup>) and calcium (Ca<sup>2+</sup>), and ultimately causing sodium (Na<sup>+</sup>) and chloride (Cl<sup>-</sup>) ions' toxicity. Under salt stress, increased Na<sup>+</sup> interferes with K<sup>+</sup> uptake which is very much important for protein synthesis by acting as binding material, and thus insufficient concentrations of K<sup>+</sup> reduces the protein synthesis (Blaha et al. 2000). Increased Na<sup>+</sup>-K<sup>+</sup> ratio and reduced K<sup>+</sup> availability result in the disruption of many enzymatic processes. Two major stresses called osmotic and ionic stresses are associated with salt stress. A usual response of plant to salt stress is growth inhibition which is caused by the changing concentration of soluble salt and osmotic potential of soil solution (Tavakkoli et al. 2011). Plant exposure to salt stress causes inhibition of water uptake and decreases cell expansion and lateral growth due to immediate osmotic stress occurring in the root medium (Munns and Tester 2008). Under salt-induced osmotic stress, development of shoot is severely affected compared to the root. Slower and reduced development of leaf area compared to root might be the reason behind it (Munns and Tester 2008). Impaired chlorophyll (chl) synthesis due to Cl- ion results in the chlorotic toxicity. Significant reduction of growth and water use efficiency are also resulting from the excess accumulation of Cl<sup>-</sup>. Germination is one of the most important phases of plant life cycle determining the final plant density. Germination and establishment of seedling are reported to decrease by salinity and considered as one of the major problems of the salt affected area. Salinity directly acts as a limiting factor for seed germination by delaying the germination time and reducing the final germination percentage and also limiting plant growth (Rahman et al. 2000). Extended salinity inhibited seed germination, while a dormant state was observed when seeds were subjected to lower level of salt stress (Khan and Weber 2008) and it was also revealed that germination process inhibited by salt stress due to lower osmotic potential of the growth medium. Salt stress also negatively affects the metabolism of nucleic acid (Gomes-Filho et al. 2008), proteins (Dantas et al. 2007), and seed food reserve utilization (Othman et al. 2006). An experiment was conducted by Kaveh et al. (2011) with S. lycopersicum, and he found significantly reduced germination when subjected to salinity. The gradual retardation and reduced germination of Hordeum secalinum were observed with an increase in NaCl concentrations. It was also concluded that 40% and 38% reductions in germination rate occur when treated with 400 and 500 mM NaCl, respectively (Lombardi and Lupi 2006). Bordi (2010) reported that different levels of NaCl treatments significantly reduced the germination percentage of B. napus. Some probable reasons of above-mentioned germination inhibition caused by salt stress are ionic imbalance, osmotic stress, and reduced seed water uptake. A study with four rice cultivars also showed remarkable germination reduction when

subjected to different salinity levels, and germination was also more significantly reduced in sensitive cultivar compared to tolerant one (Hasanuzzaman et al. 2009). Salt stress primarily affects plant by reducing the rate of the plant growth. Firstly, the water uptake capacity of the plant is reduced, and thus growth rate of plant also reduced quickly due to salinity. There are two phases involved in the salt-induced growth reduction. Osmotic stress is the reason behind the first-phase growth reduction, and second phase of growth reduction is caused by excess accumulation of salt and its toxicity to plants (Munns 2002). The second one ultimately affects the yield by decreasing the supply of photosynthate in plants and causing death of leaves. Delayed flowering and reduced crop yield are the results of this growth reduction caused by salt stress (Munns and Tester 2008). Moreover, alteration of plant water relation also caused by salinity resulting in cell turgor loss. At the same time, water uptake becomes more difficult because of the more negative water potential caused by increased salts present in the root zone (Munns 2002). Stomatal closure is one effective strategy of osmotically stressed plants for managing loss of water (James et al. 2008). Reduction in CO<sub>2</sub> uptake and restricted carboxylation reaction of leaf are executed by closing of stomata. Therefore, the reduction of carbohydrate production takes place during photosynthesis which negatively influences the plant growth and crop yield. The reduction of photosynthesis along with the reduced chl a, chl b, and carotenoid (Car) pigments were observed under salt stress in rice (Amirjani 2011), mustard (Ahmed et al. 2012), and many other crops (Hasanuzzaman et al. 2012a). Plants when under salt stress become unable to take nutrients and water from the soil due to physiological drought, reduces cell expantion, leaf growth, stomatal closure, and photosynthesis as well. Salt stress causes the premature yellowing, senescence, and ultimate death of the older leaf tissues resulting from the increased concentration of toxic ions which adversely affects photosynthesis (Munns 2002; Munns and Tester 2008). Thus, reduced photosynthesis is a remarkable effect of salt stress (Leisner et al. 2010; Raziuddin et al. 2011). Higher Na<sup>+</sup> and K<sup>+</sup> toxicity in chloroplasts also inhibits the photosynthesis process. It has been revealed that salinity involved a positive growth inhibition which is associated with a marked inhibition of photosynthesis (Fisarakis et al. 2001). Again, salt stress may affect carbon metabolism or photophosphorylation (Sudhir and Murthy 2004). High salt stress remarkably hinders crop yield due to impaired growth and physiological development. In Vigna radiata, reduction in pod per plant, seed per pod, and seed weight was observed under high salinity (Nahar and Hasanuzzaman 2009). However, plant tolerance to salt stress is a complicated process, and it depends on the plants age, growth phase, and environment. To endure the stress of salinity, plants have developed well-organized adaptive features at the biochemical level and have antioxidant defense system to fight against the adverse condition. Usually, under salt stress, plants accumulate osmoprotectants of different types like proline (Pro), betaines, glycerols, sucrose, trehalose, etc. (Budak et al. 2013). The mechanisms how plant responds to salt stress are very complex and are still a matter of further research. It is an urgent task for the plant biologists to explore the possible ways of alleviating the damaging effects of salt stress.

#### 10.3.2 Drought

Drought stress remained the greatest constraints for plant productivity throughout the world due to the increasing shortage of water. Drought stress limits plant growth significantly though the reduction of plant growth depends upon the degree of osmotic stress, stages of crop growth, and cultivar (Budak et al. 2013). Reduction in root and shoot growth is greater in susceptible soybean genotype because tolerant genotype can hold much water than susceptible one (Hossain et al. 2014). A study on growth of six bedding plants under drought stress revealed that plant dry weight, leaf area, and plant height differ significantly depending on species. Here, a significant reduction was observed in dry weight of Cineraria maritima L, Petunia x hybrida, and Plumbago auriculata under water-deficit condition, whereas leaf area reduced in Plumbago and plant height reduced in *Plumbago* and *Vinca* compared to control (Niu et al. 2006). Sapeta et al. (2013) reported the growth (stem diameter, stem length, leaf number, etc.) of two Jatropha curcas was reduced due to drought stress. Similarly, upon rehydration both genotypes showed tolerance to drought. In another study, two varieties of barley exposed to drought (50% field capacity, FC) showed significant reduction in leaf area and leaf appearance rate (Thameur et al. 2012). Reduction in water uptake and energy supply, impaired enzyme activities, loss of turgor, and reduction in cell division and expansion are considered as reasons for inhibited growth under water shortage condition (Taiz and Zeiger 2006; Hasanuzzaman et al. 2014c). Photosynthesis, the most sensitive physiological process to dehydration, is considered as physiological basis of crop yield (Luo et al. 2016). Several factors influence photosynthesis such as leaf area, stomatal opening and closure, water status in the leaf tissues, rate of CO<sub>2</sub> assimilation, electron transport and CO<sub>2</sub> assimilation reactions, and ribulose bisphosphate (RuBP) generation. Alteration in any of these factors upon dehydration condition affects photosynthesis (Ahmad et al. 2014; Hasanuzzaman et al. 2014b). The reduction in photosynthesis under deficit soil moisture condition in potato is due to stomatal closure, reduction in CO<sub>2</sub> assimilation, and excess production of ROS (Li et al. 2015; Obidiegwu et al. 2015). Comparative study between two maize cultivars revealed that photosynthetic activity was higher in drought-tolerant maize cultivar Giza 2 than susceptible Trihybrid 321 cultivar under water shortage condition (Moussa and Abdel-Aziz 2008). Reduction in photosynthetic pigments, changes in gas exchange characteristics, damage to photosystems, and reduced activity of enzymes related to photosynthesis are the common responses under water shortage condition and thus affect photosynthesis (Ashraf and Harris 2013). Marcińska et al. (2013) reported the reduction in chl content and photosynthesis under drought stress in wheat. Accumulation of compatible solutes is a common response of plant under water shortage condition. Sugar, sugar alcohol, glycine betaine, amino acids, and Pro are common compatible solutes in plant involved in osmotic adjustment, ROS scavenging, and protection in protein and cell structure (Budak et al. 2013). In recent years, Pro, glycine betaine, and total free amino acids were found to be increased in plant under dehydration condition to maintain leaf turgor and to improve water uptake in drying soil (Ajithkumar and Panneerselvam 2013). Water shortage significantly affects water

relation in plants. Water relation can be understood by some attributes such as relative water content (RWC), leaf water potential, and transpiration rate (Nahar et al. 2017).

### 10.3.3 Waterlogging

Among the abiotic stresses, excess water or flooding that causes submergence or waterlogging conditions is also harmful and even lethal for plant (Nishiuchi et al. 2012). Submergence is the condition when a plant is completely covered with water or remain under water and subjected to anaerobic from aerobic condition (Jackson and Ram 2003; Nishiuchi et al. 2012). In anaerobic submerged condition, plants also subject to other secondary stresses such as low light, impaired gas exchange, and unavailability of plant nutrients (Ram et al. 1999). On the other hand, water logging is the condition of soil when excess water limits gas diffusion in plant root zone (Setter and Waters 2003). Excess water or waterlogging condition caused by heavy rainfall, poor drainage, and irrigation practices subjected plants in complex changes in several environmental parameters and plant suffered from deficiency of oxygen, light, and nutrient. Deficiency of oxygen occurred by waterlogged condition due to limited gas diffusion and rapid consumption of oxygen by soil microorganism leads to hypoxia and progressively to anoxia within few hours. Due to hypoxia or anoxia, one of the immediate responses of water logging is closing of stomata to avoid water loss that inhibits respiration (García-Sánchez et al. 2007). Inhibited respiration consequently downregulates photosynthetic machinery which decreases chl content (Damanik et al. 2010). Water logging and submergence also decrease leaf water potential, stomatal conductance, and gas exchange which also decrease photosynthetic pigment (Arbona et al. 2008). In addition, under submerged condition, due to oxygen shortage, plant accumulates volatile ethylene which has both toxicity and signaling effect (Steffens et al. 2011). Although the mechanism is still unclear, hypoxic condition also results in oxidative stress through overproduction of ROS (Kumutha et al. 2009; Sairam et al. 2011).

Excess water damages most crops with exception of rice and some other aquatic plants (Bailey-Serres and Colmer 2014). Compared with other plants, rice has some adaptive potentiality for submergence tolerance like formation of aerenchyma and leaf gas film which contribute internal aeration during submergence. Besides these, tolerant rice cultivars survive under complete submergence using special strategies of growth control, namely, quiescence and escape strategy. Though rice can be grown well under flooded and waterlogging conditions, it is not well adapted to sudden and total submergence when sustained for several days (Nishiuchi et al. 2012; Jackson and Ram 2003). The visible injury symptoms in rice seedlings appeared with faster elongation of pseudostem and yellowing of older leaves (Jackson and Ram 2003). Banerjee et al. (2015) showed some biochemical changes in rice seedlings under submergence condition (7 days) like decrease in lipid peroxidation and increase of protein oxidation, phenol content, and flavonoid content. Rice seedlings are also damaged by oxidative stress in post submergence conditions. At recovery stage,

Ella et al. (2003) showed higher lipid peroxidation and lower chl content in rice seedlings after 7 days of submergence. Short-term (24 h) water logging condition in wheat induced transient N deficiency which reduced growth and yield (Robertson et al. 2009). After 72 h of waterlogging at three-leaf and jointing stage, growth and yield attributes of summer maize decreased in field condition (Ren et al. 2014).

Kumutha et al. (2009) observed higher lipid peroxidation and growth inhibition in pigeon pea seedlings due to activation of DPI-sensitive NADPH oxidase under 4 days of waterlogging condition. It also produced smaller and chlorotic leaves which senesce earlier. Kumar et al. (2013) studied the physiological and morphological response of tolerant and sensitive cultivars varies in *V. radiata* after 3, 6, and 9 days of waterlogging. Growth inhibition and yield reduction were higher in sensitive cultivar (Pusa Baisakhi & MH–1 K–24) compared to tolerant cultivar (T 44 & MH–96– 1) because of poor maintenance of leaf respiration rate and lower formation of adventitious root. Waterlogging and post-waterlogging condition induced oxidative stress and decrease photosynthetic rate in citrus seedlings (Hossain et al. 2009).

### 10.3.4 High Temperature

Increasing global temperatures in last few decades is responsible for severe crop loss in different countries throughout the world (Long and Ort 2010). Global temperature is expected to increase up to 2.5-5.4 °C by year 2100 (Ciscar 2012). Intensity, duration, and the rate of increase of temperature are important factors to create damage effects on plants (Wahid et al. 2007). Reduced germination and biomass, increased tillering, chlorosis, necrosis, early senescence of floral bud, premature death, and senescence of fruit are some common damage effects of high temperature (HT, Wahid et al. 2007). Heat stress during seed development results in structural disintegration and physiological disorders which further reduces germination and vigor, emergence, and seedling establishment (Akman 2009). High temperature hindered seed germination in rice by reducing a group of proteins involved in methionine metabolism, amino acid biosynthesis, energy metabolism, reserve degradation, and protein folding (Liu et al. 2014). Germination of maize is inhibited beyond 37 °C due to mutilation of protein synthesis whereas coleoptile growth is completely stopped at 45 °C (Riley 1981; Akman 2009). Increase of soil temperature beyond 45 °C causes germination failure and epicotyl emergence in sorghum (Peacock et al. 1993). In tomato, seedling emergence stops beyond 30 °C (Camejo et al. 2005). In rice, between 15 and 37 °C germination was 90%. But no germination occurred at 8 and 45 °C (Hartmann et al. 1997). Seed germination of Phacelia tanacetifolia inhibited by 2.7%, 5.8%, 84.0%, 89.0%, and 91.5% at temperatures of 20, 25, 30, 35, and 40 °C, respectively, compared to 15 °C (optimum for germination) (Tiryaki and Keles 2012). Lack of plasma membrane reorganization, cytoplasmic ion channel maintenance, and inhibition of the reactivation of the metabolic processes for mobilization of ions from a bound to a free form are responsible for germination reduction under HT in *Phacelia* seeds (Pirovano et al. 1997). High temperature adversely affects soil-plant- water relation, nutrient uptake,

photosynthesis, transpiration, and respiration, disrupts source/sink balance, and hinders translocation of assimilate. As a result, growth and development are negatively affected (Prasad et al. 2011). Plants suffer from HT damages are often characterized by decreased water content and accumulation of osmoprotectant molecules. High temperature reduced water content in trifoliate orange seedlings (Fu et al. 2014). An increase of Pro level was noticed in transgenic plant grown under HT condition (Cvikrová et al. 2013). High temperature (31/18 °C and 34/22 °C, day/night) was found to decrease total dry weight and harvest index in wheat (Prasad et al. 2011). Enzymes are thermolabile. Catalytic properties of most enzymes are lost because of which denature of enzyme under HT. Biosynthesis of proteins and enzymes are hampered under HT. Severe HT results in complete denaturation of protein, enzymes, and membrane function and causes cell death (Allakhverdiev et al. 2008). Structural disorganization of thylakoids and swelling of stromal lamellae are HT-induced damages (Zhang et al. 2005). Chlorophyll content decreased by 19% in wheat subjected to HT (31/18 °C and 34/22 °C, day/night) (Prasad et al. 2011). Increase of temperature from 22 to 32 °C decreases photosynthesis rate and transpiration (Zhang et al. 2010). Solubility of oxygen increases more compared to carbon dioxide under HT. Oxygen becomes more concentrated for which oxygenation of RuBP occurs at HT that is termed as photorespiration. Under HT stress, gross photosynthesis is inhibited but respiration and photorespiration increase for which net photosynthesis decreases (Allakhverdiev et al. 2008; Mittler et al. 2012). As HT stress continues with decreasing net photosynthesis, plant begins to use up carbohydrate reserves that cause growth reduction. Inhibition of photosynthesis during HT stress is related to reduction of activity of RuBisCo (Allakhverdiev et al. 2008). The functioning of photosystem II (PS II) is inhibited by HT (Mittler et al. 2012) due to decrease of electron transport, removal of external proteins, and release of calcium and magnesium ions from binding site (Wahid et al. 2007; Zlatev and Lidon 2012). The singlet oxygen is overproduced under HT that damage D1 and D2 proteins (Yoshioka et al. 2006). HT restricts conversion of photosynthetic assimilates into starch that ultimately hampers grain development of cereal or seed development of legume (Stone and Nicolas 1994). Reproductive development has been long recognized as extremely sensitive to heat stress and most important reason for decreasing plant productivity (Thakur et al. 2010). The male gametophyte is more sensitive to HT in contrast to pistil or the female gametophyte (Hedhly 2011). In tomato flowers due to reduction of anthers and pollen viability, the successful fertilization is seriously hampered which further hinders development of the embryo (Barnabás et al. 2008). High temperature reduced soluble sugars in the anther and pollen grains which decreased pollen viability (Ismail and Hall 1999). In barley and Arabidopsis, anther development is hampered under HT (30-35 °C) due to arrest of cell proliferation, anomalous vacuoles, and mitochondrial and chloroplast development (Sakata et al. 2010). Decrease of water use efficiency during reproductive development of wheat results in decrease of photosynthesis and leaf area. As a result grain weight and sugar content of kernels decreased (Shah and Paulsen 2003) which also modulated nutritional flour quality (Hedhly et al. 2009). High-temperature stress adversely affects xylem and phloem loading which reduces water transportation and nutrient uptake (Taiz and Zeiger 2006). High-temperature stress (38 °C, 4 days) significantly increased the transpiration rate of tomato plant (Cheng et al. 2009). Increases of temperature may result in yield reduction between 2.5 and 10% in different agronomic species throughout twenty-first century (Hatfield et al. 2011). A decrease of 6.7-10% yield in rice (Peng et al. 2004; Lyman et al. 2013) and 10% reduction of yield in wheat (You et al. 2009) has been predicted with increase of 1 °C temperature in growing periods. Maize pollen viability decreases in temperatures above 35 °C (Dupuis and Dumas 1990). High temperature above 30 °C decreased seed production in soybean (Lindsey and Thomson 2012) and common bean (Porch 2006) grown in tropical humid regions. Seed set on male-sterile, female-fertile soybean plants decreased when day time temperature increased by 30-35 °C (Wiebbecke et al. 2012). In Citrus sinensis, temperatures higher than 30 °C increased fruit drop (Cole and McCloud 1985). In wheat, HT (31/18 °C and 34/22 °C, day/night) reduced grain numbers by 56% and individual grain weight by 25% which decreased grain yield significantly (compared to control temperature, 24/14 °C) (Prasad et al. 2011). Failure of fertilization, reduced panicle size, and damaged floral primordia were correlated to 54-64% loss in seed set in sorghum (Jain et al. 2007).

### 10.3.5 Chilling

In general, chilling stress indicates the low-temperature injury without forming ice crystals, and freezing stress indicates injury due to ice formation within plant tissues. Tolerance to chilling or freezing stresses is dependable to plant species. Chilling temperature reduces crop productivity by affecting several aspects of plant growth and developmental processes (Sanghera et al. 2011). Early growth stages of plant are often adversely affected by chilling stress. Optimum temperature range for germination of rice seed is 20-35 °C. According to Yoshida (1981), the temperature of 10 °C is minimum critical value, and below this temperature, rice seeds did not germinate. In B. napus, for 50% germination, it took 3 days at 8 °C, whereas it took 13 days at 2 °C (Angadi et al. 2000). The maximum seed germination and vigor index was reported in T. aestivum plants at 20-30 °C, compared to the temperature below 20 °C (Buriro et al. 2011). Gossypium hirsutum exposed to low temperature (LT) below 20 °C showed delayed and reduced germination (Krzyzanowski and Delouche 2011). In T. aestivum, the germination was drastically reduced at temperature below 8–10 °C (Zabihi-e-mahmoodabad et al. 2011). Chilling temperature causes seedling growth inhibition and abnormal phenotype of seedlings including stem discoloration, leaf yellowing or whitening, white patches/spots, withering, and reduced tillering at their vegetative stage (Nahar et al. 2012). Seedling growth and dry weight of mung bean seedlings decreased under chilling temperature (6 °C). These seedlings also showed abnormal phenotypic appearance (Nahar et al. 2015b). Nahar et al. (2009) observed cold (11 °C) injury symptoms in rice. Stunted growth, leaf chlorosis, irregular number of tiller, and malformed and discolored grain symptoms were commonly observed in chill affected rice plant. Lower temperature reduced growth duration, decreased biomass accumulation, and harvested index,

seed number and seed weight of soybean (Calviñoa et al. 2003). Male gametophyte developmental process, meiosis, and tapetal hypertrophy are distorted under chilling stress. Pollen grain becomes distorted and short, anther protein degrades, and pollen tubes are deformed under chill temperature which causes pollen sterility. Fertilization and further development of fruit and seed are hampered due to chillinduced inhibition of male and female gametophyte development which is mainly due to reduced size of reproductive organs and anomalous structures of embryo sac (Jiang et al. 2002). Delayed flowering, bud abscission, sterile flowers, aborted embryo, and unfilled grain are evident in chill affected rice and other grain crop (Jiang et al. 2002; Thakur et al. 2010). Low temperatures  $(-2^{\circ} \text{ to } -5.5 \text{ }^{\circ}\text{C})$  reduced the number of flower bud in Simmondsia chinensis (Nelson and Palzkill 1993). Premature flowering development in Chinese cabbage is increased by chilling temperature (Kalisz and Cebula 2001). Distorted panicle initiation and emergence, delayed heading, and sterile and malformed spikelet were noticed in rice genotypes under chilling stress of 11 °C (Nahar et al. 2009). Delayed flowering, delayed blooming, and higher rate of pollen shed and pod abortion were noticed in different genotypes of canola under chilling stress (Miller et al. 2001).

Chilling temperature damages cell membrane by protein denaturation, disrupting protein lipid structure and precipitation, and disrupting membrane permeability (Wang and Li 2006). Chilling stress thus converts the membrane into solid gel phase. Ion leakage, imbalanced anion/cation exchange, disruption of anions and cataions homeostasis, disruption of osmosis, and diffusion processes become the fate of chill affected plant (Farooq et al. 2009). Chill temperature inhibits photosynthesis due to disruption of thylakoid membrane and chloroplast structure. Electron transport, carbon cycle metabolism and stomatal conductance are hampered by chilling temperature. The PS II is considered as the primary target of chill-induced damage. Chilling temperature highly decreases the quantum efficiency of PS II. Chilling temperature restricts RuBisCO regeneration and confines the photophosphorylation (Allen and Ort 2001). Total chl content reduced by 50% in rice due to exposure to LT (15/10 °C, 14 days) (Aghaee et al. 2011). Total chl (a + b) of mung bean plants reduced by 32% and 38%, after 2 and 3 days of chilling temperature (6 °C) exposure, respectively, compared to the control seedlings (Nahar et al. 2015b). Wheat plants exposed to chill temperature of 3 °C (for 48 and 72 h) showed decreased chl, CO<sub>2</sub> assimilation, and transpiration rates (Yordanova and Popova 2007). Dehydration stress may also result from freezing of cell constituents, solutes, and water (Yadav 2010). In temperatures below 0 °C, ice formation is started in intracellular spaces that are also the vital reason for hindering the solute transportation (Thomashow 1999; Yadav 2010). Damaging the root system chill temperature reduces water and nutrient uptake and causes dehydration and osmotic stress (Chinnusamy et al. 2007). Damaged root system and stomatal closure were described as cause of chill-induced dehydration stress (Yadav 2010). Cucumber root showed chill-induced damage in cortical cells. Chill temperature also increased density of cytoplasm and damaged the endoplasmic reticulum (Lee et al. 2002). Decreased root hydraulic conductance, leaf water, and turgor potentials are common effects of chill temperature in sensitive plants (Aroca et al. 2003). During chillinduced dehydration, stress plant metabolic functions are altered which include accumulation of enzymes and isozymes (Hurry et al. 1994). Low-temperatureinduced yield reduction is a common occurrence to plants due to its adverse effects on vegetative and reproductive phases (Nahar et al. 2009; Kalbarczyk 2009; Riazud-din et al. 2010). In rice, chilling temperature significantly reduced yield which was due to flower abortion, pollen and ovule infertility, distorted fertilization, poor seed filling, and seed setting (Thakur et al. 2010). Other study revealed that chilling temperature reduced yield by 30-40% in temperate regions (Andaya and Mackill 2003). Rice varieties of BRRI dhan46 and BRRI dhan31 showed 16 and 37% yield reduction, respectively, due to late sowing mediated chilling stress (Nahar et al. 2009). Low temperature induced anomalous seed structure in B. napus and B. rapa. Low temperature reduced diameter and created white patches, white reticulation, red-brown pigmentation, folded seed, and shriveled seed (Angadi et al. 2000). Seed weight in G. max plants decreased by 5% under chill temperature of 13/23 °C (day/ night) as reported by Rasolohery et al. (2008). Chilling stress of 11 °C caused yield reduction in maximum genotypes of rice, and only 23 genotypes were screened out among the 244 genotypes which showed higher yield and had better phenotypic appearance in terms of vegetative and reproductive development (Nahar et al. 2009).

### 10.3.6 Toxic Metals

World population is increasing day by day together with fast industrialization. As a result, big amount of toxic metals is turned out and enter into the environment (Sarma 2011). Increasing environmental pollution caused by toxic metals is becoming a significant problem in the modern world (Sun et al. 2005). Nowadays, losses in agricultural yield are very common because of soil contamination by toxic metals, and it is a serious threat for wildlife and humans health (Sharma and Dubey 2007; Sharma and Dietz 2008). Due to high reactivity of toxic metal, they can easily influence growth, development, and energy synthesis processes of organisms. So, metal toxicity is one of the key abiotic stresses leading to dangerous health effects in plants and animals (Maksymiec 2007). Excessive toxic metal uptake may occur by plants, which possibly will part take in many physiological and biochemical reactions of plants that will be able to break the normal growth of the plant by upsetting absorption, translocation, or their synthetic processes (Hasanuzzaman and Fujita 2012a,b). Plant suffered a lot by toxic metal/metalloids from germination to final seed yield. Seed germination is the primary stage of plant life, and so it is very sensitive to many environmental stresses. Germination of seeds of Salicornia brachiata was affected badly by different doses of Cd, Ni, and As (Sharma et al. 2011). In addition, some scientists reported that growth of seedling is very susceptible to heavy metals (Hg, Pb, Cu, Zn, etc.) in comparison to germination of seed, while Cd is the exception, because it disturbed both processes at same concentrations (Li et al. 2005). Different toxic metal/metalloids cause oxidative stress in plants. The generation of ROS is the primary response of plants under metal stress. A variety of metals can directly generate ROS through

Haber-Weiss reactions. Moreover, ROS overproduction and oxidative stress occurrence in plants may occur due to indirect consequence of heavy metal toxicity (Wojtaszek 1997; Mithofer et al. 2004). Lipid peroxidation of cells is the most detrimental effects under heavy metal stress, which can cause biomembrane deterioration directly. Hasanuzzaman et al. (2012b) observed that Cd stress (1 mM CdCl<sub>2</sub>, 48 h) increased malondialdehyde (MDA) content by 134% and H<sub>2</sub>O<sub>2</sub> content by 60% in rapeseed seedlings. Toxic metals/metalloids also altered the activities of antioxidant enzymes of plants as reported by several researchers. Nahar et al. (2016) reported that Cd stress in mung bean plants reduced growth, damaged chl, decreased leaf RWC and altered proline (Pro), and enhanced oxidative damage [lipid peroxidation, H<sub>2</sub>O<sub>2</sub> content, O<sub>2</sub><sup>--</sup> generation rate] by disrupting activities of nonenzymatic (AsA and GSH) and enzymatic [catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), mono dehydro-ascorbate (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), and glutathione S-transferase (GST)] antioxidants. Similar kinds of physiological disorders were

observed in rice plant under Cd stress (Rahman et al. 2015) and wheat plant under

arsenic (As stress) (Hasanuzzaman and Fujita 2013).

### 10.3.7 Ozone

Ozone  $(O_3)$  is a heterogenous air pollutant framed in the troposphere layer. In presence of sunlight, O<sub>3</sub> is developed due to oxidation of oxides of nitrogen, volatile organic hydrocarbons, and carbon monoxide those generate primarily from gas motors and burning/blazing of other fossil fuels (Kesselmeier and Staudt 1999). Expanding levels of surrounding ozone may force destructive impacts on human, animals, and plants. The harming influence of  $O_3$  to plant species might be acute or chronic. Acute damage is created by a high concentration of O<sub>3</sub> (>150 ppb) inside a brief timeframe (Gillespie et al. 2011) and brought about foliar injuries and impels an array of biochemical and physiological reactions in plants (Tsukahara et al. 2015). Chronic damage to lower  $O_3$  concentrations is portrayed by decreasing growth and development without noticeable harm (Gillespie et al. 2011). Crops demonstrate differential intra and interspecific phenotypic responses to O<sub>3</sub> (Biswas et al. 2008; Brosche et al. 2010). The obvious indications of  $O_3$  damage have been evaluated in foliage part. Chlorotic or necrotic injuries on leaves, reduced biomass production, and yield reduction are common consequences of O<sub>3</sub> stress (Wilkinson et al. 2012). The reproduction process of plants is greatly hampered due to exposure of tropospheric O<sub>3</sub>. Grain characteristics of rice, wheat, and maize crops are negatively affected under O<sub>3</sub> stress (Biswas and Jiang 2011). It is estimated that elevated O<sub>3</sub> can reduce grain yield of different rice cultivars by 4.2–5.2% (Sawada et al. 2016) and yield of soybean by 23-27% (Wang and Mauzerall 2004). The fruits of different types of plants are affected differentially under O3 stress. Pod development is adversely affected by O<sub>3</sub> which results in reduction of number and size of pod. Tuber number and yield have been demonstrated to decrease as affected by  $O_3$  in tuber crops (Wilkinson et al. 2012). In potato, tuber number and total tuber yield decreased by 38% and 45%, respectively, due to exposure of  $O_3$  (Foster et al. 1983). Pollen germination and tube development are adversely affected by  $O_3$ ; abscissions of bud or flower and individual ovules or seeds are commonly occurred phenomenon under  $O_3$  stress (Black et al. 2000).

### 10.3.8 Ultraviolet Radiation

Solar radiation supplies the essential energy for growth and development of plant via photosynthesis but high light and particularly its integral ultraviolet (UV) fraction cause stress potentially leading to severe injury to cellular components of plants even the DNA and proteins (Müller-Xing et al. 2014). The ultraviolet radiation from sunlight is divided into three broad classes: UV-A (320-400 nm), UV-B (290-320 nm), and UV-C (280-100 nm) light. UV-A and UV-B can easily reach to the surface of earth, but UV-C is filtered out in the atmosphere (Biedermann et al. 2011). Stratospheric ozone layer does not affected by the UV-A, because it is not attenuated by ozone layer. The wavelength of UV-C is shorter than 280 nm, and it cannot arrive at ground level, and this is not expected to change. The UV-B radiation gets top most importance by the researcher and geologist, because ozone absorbed it. Among UV radiation types, even though UV-B is only a negligible constituent of the total solar radiation (less than 0.5%), due to its high energy, its potential for causing biological damage is remarkably high, and even little raise could lead to considerable biological damage (Zlatev et al. 2010). Due to large-scale production of anthropogenic pollutants, intensities of UV-B radiation in the sunlight are slowly increasing in the world as a result of depletion is going on in the stratospheric ozone layer. Previous research on UV-B radiation confirmed that it has significant photobiological consequences on growth, development, and other biochemical activities of plants (McNamara and Hill 2000). The intensities of UV-B vary with the angle of sun and thickness of stratospheric ozone layer. So, all organisms of the earth are exposed to UV-B radiation in different intensities. The rate of enhance UV-B intensity depends on latitude, and higher amount of UV-B is recorded in antarctic and arctic regions (Zlatev et al. 2010).

Frequent discharge of chlorofluorocarbons and other pollutants due to anthropogenic activities is increasing the amount of ultraviolet radiation in the earth surface which is the main reason of stratospheric ozone layer depletion (Dai et al. 1997; Sharma et al. 1998). The stratospheric ozone depletion and increased solar UV radiation cause injury to plants and animals (Costa et al. 2002; Ravindran et al. 2010). Sunlight is obligatory for photosynthesis of terrestrial plants, so they are mostly vulnerable to UV radiation (Greenberg et al. 1996; Sharma et al. 1998). The UV-A radiation shows less harmful effect to organism among all the UV radiations. In addition, also UV-C radiation does not show much harmful effects on the biota because it is observed by the oxygen and ozone layer (Barta et al. 2004). The impact of UV radiation on most cultivated plants is negative and unfavorable to plant growth and development (Vyšniauskienė and Rančelienė 2014). UV radiation creates oxidative stress (Costa et al. 2002), which come up from the detrimental effects of ROS, and they react with lipids, proteins, and nucleic acid (Dai et al. 1997). Plants have many enzymatic and nonenzymatic detoxification systems under normal healthy growth condition to efficiently scavenge or detoxify the ROS or their secondary reaction products (Bartling et al. 1993). Nasibi and M-kalantari (2005) carried out an experiment regarding the action of the antioxidant defense system in Brassica napus, under different ultraviolet radiation (UV-A, UV-B, and UV-C). This experiment demonstrated that UV-B and UV-C radiation induced oxidative stress. Because, they increased the lipid peroxidation and total ascorbate content of cells. The treatments of UV-B and UV-C significantly increased flavonoids and anthocyanins levels compared with control and UV-A-treated plants. These compounds perform as internal filters and also have an antioxidant action against ROS such as H<sub>2</sub>O<sub>2</sub>. Protein content increased under UV-B and UV-C, which probably related to the synthesis of different defense proteins such as HSP. On the other hand, treatment of UV-B radiation for 8 days on maize plants (Zea mays L. cv. SC. 704, 21 days old) increased lipid peroxidation (MDA content) and decreased RWC. UV-B stress also increased carotenoid content and activity of some enzymes (APX and GPX) Javadmanesh et al. (2012). In addition, plants under adverse conditions decreased their protein content in root tissue but not in shoot tissue. Vyšniauskienė and Rančelienė (2014) reported that compared to the control, the plant height of early potato cultivars reduced after the UV-B exposure. However, fresh and dry weight of leaves, chlorophyll a and b, and carotenoid contents in potato cultivars remained unaffected after UV-B treatment. Antioxidative enzymes also increased due to exposure of UV-B in potato cultivars which prove the active response of plant to UV-B-induced stress. They also suggested that response and tolerance depend on the plant genotype. Similar kind of reduction in photosynthetic parameters was observed in cotton plant under UV-B stress (Reddy et al. 2003). UV radiation reduces the total mass and yield of different plants (Gao et al. 2004; Liu et al. 2013). A field experiment was carried out with three soybean cultivars [Hai339 (H339), Heinong 35(HN35), and Kennong18 (KN18)] by exposing them to higher UV-B radiation. The UV-B radiation reduced height of plant, dry weight of individual stem, and yield per plant. Pod number per plant was the most responsible component for yield change under UV-B radiation in the 2-year study. UV-B radiation reduced pod number per plant of three soybean cultivars by 43.5% for KN18, 30.4% for HN35, and 29.6% for H339. They also stated that seed number per pod was less affected than the pod number per plant under UV-B light treatment. The UV-B radiation had no noteworthy effect on effective filling period, but seed size was negatively impacted by this radiation, and it reduced 12.3% for all the cultivars of soybean. UV-B radiation decreased the cotyledon cell number, as a result seed size was decreased. No significant effect on cell volume of cotyledon, cell weight, or cell growth rate of soybean varieties was observed under enhanced UV-B radiation (Liu et al. 2013). Similarly Gao et al. (2004) reported that higher UV-B radiation caused a considerable declination in the growth, yield, and quality of maize. Besides the yield and biomass reduction, UV-B radiation altered the nutrient status of plants (Yue et al. 1998).

#### 10.4 Abiotic Stress-Induced Oxidative Stress

Reactive oxygen species are unavoidable by-products derived from the reduction of molecular oxygen  $(O_2)$  and include some free radicals: superoxide  $(O_2^{-})$ , hydroxyl radical (OH<sup>•</sup>), alkoxyl (RO<sup>•</sup>), and peroxyl (ROO<sup>•</sup>) and some non-radical products, H<sub>2</sub>O<sub>2</sub>, singlet oxygen (1O<sub>2</sub>), etc. (Gill and Tuteja 2010; Sandalio et al. 2013). Chloroplast, mitochondria, and peroxisomes are the main source of ROS production, chloroplast being the main source (Apel and Hirt 2004). Physical and chemical activation is involved in ROS generation. Physical activation involves transfer of energy from photo activated pigment such as excited chl (chl triplet state, 3chl) that involved in the transfer of its excitation energy onto  $O_2$  to make  ${}^1O_2$ . Chemical activation involves univalent reduction of dioxygen or triplet oxygen (molecular oxygen) to water; four electrons and four protons are engaged which leave three major ROS, viz. O<sub>2</sub><sup>-</sup>, H<sub>2</sub>O<sub>2</sub> and •OH (Gill and Tuteja 2010; Sandalio et al. 2013). Under normal or nonstress environment, electron flow from excited PS centers is transferred to NADP+ which is reduced to NADPH. This NADPH enters Calvin cycle where it reduces final electron acceptor (CO<sub>2</sub>). Calvin cycle recycles NADP (Vašková et al. 2012). But under stress conditions, NADP recycling is impaired, electron transport chain (ETC) can be over loaded, and electron leakage from ferredoxin is converted to O<sub>2</sub>, reducing it to O<sub>2</sub><sup>-</sup> through Mehler reaction (Elstner 1991). The  $O_2^{-}$  can be converted into more reactive  $H_2O_2$  by SOD activity in outer stromal membrane surface (Gill and Tuteja 2010). In presence of Fe<sup>2+</sup>, H<sub>2</sub>O<sub>2</sub> is transformed into extreme reactive OH• through Fenton reaction (at Fe-S centers) (Gill and Tuteja 2010; Sharma et al. 2012). Peroxisome metabolic processes are chiefly involved in the production of  $H_2O_2$ . The  $O_2$  - can also be produced in peroxisome (Noctor et al. 2002). Mitochondrial electron transport chain (ETC) is also an important source of ROS production in plant cells. Mitochondrial ETC and ATP syntheses are coupled strongly, and stress-induced imbalance between these two may lead to over-reduction of electron carriers as a result of which ROS overproduce (Noctor et al. 2007; Blokhina and Fagerstedt 2010). NADPH-dependent electron transport process is involved with Cyt  $P_{450}$  and  $O_2^{-}$  generation in the endoplasmic reticulum (Mittler 2002). In cell wall, plasma membrane, and apoplastic area, ROS including OH and  $H_2O_2$  can be overproduced through ranges of biochemical reactions (Heyno et al. 2011).

Under normal growing (nonstress) condition, ROS is kept in a balance state by wellequipped antioxidant defense system. In contrast, under environmental stress condition, excess ROS generation leads to oxidative stress. The ROS can cause membrane lipid peroxidation, protein oxidation, and DNA damage. Cell structure and biochemical and physiological process are disrupted by ROS-induced oxidative stress and, at extreme state, gradually lead to programmed cell death (Gill and Tuteja 2010; Hasanuzzaman et al. 2012a). ROS-induced oxidative stress is a common phenomenon under different abiotic stresses. The ROS production under salt stress might be increased by three-fold. The level of  $H_2O_2$  can be increased by 30-fold under salt stress (Singh and Flowers 2010). Salinity-induced oxidative stress was documented in different plant species. Salt stress significantly increased  $H_2O_2$  and MDA levels in mung bean seedlings (Nahar et al. 2014). Salt affected wheat seedlings showed high level of  $H_2O_2$  by 60%, compared to control. Lipid peroxidation in those wheat seedlings increased by 27 and 73% at 150 mM and 300 mM NaCl, respectively (Hasanuzzaman et al. 2011a, b). Drought is one of major stresses contributing the major ROS and causing severe oxidative stress within the plants. More than 70% of total H<sub>2</sub>O<sub>2</sub> were demonstrated to produce due to photorespiration under drought stress condition (Noctor et al. 2002). Cellular membrane damage was related to significant rise in  $O_2^{-}$  and  $H_2O_2$  in leaves of drought affected *Malus* spp. (Wang et al. 2012). Similar results were demonstrated in mung bean seedlings under PEG-induced drought stress (Nahar et al. 2017). High-temperature raised ROS production in wheat seedlings. The  $H_2O_2$  contents in wheat seedlings were 0.5, 0.58, 0.78, and 1.1 µmol g<sup>-1</sup> FW in response to 22, 30, 35, and 40 °C (2 h) temperature stresses, respectively (Kumar et al. 2012). Mung bean seedlings exposed drought and high-temperature stress separately or in combined increased H2O2 and O2 - production which was evidenced from higher cellular H<sub>2</sub>O<sub>2</sub> and O<sub>2</sub><sup>--</sup> contents and increased number of spots of these ROS in leaves, compared to control. The  $H_2O_2$  level,  $O_2^{-}$  generation rate, lipoxygenase (LOX) activity, and MDA contents under combined HT and drought stress were 122, 146, 108, and 120%, respectively, in contrast to control (Nahar et al. 2016a). Low temperature creates imbalance between light absorption and light use due to inhibition of  $C_3$  cycle which enhances ROS production. ROS generation also increased due to increased photosynthetic electron flux to  $O_2$  as well as the over-reduction of respiratory ETC (Hu et al. 2008). Waterlogging or flooding induces hypoxic or anoxic environment. Under waterlogging stress, ROS can be produced when plants go through a hypoxia/anoxia from normoxic conditions and also under the condition when plants return to an aerobic environment (Irfan et al. 2010). Enhanced accumulation of H<sub>2</sub>O<sub>2</sub> or lipid peroxidation under anoxic conditions was reported previously (Sairam et al. 2011). Plants under heavy metal exposure cause a significant increase of ROS production and subsequent oxidative stress. Redox-active metals such as Fe, Cu, Cr, V, and Co initiate redox reactions in the cell and directly involved in the formation of OH' via Haber-Weiss and Fenton reactions (Sharma and Dietz 2008). Other metals also generate ROS and cause oxidative stress in different ways (Hasanuzzaman et al. 2012a; Nahar et al. 2016). Heavy metal-dependent activation of LOX also leads to lipid peroxidation (Nahar et al. 2016). Mung bean seedlings exposed Cd stress showed a higher level of ROS generation including  $H_2O_2$  and  $O_2^{-}$ , a higher LOX activity, and increased lipid peroxidation (Nahar et al. 2016). Wheat seedlings exposed to As; 0.25 and 0.5 mM showed 41 and 95% increase of H<sub>2</sub>O<sub>2</sub> and 58 and 180% increase of lipid peroxidation level, respectively, compared to control (Hasanuzzaman and Fujita 2013). Ozone (O<sub>3</sub>) being strong oxidant interacts with apoplastic constituents in generating ROS (Yan et al. 2010). Different studies designated that elevated O<sub>3</sub> highly increased the levels of O<sub>2</sub><sup>--</sup>, H<sub>2</sub>O<sub>2</sub> and lipid peroxidation in plants (Yan et al. 2010; Feng et al. 2011). UV-B radiation also generates ROS and results in damage to proteins, lipids, nucleic acids, and associated enzymes (Du et al. 2011; Singh et al. 2011).

# **10.5** Highlights of Potent Micronutrients and Trace Elements Associated with Plants' Functions

Micronutrients and trace elements are required in small amount but equally important for plant functions as like macronutrients. Their major functions in plants are summarized in Table 10.1. Plants show some deficiency symptoms due to lack of these nutrients as shown in Fig. 10.2.

Elements	Functions
Copper	Essential for carbohydrate and nitrogen metabolism also plays roles in lignin synthesis for cell wall strengthening. It plays an important role in chl synthesis. It also activates some enzymes by playing role as coenzyme
Iron	It plays role in nitrogen reduction and fixation and lignin formation. Important for chlorophyll synthesis and energy transfer
Zinc	Important for energy production, formation of chlorophyll, and plant hormone like indole acetic acid (IAA). Helps in protein synthesis, better seed quality, and uniform crop maturity
Boron	Helps in carbohydrate transport, cell wall formation, pollen formation
Manganese	Important for enzyme activity and other metabolic processes. Important for nitrogen metabolism, pollen tube growth, and root hair formation
Molybdenum	Essential for pollen formation, fruit and grain formation. It can convert nitrate into usable form
Cobalt	Promotes to auxin formation and nitrogen fixation. It is also essential for the development of bud, plant stem, and coleoptiles. It also increases drought resistance to seed
Nickel	Component of some plant enzymes, most notably urease, which metabolizes urea nitrogen into useable ammonia within the plant. It plays role in root nodule growth. Essential part of glyoxalase system
Silicon	Strengthens cell walls, stimulates plant growth. Performs as essential function in healing plants in response to environmental stress
Selenium	It stimulates nitrogen assimilation and regulates the water status of plants. Acts as antioxidant and stress protectants

Table 10.1 Major functions of trace elements/micronutrients in plants

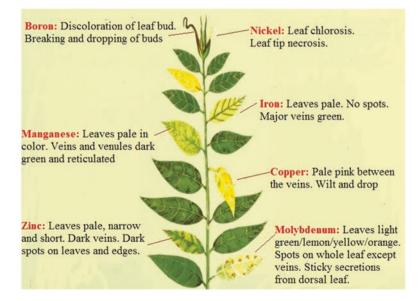


Fig. 10.2 Visualization of deficiency symptoms of major trace elements in plants

# **10.6 Functional Role of Trace Elements in Conferring** Abiotic Stress Tolerance

Although trace elements are required in small amount, their essentialities are the same as macronutrients. Although several trace elements have not yet been identified as essential elements, they have some vital functions in plant growth and development (Fig. 10.3). In addition, these elements have specific metabolic functions and diverse roles in stress tolerance (Table 10.2). However, these elements showed toxicity in plants when exposed to high concentration.

### 10.6.1 Copper

Due to its presence in multiple oxidation states in vivo, Cu is involved in many physiologic conditions. The role of Cu in plants stress tolerance is well considered due to its functions as structural element of photosynthetic electron transport, cell signaling, and metabolism as well as participation in enzymatic activities (Yruela 2005). It is important that both deficiency and abundance of Cu negatively affect plant processes. For instance, photosynthetic ETC is hampered under both Cu

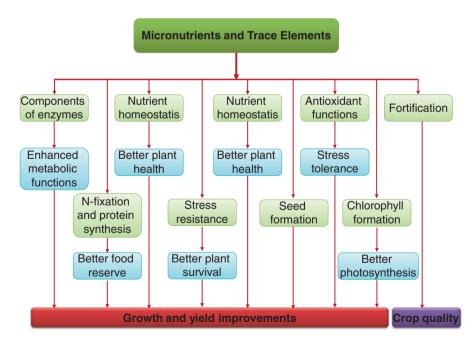


Fig. 10.3 Different aspects of the beneficial roles of trace elements in boosting plant growth, yield, and quality

Plant species	Trace elements	Stress	Be	eneficial effects	References
Hordeum vulgare	300 μM ZnSO <sub>4</sub>	0.1–10 μM CdCl <sub>2</sub> (10–22 DAS)	•	Reduced Cd uptake and MDA	Wu and Zhang (2002)
Capsicum annuum	$\begin{array}{c} 2 \text{ and } 10 \text{ mg} \\ \text{ZnSO}_{4} \text{ kg}^{-1} \\ \text{soil} \end{array}$	Salt, 0.5 and 1.5%, NaCl, 20 days	•	Increased biomass Reduced Na uptake	Aktaş et al. (2006)
Pistacia vera	$\begin{array}{c} 520 \text{ mg} \\ \text{ZnSO}_4 \text{ kg}^{-1} \\ \text{soil} \end{array}$	Salt, NaCl 0.8–3.2 g kg <sup>-1</sup> soil, 100 days	•	Reduced lipid peroxidation and LOX activity Reduced electrolyte leakage Increased	Tavallali et al. (2010)
			•	phenolic contents	
Triticum aestivum	Zn and Fe	Drought, stop watering at pollination and seed-filling stage	•	Increased seed yield and kernel weight	Monjezi et al. (2012)
T. aestivum	50 mg B L <sup>-1</sup>	Drought, 50, 75, and 100% irrigation	•	Increased chl and Car	Abdel- Motagally and
			•	Decreased H <sub>2</sub> O <sub>2</sub> and Pro content	El-Zohri (2016)
T. aestivum	B (0, 0.5, 1%)	Drought, irrigation withdrawal	•	Improved LAI, CGR, and NAR	Moeinian et al. (2011)
Zea mays	Foliar spray of 50 and 100 ppm boric acid	Salt, 4% NaCl	•	Increased plant height, leaf number, shoot dry weight, and grain weight	Salim (2014)
Citrus grandis	2.5 and 20 μM H <sub>3</sub> BO <sub>3</sub>	Al stress, 1.2 mM AlCl <sub>3</sub> , 18 week	•	Higher dry weight, root citrate secretion, root malate secretion	Zhou et al. (2015)
H. vulgare	2.0 mmol m <sup>-3</sup> Mn	Salt stress, 125 mM NaCl and 9.6 mM CaCl <sub>2</sub> , 24 days	•	Increased NAR, RGR, photosynthesis, Mn uptake in salt-stressed seedlings	Cramer and Nowak (1992)
H. vulgare	3 mM Mn, 1 WAS	Salinity, 8 dS m <sup>-1</sup> ; two weeks after sowing (WAS)	•	Increased dry weight, NAR, RGR, leaf area ratio	Pandya et al. (2004)
Oryza sativa	5 and 25 μM MnCl <sub>2</sub>	Cd, 5 and 25 $\mu$ M CdCl <sub>2</sub> , 7 days	•	Increased chl, Car, AsA, and sugar content	Sebastian and Prasad (2015)
			•	Decreased Cd uptake, MDA content, CAT, and POD activity	

 Table 10.2 Beneficial effects of trace elements supplementation in plants grown under adverse environmental conditions

Plant species	Trace elements	Stress	Beneficial effects References
Z. mays	100 μM MnSO <sub>4</sub>	Cd, 10 µM CdCl <sub>2</sub> , 12 h	• Increased root Pal'ove-Balang length and decrease Cd uptake et al. (2006)
Phytolacca americana	1–5 mM MnCl <sub>2</sub>	Cd, 10 and 50 µM CdCl <sub>2</sub>	• Increased root, stem, and leaf dry weight and decreased Cd content
Camellia sinensis	50 and 100 µM MnCl <sub>2</sub>	Drought, Irrigation withdrawal	Increased dry mass and RWC, total phenolic and AsA content     Upadhyaya et al. (2012)
C. annuum	uum 1.8 mM Salinity, 50 mM K <sub>2</sub> SiO <sub>3</sub> NaCl	<ul> <li>Improved growth</li> <li>Increased photosynthesis rate, stomatal conductance</li> <li>Decreased electrolyte leakage</li> </ul>	
			<ul> <li>Decrease ROS production and lipid peroxidation</li> <li>Increased activities of antioxidant</li> </ul>
Anethum graveolens	1.5 mM Na <sub>2</sub> Si <sub>3</sub> O <sub>7</sub>	Salinity, 10 dS m <sup>-1</sup>	<ul> <li>enzymes</li> <li>Improved growth</li> <li>Shekari et al. (2015)</li> <li>(2015)</li> <li>(2015)<!--</td--></li></ul>
Z. mays	1.5 mM Na <sub>2</sub> O <sub>3</sub> Si.5H <sub>2</sub> O	Alkalinity, 25–75 mM Na <sub>2</sub> CO <sub>3</sub>	<ul> <li>Improved growth</li> <li>Enhancement in leaf RWC and levels of photosynthetic pigments</li> <li>Increased soluble sugars, soluble proteins, total free amino acids and K</li> <li>Enhanced</li> </ul>
			activities of SOD, CAT, and POD

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects References
O. sativa	350 kg ha <sup>-1</sup> of Si fertilizer	Drought, -0.050 or -0.025 MPa	• Increased Pro Mauad et al. (2016)
			Increased     peroxidase activity
Saccharum officinarum	2 mM Ca <sub>2</sub> SiO <sub>4</sub>	Salinity, 100 mM NaCl	Reduced tissues Ashraf et al. Na <sup>+</sup> (2010) (2010)
			Improved K <sup>+</sup> uptake, K <sup>+</sup> /Na <sup>+</sup> ratios and Ca <sup>2+</sup> content
			Increased shoot and root dry matter
Vitis vinifera	4 mM Si Na <sub>2</sub> Si <sub>3</sub> O <sub>7</sub>	Salinity, 20 mM NaCl	Reduced stomatal resistance     Soylemezoglu et al. (2009)
			Reduced MDA and H <sub>2</sub> O <sub>2</sub> contents
			Increased APX     activity
Brassica napus	2 and 4 mM K <sub>2</sub> SiO <sub>3</sub>	nM Salinity, 300 mM NaCl	• Increased leaf area, leaf fresh weight, seed yield, and photosynthesis
			Increased APX     and NR activities
			Increased chl     content
Z. mays	0.4, 0.8, 1.2, 1.6, 2.0, 2.4,	Salinity, 150 mM NaCl	Improved Parveen and growth Ashraf (2010)
	2.8, and 3.2 mM Si(OH) <sub>4</sub>		• Increased net CO <sub>2</sub> assimilation rate, stomatal conductance (g <sub>s</sub> ), transpiration, and leaf sub-stomatal CO <sub>2</sub> concentration
Spartina densiflora	500 μM Na <sub>2</sub> SiO <sub>3</sub>	Salinity, 171 and 680 mM NaCl	• Improved Mateos-Naranjo growth et al. (2013) associated with higher net photosynthetic rate, water-use efficiency, and $g_s$
			Reduced tissue     Na <sup>+</sup> content

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
Solanum lycopersicum	2.5 mM K <sub>2</sub> SiO <sub>3</sub>	Drought, 10% PEG	<ul> <li>Improved water balance</li> <li>Increased growth and photosynthesis</li> <li>Decreased ROS production</li> <li>Enhanced activities of SOD and CAT</li> <li>Increased level of AsA and GSH</li> </ul>	Shi et al. (2016)
T. aestivum	Si 50 mg kg <sup>-1</sup> and 150 mg kg <sup>-1</sup>	Drought, 50%, 75% and 100% FC	<ul> <li>Increased plant biomass, plant height, and spike weight</li> <li>Increased tissue Si concentration and uptake</li> </ul>	Ahmad et al. (2007)
Z. mays	0.8 mM Na <sub>2</sub> SiO <sub>3</sub>	Drought, 50% water deficit	<ul> <li>Increased dry mass, tissue nutrient content, water use efficiency</li> <li>Reduced leaf wilting</li> </ul>	Janislampi (2012)
Glycine max	1.70 mM Na <sub>2</sub> SiO <sub>3</sub>	Drought, -0.5 MPa	<ul> <li>Increased root and shoot dry matter and the ratio of root/ shoot</li> <li>Increased leaf water potential, growth</li> <li>Increased net photosynthetic rate, gs, chl content</li> <li>Decreased free Pro content, lipid peroxidation, and electrolytes leakage</li> </ul>	Shen et al. (2010)
S. bicolor	200 mg L <sup>-1</sup> Si	Drought, withholding irrigation	<ul> <li>Increased net photosynthetic rate</li> <li>Decreased shoot to root ratio by increasing root growth</li> </ul>	Ahmed et al. (2011)

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects References
Oryza sativa	1.5 mM Na <sub>2</sub> SiO <sub>3</sub>	нт, 39 °С	• Increased Li et al. (2005) number of pollen grain those were with higher diameter
			• Increased anther dehiscence percentage, pollination, and fertilization
Z. mays	10 mM K <sub>2</sub> SiO <sub>3</sub>	Chilling, $2/3 \pm 1$ °C	Enhanced Habibi (2016)      photosynthesis
			Reduced ROS     production
			Enhanced AsA     and GSH pool
Cucumis sativus	0.1 and 1 mM C $K_2SiO_3$	Chilling (15/8 °C)	• Reduced leaves Liu et al. (2009) withering
			<ul> <li>Increased activities of SOD, GPX, APX, MDHAR, GR, GSH</li> </ul>
			Increased AsA content
			<ul> <li>Decreased levels of H<sub>2</sub>O<sub>2</sub>, O<sub>2</sub><sup>-</sup> and MDA</li> </ul>
T. aestivum	0.1 and 1.0 mM K <sub>2</sub> SiO <sub>3</sub>	Freezing, -5 °C	• Increased leaf Liang et al. (2008)
			• Improved activities of antioxidant enzymes AsA, GSH, SOD, and CAT
			• Reduced H <sub>2</sub> O <sub>2</sub> , free Pro, and MDA content
C. limon	50, 150 and 250 mg $L^{-1}$ $K_2SiO_3$	Freezing, 0.5 °C for 28 days	• Increased Mditshwa et al. (2013) flavonoids concentration
			• Improved fruit quality
			Reduced chilling     injury

Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
O. sativa	0.6 mM Si(OH) <sub>4</sub>	Heavy metal (HM), 10 µM CdCl <sub>2</sub> , 4 days	<ul> <li>Improved plant growth</li> <li>Improved photosynthesis</li> <li>Maintenance of nutrient homeostasis</li> <li>Stimulation of the AsA-GSH pathway</li> </ul>	Farooq et al. (2016)
S. nigrum	1.0 mM Na <sub>2</sub> SiO <sub>3</sub>	HM, 100 μM CdCl <sub>2</sub>	<ul> <li>Decreased Cd accumulation</li> <li>Reduced electrolyte leakage</li> <li>Increased activities of SOD, POD, CAT, and APX</li> </ul>	Liu et al. (2013)
O. sativa	1.25, and 2.5 mM Na <sub>2</sub> SiO <sub>3</sub>	HM, 100 μM K <sub>2</sub> Cr <sub>2</sub> O <sub>7</sub>	<ul> <li>Increased seedling height, dry biomass, and soluble protein content</li> <li>Reduced Cr uptake and translocation</li> <li>Improved antioxidant defense</li> </ul>	Zeng et al. (2011)
B. chinensis	1.5 mM K <sub>2</sub> SiO <sub>3</sub>	HM, 0.5 and 5 mg $L^{-1}$ CdCl <sub>2</sub>	<ul> <li>Increased shoot and root biomass</li> <li>Decreased Cd uptake and root-to-shoot transport</li> <li>Increased SOD, CAT, APX, reduced MDA, and H<sub>2</sub>O<sub>2</sub> concentrations</li> </ul>	Song et al. (2009)
C. sativus	1 mM Na <sub>2</sub> SiO <sub>3</sub>	HM, 100 μM CdCl <sub>2</sub>	<ul> <li>Reversed chlorosis, protected the chloroplast from disorganization</li> <li>Increased pigment contents, intercellular CO<sub>2</sub> concentration, gs and net photosynthetic rate</li> <li>Improved water use efficiency</li> </ul>	Feng et al. (2010)

Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
Z. mays	1 mM Si as Si(OH) <sub>4</sub>	HM, 200 or 500 μM MnSO <sub>4</sub>	<ul> <li>Ameliorated chloroplast damage and photoinhibition</li> <li>Improved detoxification and compartmentation of Mn</li> </ul>	Doncheva et al (2009)
Picea abies	0.2, 0.5 and 1.0 mM Si	HM, 0.2, 0.5 and 1.0 mM Al	<ul> <li>Ameliorated adverse effects on cell wall thickening, degree of vacuolation, and the degeneration of mitochondria, golgi bodies, endoplasmic reticulum, and nucleus</li> <li>Reduced cell death</li> </ul>	Prabagar et al. (2011)
V. vinifera	4 mM Na <sub>2</sub> Si <sub>3</sub> O <sub>7</sub>	HM, 20 mg kg <sup>-1</sup> H <sub>3</sub> BO <sub>3</sub>	<ul> <li>Reduced tissue B concentration</li> <li>Increased activities of CAT and APX</li> <li>Reduced Pro, H<sub>2</sub>O<sub>2</sub>, and MDA content</li> </ul>	Soylemezoglu et al. (2009)
O. sativa	Si fertilizer (CaSiO <sub>3</sub> ) @ 40 g m <sup>-2</sup>	UV-B radiation, 250–350 nm	<ul> <li>Improved cell walls of sclerenchyma, vascular bundle sheath, and metaxylem vessel cells, cellulose, non-cellulosic polysaccharides, lignin, and phenolic acids</li> </ul>	Goto et al. (2003)
G. max	1.70 mM Si	UV-B radiation, 290–320 nm	<ul> <li>Increased root and shoot dry weight and their ratio</li> <li>Increased net photosynthetic rate and gs</li> <li>Decreased H<sub>2</sub>O<sub>2</sub> content</li> </ul>	Shen et al. (2010)

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
Vigna unguiculata	5–10 μM Na <sub>2</sub> SeO <sub>4</sub>	Salinity, 100 mM NaCl	Improved     photosynthetic     pigments	Manaf (2016)
			• Increased Pro and soluble sugar content and PAL	
			• Improved growth and yield	
L. esculentum	5–10 μM Na <sub>2</sub> SeO <sub>3</sub>		• Improved the integrity of cell membrane	Mozafariyan et al. (2016)
			<ul> <li>Increased leaf RWC</li> </ul>	
			Enhanced antioxidant defense system	-
L. esculentum	50 μM Na <sub>2</sub> SeO <sub>3</sub>	Salinity, 100 mM NaCl	Improved     photosynthetic     efficiency	Diao et al. (2014)
			Decreased ROS     production	
			Enhanced antioxidant defense	-
B. napus	25 μM Na <sub>2</sub> SeO <sub>4</sub> , 48 h	Salinity, 100 and 200 mM NaCl, 48 h	<ul> <li>ncreased AsA and GSH contents, GSH/ GSSG ratio, and activities of APX, MDHAR, DHAR, GR, GST, GPX, and CAT</li> </ul>	Hasanuzzamar et al. (2011b)
			• Reduced levels of H <sub>2</sub> O <sub>2</sub> and MDA	-
C. sativus	5, 10, or 20 μM Na <sub>2</sub> SeO <sub>4</sub> , 11 days	Salinity, 50 mM NaCl, 11 days	<ul> <li>Decreased content of Cl<sup>-</sup> in the shoots tissues</li> </ul>	Hawrylak- Nowak (2009)
			Increased Pro accumulation	
			• Enhanced antioxidant defense	
			Decreased lipid     peroxidation	

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
Rumex patientia x R. tianshanicus	$1-5 \ \mu M$ Na <sub>2</sub> SeO <sub>4</sub> , 43 days	Salinity, 100 mM NaCl, 43 days	<ul> <li>Stimulated growth</li> <li>Increased activities of SOD and POD</li> <li>Increased accumulation of water-soluble</li> </ul>	Kong et al. (2005)
S. vulgare	20 mg L <sup>-1</sup> Se	Drought, 35–70% FC	<ul> <li>sugar</li> <li>Improved growth</li> <li>Increased photosynthesis</li> <li>Increased yield</li> </ul>	Aissa et al. (2016)
T. aestivum	15 μg L <sup>-1</sup> Na <sub>2</sub> SeO <sub>4</sub>	Drought, 20% FC	<ul> <li>Increased dry matter accumulation</li> <li>Protection of leaf photochemical event</li> <li>Increased photosynthesis</li> </ul>	Hajiboland et al (2016)
T. aestivum	7.06 µM Se	Water deficit	<ul> <li>Increased stress tolerance index</li> <li>Increased biomass</li> </ul>	Nawaz et al. (2014)
Trifolium repens	5 μM Na <sub>2</sub> SeO <sub>4</sub> , 0–5 days	Drought, PEG 6000 (-1.0 MPa), 0-5 days	<ul> <li>Decreased levels of H<sub>2</sub>O<sub>2</sub>, TBARS, DHA, and GSSG</li> <li>Increased the levels of AsA and GSH and AsA/ DHA and GSH/ GSSG ratios</li> <li>Improved the activities of MDHAR, DHAR, and GR</li> </ul>	
B. napus	$\begin{array}{c} 15 \text{ and } 30 \text{ g} \\ L^{-1} \text{ as} \\ Na_2 SeO_3 \end{array}$	Drought, limited irrigation at early stem elongation	<ul> <li>Increased plant height</li> <li>Increased pod and seed development</li> <li>Increased yield</li> </ul>	
T. aestivum	Se (Na <sub>2</sub> SeO <sub>3</sub> ) 0.5 mg kg <sup>-1</sup> , 20 days	Drought, 30% FC	<ul> <li>Increased root activity</li> <li>Increased Pro content</li> <li>Increased activities of POD and CAT</li> </ul>	Xiaoqin et al. (2009a)

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
T. aestivum	1.0, 2.0, and 3.0 mg kg <sup>-1</sup>	Water stress of 30% FC, 20 days	Increased root     activity	Xiaoqin et al. (2009b)
	Na <sub>2</sub> SeO <sub>3</sub> , 20 days		• Increased chl, carotenoids and Pro content	
			Increased activities of POD and CAT activities	-
			Decreased MDA content	-
Fagopyrum esculentum	1 g m <sup>-3</sup> Na <sub>2</sub> SeO <sub>4</sub> , 7–8 weeks	Reduction of water by 50%, 8 weeks	• Improved <i>gs</i> , potential photochemical efficiency of PS II, respiratory potential	Tadina et al. (2007)
			Increased yield	
Z. mays	20 g ha <sup>-1</sup> Na <sub>2</sub> SeO <sub>4</sub>	Drought, withholding water	Enhanced activities of SOD	Sajedi et al. (2011)
			Reduced MDA content	
			Improved grain yield	
T. aestivum		withholding water	Increased root length and total biomass	Nawaz et al. (2013)
			Increased stress     tolerance index	-
			• Increased total sugar content and total free amino acids	-
1	$\begin{array}{c} 25 \ \mu M \ Se \\ (Na_2SeO_4), \ 48 \\ h \end{array}$	Drought, 10 and 20% PEG-6000, 48 h	Increased activities of APX, DHAR, MDHAR, GR, GST, GPX, and CAT	Hasanuzzamar and Fujita (2011)
			• Decreased GSSG content, H <sub>2</sub> O <sub>2</sub>	
			Decreased lipid peroxidation	
Z. mays	$5-15 \ \mu M$ Na <sub>2</sub> SeO <sub>3</sub> ·	Drought, 25% PEG	Unregulated     AsA-GSH cycle	Yildiztugay et al. (2016)
	5H <sub>2</sub> O		Decreased ROS     production	

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
Z. mays	$\begin{array}{c} 5-15 \ \mu M \\ Na_2 SeO_3 \cdot \\ 5H_2 O \end{array}$	HT (24–44 °C)	<ul> <li>Upregulated AsA-GSH cycle</li> <li>Decreased ROS</li> </ul>	Yildiztugay et al. (2016)
	- 2 -		production	
T. aestivum	2–4 mg L <sup>-1</sup> Se HT, 38 $\pm$ 2 °C	HT, 38 ± 2 °C	• Improved growth and photosynthesis	Iqbal et al. (2015)
			Increased yield attributes and yield	
		Increased     nonenzymatic     antioxidants	_	
			Enhanced activities of antioxidant enzymes	
S. bicolor	Na <sub>2</sub> SeO <sub>4</sub> (75 mg L <sup>-1</sup> ), 7–28 days	HT, 40/30 °C, 7–28 days	Increased antioxidant enzyme	Djanaguiraman et al. (2010)
			Decreased ROS levels and membrane damage	
		Increased antioxidant defense	_	
			Increased grain yield	-
C. sativus	2.5, 5, 10, or 20 μM Na <sub>2</sub> SeO <sub>4</sub>	LT, 10 °C/5 °C for 24 h, day	Improved shoot fresh weight	Hawrylak- Nowak et al.
			Increase of Pro content	(2010)
			Reduced MDA     level	
3.0 mg	0.5, 1.0, 2.0, 3.0 mg kg <sup>-1</sup>	LT, 4 °C, 72 h	Increased     biomass	Chu et al. (2010)
	Na <sub>2</sub> SeO <sub>3</sub> , 72 h		Increased chl, anthocyanins, flavonoids, and phenolic compounds	
			Increased activities of POD and CAT	

 Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
T. aestivum	Se (5 mg Se L <sup>-1</sup> ), 5, 10, and 15 h	LT, 3 or 5 °C, 14 days	Enhanced     growth	Akladious (2012)
			Increased chl, anthocyanin, sugar, and Pro contents	
			Enhanced antioxidant defense system	
			Decreased membrane damage	
S. bicolor	Se (3 and 6 μM L <sup>-1</sup> Na <sub>2</sub> SeO <sub>4</sub> ), 6 h	LT, 4–8 °C, 7 days	Enhanced     growth	
			• Increased levels of chl, anthocyanin, sugar, Pro, and AsA	
			Increased     enzymatic activities	
			• Diminished lipid peroxidation	
C. frutescens	0, 3 and 7 μM Na <sub>2</sub> SeO <sub>3</sub>	HM, 0.25–0.5 mM CdCl <sub>2</sub>	• Improved growth	Shekari et al. (2016)
			• Improved photosynthetic pigments	
			Decreased Pro     Enhanced CAT     activity	
B. napus	50 and 100 μM Se (Na <sub>2</sub> SeO <sub>4</sub> ), 24 h	HM. 0.5 and 1.0 mM CdCl <sub>2</sub> , 48 h	<ul> <li>activity</li> <li>Increased the AsA and GSH contents, the GSH/GSSG ratio</li> </ul>	Hasanuzzaman et al. (2012b)
			Increased activities of APX, MDHAR DHAR, GR, GPX and CAT	
			• Reduced the MDA and H <sub>2</sub> O <sub>2</sub> levels	
B. napus	2 μM Na <sub>2</sub> SeO <sub>4</sub> , 14 days	HM, 400 and 600 μM, CdCl <sub>2</sub> , 14 days	Reduced     oxidative stress     by modulating     SOD, CAT, APX,     GPX activities	Filek et al. (2008)
			Prevented Cd-induced alteration of DNA methylation pattern	

Table 10.2 (continued)

Plant species	Trace elements	Stress	Beneficial effects	References
Pteris vittata	5, 10 $\mu$ M of Na <sub>2</sub> SeO <sub>4</sub> , 5 and 10 days	HM, 150 or 300 μM of Na <sub>2</sub> HAsO <sub>4</sub> , 10 days	• Improved antioxidant system including thiol and GSH levels	Srivastava et al. (2009)
			Reduced As     uptake	
B. oleracea	$\frac{1 \text{ mg } \text{L}^{-1}}{\text{Na}_2 \text{SeO}_3, 10}$ and 40 days	HM, 1 mg $L^{-1}$ CdCl <sub>2</sub> , 40 days	Increased chl     content	Pedrero et al. (2008)
			Improved     α-tocopherol level     and reduced     oxidative damage	
Lolium perenne	1.0, 1.5, 2.0, 5.0 and 10 μM Na <sub>2</sub> SeO <sub>3</sub> , 20 days	HM, 0.2 mM AlCl <sub>3</sub> , 20 days	Improved POD activity	Cartes et al. (2010)
			Reduced O <sub>2</sub> <sup></sup> and lipid peroxidation	
T. aestivum	1.0 and 2.0 mg Se kg <sup>-1</sup> , 8 h	UV-B, 40 W, 305 nm, 8 h	Increased root     weight and root     activity	Yao et al. (2009
			Increased flavonoids and Pro content	
			Increased activities of POD and SOD	
			• Reduced MDA and O <sub>2</sub> -	
Euglena gracilis	$\begin{array}{c} 10^{-7}, 10^{-8}, \\ 10^{-9} \text{ and } 10^{-10} \\ \text{M}, \text{Na}_2\text{SeO}_3 \cdot \\ 5\text{H}_2\text{O}, 40 \text{ min} \end{array}$	UV-A, 320–400 nm, 40 min	• Improved light-enhanced dark respiration and photosynthesis	Ekelund and Danilov (2001)

 Table 10.2 (continued)

deficiency and excess Cu conditions (Yruela 2005). Copper is found to be actively involved in many antioxidant enzymes in plants. Growth, protein content, and antioxidant enzymes' activities showed differential responses under different concentrations of copper (0–800  $\mu$ M) as reported by Gao et al. (2008). Higher activities of enzymes in *Jatropha curcas* seedlings were observed at the concentration of 200– 400  $\mu$ M. However, it was also dependent of plant organs. Azooz et al. (2012) observed the effect of Cu in wheat and found that 2 mM Cu showed optimum growth and biochemical parameters, while no changes were observed up to 10 mM Cu, and thereafter, the growth and biochemical parameters were significantly reduced. The activities of antioxidant enzymes such as CAT, POD, APX, and SOD were increased in dose-dependent manners. This effect of Cu in plants was associated with the biosynthesis of free amino acids and Pro (Azooz et al. 2012).

### 10.6.2 Zinc

Since 1932, Zinc has been considered as a vital micronutrient for plants because its participation as a functional component of around 200 enzymes and transcription factor involved in biomolecule synthesis and metabolism of nucleic acid and lipid. Furthermore, Zn plays role in biomass production, chl formation, pollen function, and fertilization (Ebrahimian and Bybordi 2011; Hafeez et al. 2013). Zn (at low concentration 1-2 µM) increases plant growth, chl content, and crude protein (Samreen et al. 2013). Role of Zn in conferring drought stress tolerance maintaining water use efficiency was described by Waraich and his group (Waraich et al. 2011a, b). They proposed that Zn can enhance the auxin level directly or indirectly by increasing tryptophan which is a precursor of auxin. Then auxin increased the root growth under drought condition. In addition, Zn decreases the activity of membranebound NADPH oxidase; for this reason, ROS generation decline and SOD, CAT, and POD activities increase to protect cell from oxidative damage under drought stress. Cd-induced damage can be restored by using Zn. Wu and Zhang (2002) reported Cd-induced reduction in root and shoot biomass, micronutrient imbalance (Cu, Fe, and Zn), and higher amount of Cd uptake reduced by the application of 300 µmol L<sup>-1</sup> Zn. Exogenous Zn prevented the Cd uptake by making block, maintained micronutrient (Cu, Fe, and Zn), reduced MDA, and, at the same time, increased antioxidant enzyme activity to protect barley plant from Cd toxicity. Supplemental Zn can reduce salinity-induced oxidative stress by reducing MDA, H<sub>2</sub>O<sub>2</sub>, and lipoxygenase activities as well as increasing APX and CAT activity in pistachio seedling (Tavallali et al. 2010). Application of Zn increased fresh and dry weight and Pro content and enhanced the activities of CAT, SOD, and GST under salt stress in sunflower leaves (Ebrahimian and Bybordi 2011). Role of Zn in abiotic stress tolerance is still ambiguous. Further study is required to find out mechanism of Zn-induced abiotic stress tolerance and elucidate nature of interaction among Zn and other nutrient elements.

#### 10.6.3 Nickel

Although the biological functions of Ni in plants have been reported since long time, its essentiality has been established recently due to its role as an activator of the enzyme urease (Fabiano et al. 2015). However, its role as protectants of plant stress is rarely available rather than its toxic effects. Recent studies have shown that Ni may activate *OsGLY11.2* (an isoform of glyoxalase I), which is the first line of enzymes in the degradation of cytotoxic methylglyoxal (MG) (Mustafiz et al. 2014), a cytotoxic compound which is produced in high concentration under stress. This MG is detoxified via glyoxalase system where both Gly I and Gly II enzymes are involved. Importance of Ni for the activity of Gly I not only suggest its role in MG detoxification but also the redox state of GSH which is a strong antioxidant and vital player in metal tolerance. Fabiano et al. (2015) studied the role of Ni in the

relationship between the MG cycle and GSH homeostasis and stated that Ni may have a key participation in plant antioxidant metabolism, especially in stressful situations (Fabiano et al. 2015). However, further study is necessary to elucidate the actual functions of Ni in conferring stress tolerance to plants.

#### 10.6.4 Boron

Though the physiological role of B in plant is still unclear, it is evident that both the deficiency and toxicity of B resulted in many anatomical, biochemical, and physiological changes in plants (Herrera-Rodrígueź et al. 2010). The deficiency of B in plant affects growth and reduces yield, whereas sufficient supply results in better growth and good yield (Shabaan 2010). As an essential element, B is required for many essential functions of plant such as maintaining cell structures and functions as well as cell division, sugar transport, hormone development, respiration, carbohydrate metabolism, membrane transport, and transportation and metabolism of other essential plant nutrients (Shabaan 2010, Herrera-Rodrígueź et al. 2010). Boron can also play role in fruit and seed development by increasing fertility, pollen tube growth, and carbohydrate utilization (Blevins and Lukaszewski 1994). Therefore, deficiency of B causes many physiological and biochemical changes in plant that affect plant growth and yield (Shabaan 2010). It is also revealed that exogenous B can develop stress tolerance by regulating physiological and biochemical attributes under environmental stress condition. Foliar application of B improves growth and yield of wheat by increasing chl and Car content and decreasing  $H_2O_2$ and Pro content under drought stress condition (Abdel-Motagally and El-Zohri 2016). Moeinian et al. (2011) also showed that foliar application of B improve growth, yield, and grain quality of *T. aestivum* under drought stress condition by improving leaf area index (LAI), crop growth rate (CGR), and net assimilation rate (NAR). Foliar application of B alleviates salinity and improves growth and yield attributes in maize seedlings under salt stress by regulating phenols, proline, amino acids, and soluble sugar (Salim 2014). Zhou et al. (2015) reported that gene related to ROS and aldehyde detoxification and metabolism, cell transport, Ca signaling, and hormone and gene regulation play role in B-induced alleviation of aluminum toxicity in Citrus grandis seedlings.

#### 10.6.5 Manganese

As an essential trace element, manganese (Mn) is associated with various plant metabolic processes. It plays an important role in plant photosynthesis, respiration, and hormone activation. It also takes part in synthesis of protein, lipid, fatty acids, amino acids, ATP, flavonoids, etc. (Lidon et al. 2004; Millaleo et al. 2010). Usually Mn presents in soil as free Mn<sup>2+</sup> which is only available form for plant and readily taken up by plant via an active transport system in epidermal root cells. Deficiency of Mn is dangerous for plant, because it weakens structural resistance against pathogen and decreased tolerance ability toward abiotic stresses such as heat and drought stress. In addition, Mn deficiency also affects the water-splitting system of photosystem II (PS II) that provides electron directly for photosynthesis which also makes plant vulnerable toward stress (Gherardi and Rengel 2003; Millaleo et al. 2010). On the other hand, the presence of excess Mn in plant root zone also extremely toxic to plant. Higher accumulation of Mn by plant alters various physiological and metabolic processes which causes chlorosis, necrosis, oxidative stress, and growth and yield reduction (Ducic and Polle 2005; Millaleo et al. 2010; Arya and Roy 2011). Considering the beneficial role of lower amount and toxic effect of excess amount, Mn plays dual role in plant system: essential micronutrient and toxic element, respectively (Ducic and Polle 2005; Millaleo et al. 2010).

However, among the beneficial roles that we discussed. Mn also plays role directly against various abiotic stresses. Being a divalent cation, Mn can compete with other divalent toxic ion and reduced their uptaken and transportation within plant as they are uptaken by active transporter and have some common transporter during uptake and transportation (Hirschi et al. 2000; Pittman 2005). In addition, Mn also acts as cofactor in Mn-CAT and Mn-SOD enzymes that participates in plant antioxidant defense system. Although it is not clear but assumed that Mn acts as O<sub>2</sub><sup>--</sup> and H<sub>2</sub>O<sub>2</sub> scavenger (Ducic and Polle 2005). Moreover, many studies revealed that supplemental Mn plays positive role in conferring stress tolerance under various abiotic stress conditions (Table 10.2). Supplementation of Mn in Cd-treated plant improves growth and chl and Car contents and decrease lipid peroxidation by reducing Cd uptake and enhancing antioxidant defense system (Pal'ove-Balang et al. 2006; Peng et al. 2008; Sebastian and Prasad 2015). Exogenous application of Mn in barley seedlings confer salt stress tolerance and improve growth by increasing net assimilation and photosynthetic rate under salt stress condition (Cramer and Nowak 1992; Pandya et al. 2004). Upadhyaya et al. (2012) reported that Mn plays positive role on post-drought stress recovery in tea by influencing growth and antioxidative response. To observe the protective effect of Mn under salt stress condition, we have grown 12-day-old O. sativa seedlings under 150 mM NaCl for 3 and 6 days under controlled environment. Salt stress resulted in marked increase in Na<sup>+</sup>, MDA, H<sub>2</sub>O<sub>2</sub>, O<sub>2</sub><sup>--</sup>, and Pro and MG content which in turns exhibited chlorosis and growth inhibition in time-dependent manner (Rahman et al. 2016). On the other hand, Mn supplementation (0.5 mM MnSO4) reduced oxidative stress by lowering the levels of MDA and H<sub>2</sub>O<sub>2</sub> and enhancing the activities MDHAR, DHAR, SOD, CAT, Gly I, and Gly II and improving the contents of nonenzymatic antioxidants. Exogenous Mn also maintains low Na<sup>+</sup> and high K<sup>+</sup> content and thus maintained ion homeostasis.

#### 10.6.6 Silicon

Although it is not considered as essential for plant function, in rice, Si showed some essential functions, and it is absorbed from soil in amounts that are even higher than those of the essential macronutrients (Datnoff et al. 2001). There are plenty of

evidences on the role of Si in plant stress tolerance (Hasanuzzaman et al. 2014b). Beneficial effects of exogenous Si in enhancing abiotic stress resistance are reported in many plant studies (Table 10.2). The protective effect of Si under abiotic stress are mainly due to the deposition of Si as  $SiO_2.nH_2O$  in leaves and stems of plants and partly by the interaction between  $Si(OH)_4$  and other elements such as Al. It is also suggested that the function of Si in plants might involve mechanical defense rather than physiological changes (Fig. 10.4; Ma and Yamaji 2008; Hasanuzzaman et al. 2014b).

Hydroponically supplemented Si (1.8 mM  $K_2SiO_3$ ) significantly increased growth and alleviated salinity stress (50 mM NaCl) in *C. annuum* which was due the enhancement of antioxidant defense, improvement of photosynthesis, and maintenance of the nutrient balance (Manivannan et al. 2016). For example, electrolyte leakage potential in salt stress treatment by 38% upon exposure illustrated the NaCl-induced cell membrane damage, which, in turn, was reduced by 33% upon Si supplementation. Similarly, the addition of Si mitigated the oxidative damage by decreasing the MDA content by 29% and H<sub>2</sub>O<sub>2</sub> content by 26% which efficiently minimized the oxidative burst. While investigating the beneficial role of Si in salt stressed (10 dS/m) *Anethum graveolens*, Shekari et al. (2015) observed that exogenous Si (1.5 mM) could be able to improve the salt-induced inhibition of growth and

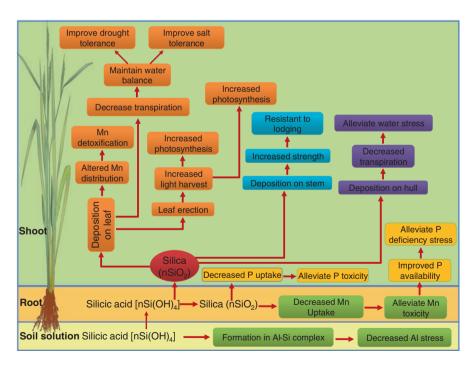


Fig. 10.4 Silicon-induced abiotic stress tolerance in plants (Source: Hasanuzzaman et al. 2014b, with permission from Elsevier)

Na/K ratio. Silicon also reduced lipid peroxidation which was associated with enhanced activities of antioxidant enzymes. Mateos-Naranjo et al. (2013) observed that Si could ameliorate nutrient imbalances in salt affected Spartina densiflora. The K<sup>+</sup>/Na<sup>+</sup> ratio of leaves of Spartina densiflora was greater in Si-treated plants, and these plants also had higher levels of essential nutrients (Si, Al, Cu, Fe, K, and P) in their tissues (Mateos-Naranjo et al. 2013). In B. napus, Si (2 and 4 mM) was found to be effective in enhancing antioxidative enzyme activities and photosynthesis (Bybordi 2012). Protective role of Si in drought stress tolerance was reported by many authors. These effects were mainly due to the maintenance of water balance, cellular integrity, and antioxidant defense. However, little information is available on its role in water uptake and in less Si-accumulating plants. Silicon also provided better protection under alkali stress (25-75 mM Na<sub>2</sub>CO<sub>3</sub>). After 25 days of stress growth parameters, leaf RWC, and the contents of photosynthetic pigments, soluble sugars, total phenols and potassium ion (K<sup>+</sup>), as well as potassium/sodium ion (K<sup>+</sup>/ Na<sup>+</sup>) ratio were decreased, while the contents of soluble proteins, total free amino acids, proline, Na<sup>+</sup> and MDA, as well as the activities of SOD, CAT, and POD were increased. On the other hand, seed priming with 1.5 mM Na<sub>2</sub>O<sub>3</sub>Si.5H<sub>2</sub>O improved growth of stressed plants, which was accompanied by the enhancement in leaf RWC and levels of photosynthetic pigments, soluble sugars, soluble proteins, total free amino acids and K<sup>+</sup>, as well as activities of SOD, CAT, and POD enzymes. Furthermore, Si supplement resulted in a decrease in the contents of Pro, MDA, and Na<sup>+</sup>, which together with enhanced K<sup>+</sup> level led to a favorable adjustment of K<sup>+</sup>/Na<sup>+</sup> ratio, in stressed plants relative to plants treated with alkaline stress alone. In a recent report, Shi et al. (2016) found increased water uptake and less oxidative damage in S. lvcopersicum under drought stress (10% PEG) when Si (2.5 mM) was applied. Silicon addition significantly recovered the growth and photosynthetic inhibition and improved water status in plants compared to water stress alone. There was a marked increase in ROS accumulation under water stress, while added Si ameliorated these by enhancing the activities of SOD and CAT and maintaining the AsA and GSH levels higher (Shi et al. 2016). Mauad et al. (2016) reported that Si-induced drought stress tolerance was developed due to increased Pro synthesis and peroxidase (POX) activity.

In *Z. mays*, foliarly applied Si (10 mM K<sub>2</sub>SiO<sub>3</sub> metasilicate) could enhance chilling tolerance to low-temperature ( $3 \pm 1$  °C) stress (Habibi 2016). Maize plants grown under low temperature resulted in marked reduction of plant growth and RWC, increased the production of ROS, and depleted the photosynthetic parameters. However, Si supplemented plants showed revisable effect, i.e., decrease in lipid peroxidation and increase in maximum quantum yield of PS II (Fv/Fm) and photosynthetic pigments. Silicon supplementation also maintained the AsA and GSH pool (Habibi 2016). Several studies indicated that Si is also effective in mitigating metal toxicity in plants. Hydroponically grown rice plants exposed to 10  $\mu$ M CdCl<sub>2</sub> showed inhibition of plant growth and photosynthesis as well as disruption of ion homeostasis and antioxidant defense (Farooq et al. 2016). However, when the plants were supplemented with 0.6 mM Si(OH)<sub>4</sub>, it reversed the effects of Cd by improving plant growth, photosynthesis, nutrient homeostasis, and enhancement of antioxidant defense system, especially AsA-GSH cycle, and thus readjusting cell redox homeostasis (Farooq et al. 2016). In *S. nigrum*, Si-induced Cd stress tolerance was associated with the activation of antioxidant defense and reduction of Cd uptake as reported by Liu et al. (2013). They observed that Cd markedly enhanced the production of ROS and showed higher electrolyte leakage and accumulated higher amount of Cd in shoot and root. In contrary, Si reduced  $H_2O_2$  accumulation and prevented cell death and the electrolyte leakage and  $H_2O_2$  concentration in functional leaves. Si supplementation also enhanced the activities of SOD, CAT POD, and APX (Liu et al. 2013).

## 10.6.7 Selenium

After the intense research of past few decades, the beneficial roles of Se in plants have been observed, but the question is still unresolved whether Se is an essential micronutrient for plants (Terry et al. 2000). However, it is still recognized as an essential micronutrient (Hasanuzzaman et al. 2014b). In many plant species, Se exerts a positive effect on plant growth, physiology, and productivity under abiotic stress (Hasanuzzaman et al. 2010, 2011b, 2012b, 2014a, b; Table 10.2). One of the roles of Se in exerting beneficial effects on the stress tolerance is the enhancement of the antioxidant capacity (Hasanuzzaman et al. 2014a, b).

Several research results have shown that Se at low concentration provided protection to different plant species against salt stress. Selenium-induced growth promotion and improvement of photosynthesis and antioxidant defense system in salt-treated tomato plants were reported by Diao et al. (2014). Under salt stress (100 mM NaCl), plant growth and photosynthetic attributes were inhibited while Se supplementation (50  $\mu$ M Na<sub>2</sub>SeO<sub>3</sub>) reversed the effects. Se treatment also limited the ROS generation which was mainly due to the enhanced activities of SOD, GR, DHAR, MDHAR, and GPX and the redox pool of AsA and GSH (Diao et al. 2014). In pot culture Se (5-10 µM) supplemented V. unguiculata showed enhanced tolerance to salt stress (50 mM NaCl) through the highest values of photosynthetic pigments, proline, phenylalanine ammonia lyase (PAL), and total soluble sugar as well as growth and yield attributes (Manaf 2016). In a recent study, we found that exogenous Se (5-10 µM) could alleviate salt (25-50 mM NaCl)-induced damages by improving the integrity of cell membranes and by increasing leaf RWC, and photosynthetic pigments under stress conditions and subsequently increasing plant biomass and yield (Mozafariyan et al. 2016). Under high salt concentration (50 mM NaCl) 10 µM Se performed well than other dose.

Kong et al. (2005) reported that low concentrations (1–5  $\mu$ M) of Se stimulated growth and enhanced antioxidant enzyme (SOD and POD) activities in leaves of sorrel (*R. patientia* × *R. tianshanicus*) seedlings under salt stress. In contrast, at higher concentrations (10–30  $\mu$ M), Se showed fewer beneficial effects. In *C. sativus* leaves, Se treatments (5–10  $\mu$ M) increased the growth, synthesis of photosynthetic pigments, and Pro levels under salt stress (Hawrylak-Nowak 2009). In our recent

study, we observed beneficial effects of exogenous Se ( $25 \mu$ M Na<sub>2</sub>SeO<sub>4</sub>) in salt (100 and 200 mM NaCl)-stressed *B. napus* seedlings (Hasanuzzaman et al. 2011a, b). Selenium treatment increased the components of AsA-GSH cycle and other antioxidant enzymes and maintained the AsA and GSH pool which reduced levels of H<sub>2</sub>O<sub>2</sub> and MDA when compared to plants exposed to salt stress alone (Hasanuzzaman et al. 2011a, b). So far the confirmation about which form of Se is more effective is yet to be elucidated. In a recent study Hawrylak-Nowak (2015) reported that Se application, especially in the form of selenite, could upregulate the antioxidant defense in salt-treated lettuce. It was also found that the root growth and increase in photosynthetic pigment were increased upon Se supplementation.

Several plant studies that focused on the protective effects of Se under drought stress indicated that the effects of Se are due to its ability to regulate the water status of plants under water-deficit condition. In wheat, Se supplementation improved dry matter and grain yield under both well watered and a drought condition which was mainly due to enhancement of photosynthesis rate, protection of leaf photochemical events, accumulation of organic osmolytes, and improvement of water use efficiency. Selenium was also able to increase root length and diameter which made the plant able to uptake more water and maintaining higher water content in leaves (Hajiboland et al. 2016). Nawaz et al. (2014) reported that the growth and biomass of wheat seedlings increased under drought due to Se fertigation. Se supplemented seedlings showed higher stress tolerance index and biomass with 7.06 µM Se. Kuznetsov et al. (2003) reported that the addition of 0.1 or 0.25 mM Se caused a 2-6% increase in leaf water content, thereby increasing the drought resistance. The Se-induced improvement in leaf tissue water status was accompanied by a sharp (two to fourfold) inhibition of stress-induced accumulation of Pro and a significant inhibition of POX activity (Kuznetsov et al. 2003). Wang et al. (2011) examined the effect of Se (5 µM Na<sub>2</sub>SeO<sub>4</sub>) on the AsA-GSH cycle in *Trifolium repens* seedlings subjected to drought. They observed that Se application decreased the lipid peroxidation and H<sub>2</sub>O<sub>2</sub> by maintaining the higher AsA and GSH pool higher. Selenium supplementation significantly increased the activities of MDHAR, DHAR, and GR. Among the enzymes, GR showed the highest increase in activity compared to DHAR and MDHAR. In our laboratory, we studied the beneficial role of Se pretreatment (25 µM Na<sub>2</sub>SeO<sub>4</sub>, 48 h) in B. napus seedlings under drought stress (10 and 20% PEG-6000) (Hasanuzzaman and Fujita 2011). Drought-stressed seedlings showed increases in GSH and GSSG content; however, the AsA content increased only under moderate stress (Table 8). The MDHAR and GR activities increased only under moderate stress (10% PEG). The activities of DHAR, GST, and GPX significantly increased at all levels of drought, while CAT activity decreased. Drought stress resulted in a marked increase in the levels of H<sub>2</sub>O<sub>2</sub> and MDA. In contrast, Se-pretreated seedlings exposed to drought stress showed a rise in AsA and GSH content and upregulated activities of CAT, APX, DHAR, MDHAR, GR, GST, and GPX when compared with the drought-stressed seedlings without Se. In turn, the Se-treated seedlings showed a considerable decrease in the levels of H<sub>2</sub>O<sub>2</sub> and MDA and considerable alleviation of oxidative stress (Hasanuzzaman and Fujita 2011). Very recently, Nawaz et al. (2013) found beneficial role of Se priming in conferring drought stress tolerance. In their experiment, seeds of *T. aestivum* were soaked in distilled water or Na<sub>2</sub>SeO<sub>4</sub> solutions (25, 50, 75, and 100  $\mu$ M) for 30 or 60 min, followed by re-drying and subsequent sowing. Priming with Se significantly increased root length, stress tolerance index, and total biomass of germinated seed-lings. Yildiztugay et al. (2016) observed that exogenous Se could upregulate the AsA-GSH cycle in heat-exposed *Z. mays* plants and minimized the overproduction of ROS which in turns protected the plants from oxidative stress induced by drought (25% PEG).

Recent studies also indicated the protective role of Se under HT stress. Yildiztugay et al. (2016) observed that exogenous Se could upregulate the AsA-GSH cycle in heat-exposed Z. mays plants and minimized the overproduction of ROS which in turns protected the plants from oxidative stress induced by HT (24-44 °C). Exogenously applied Se also found to be effective under HT stress in spring wheat under field condition. Heat stress  $(38 \pm 2 \degree C)$  significantly depleted the antioxidative potential, affected growth, photosynthetic pigments, and grain yield of wheat which were satisfactorily reversed by Se supplementation which helped the wheat plants to increase fertility and hence avoid reduction of grain yield under HT stress (Iqbal et al. 2015). Djanaguiraman et al. (2010) reported that beneficial effect of foliarly applied Se (75 mg L<sup>-1</sup>) could enhance photosynthesis, membrane integrity, and antioxidant defense which improved the yield components and grain yield of S. bicolor plants grown under HT stress (40/30 °C). Se application increased photosynthetic rate and stomatal conductance in HT-stressed plants by 13.2 and 12.4%, respectively, compared to non-supplemented plants under stress, while the  $O_2$ ,  $H_2O_2$  and MDA content decreased by 11.5, 35.4 and 28.4%, respectively. Recently, we found that Se could minimize HT-induced damages to B. napus seedlings by enhancing antioxidant defense and glyoxalase systems (Hasanuzzaman et al. 2014b). Heat (38 °C, 24 and 48 h)-exposed seedlings exhibited marked decrease in the chl content and increased RWC, MDA, H<sub>2</sub>O<sub>2</sub>, Pro, and MG contents in time-dependent manners. Selenium supplemented HT-treated seedlings recovered these damages which were evident with decrease level of MDA, H2O2, and MG which was correlated with enhanced ecaivities of CAT, GPX, MDHAR, DHAR, GR, Gly I, and Gly II as well as higher redox balance of AsA and GSH (Hasanuzzaman et al. 2014b). Protective role of Se under LT stress has been reported in few plant studies, but the effect was mostly dose dependent. According to Djanaguiraman et al. (2005), Se was able to increase the tolerance of G. max plants to LT stress by promoting antioxidant capacity, and it improved growth and developmental processes of that plant under LT. Recently, Abbas (2012) found that  $SeO_4^{2-}$  at low concentrations (3 and 6 mg L<sup>-1</sup>) enhanced growth, levels of chl, anthocyanin, sugar, Pro, and AsA, and enzymatic activities in S. bicolor seedlings subjected to LT stress. However, high levels of  $\text{SeO}_4^{2-}$  (12 mg L<sup>-1</sup>) resulted in toxic effects. Low levels of  $\text{SeO}_4^{2-}$  (3 and 6 mg  $L^{-1}$ ) also diminished lipid peroxidation by enhancing the activities of APX and GPX.

Selenium has been documented to reduce metal toxicity in several research studies. The modes of action were varied and are still unclear; however, some suggested reasons included improvement of the antioxidant defense system, reduction of metal uptake, formation of nontoxic Se-metal complexes, and phytochelatin activity (Vorobets and Mykivevich 2000; Sun et al. 2010). Moreover, Se is effective at sustaining physiological activities, growth, and developmental processes even in HM toxic environments (Pedrero et al. 2008; Cartes et al. 2010). A study on peeper showed that Se supplementation diminished Cd toxicity on photosynthesis pigment (Shekari et al. 2016). The application of Selenium at 7 µM significantly increased leaf area in the plants grower at 0.25 mM Cd. The application Se at 3 µM with 0.25 mM Cd and Se 3 and 7 µM with 0.5 mM Cd increased the activity of CAT. Selenium 7 µM decreased Pro content of pepper leaves exposed to Cd 0.5 mM (30%). Selenium significantly enhanced antioxidant activity of leaves which was diminished by Cd toxicity. In general, Se has beneficial effect on plant growth and antioxidant enzymes of pepper under Cd stress and nonstress conditions (Shekari et al. 2016). In B. oleracea, Cd phytotoxicity resulted in elevated MDA level and decreased photosynthetic pigment and tocopherol concentrations, but Se treatment effectively alleviated these adverse effects (Pedrero et al. 2008). In B. napus, Se (2 µM) conferred tolerance to Cd (400 and 600 µM) stress by reducing lipid unsaturation and peroxidation, modulating the activity of antioxidative enzymes (SOD, CAT, APX, GPX), and preventing Cd-induced changes in the DNA methylation pattern (Filek et al. 2008). Sun et al. (2010) showed that enhanced Cd tolerance by Se might be due to removal of Cd from metabolically active cellular sites, induction of Se to scavenge the Cd-induced ROS generated, and the regulation phytochelatin synthesis associated enzymes induced by of Se. In our recent study, we observed that rapeseed seedlings grown under Cd stress (0.5 and 1.0 mM CdCl<sub>2</sub>) showed substantial increases in MDA and H<sub>2</sub>O<sub>2</sub> levels (Hasanuzzaman et al. 2012b). The AsA content of the seedlings decreased significantly upon exposure to Cd stress. The amount of GSH increased only at 0.5 mM CdCl<sub>2</sub>, while GSSG increased at any level Cd with concomitant decreases in the GSH/GSSG ratio. The activities of antioxidant enzymes also reduced under Cd stress. Importantly, Se-pretreated seedlings exposed to Cd showed increases in the AsA and GSH contents, GSH/GSSG ratio, and the activities of APX, MDHAR, DHAR, GR, GPX, and CAT. However, in most of the cases, pretreatment with 50 µM Se showed better results compared to 100 µM Se. These results indicated that the exogenous application of Se at low concentration increased the tolerance of the plants to Cd-induced oxidative damage by enhancing their antioxidant defenses (Hasanuzzaman et al. 2012b).

Selenium improves plant growth and survival under UV radiation, as reported in several studies. Se (0.01 and 0.05 mg kg<sup>-1</sup> soil) improved the antioxidative capacity, protected chloroplast enzymes, and increased shoot yield in *Lactuca sativa* under combined UV-B and UV-C stress (Pennanen et al. 2002). Significant increases in the activities of POD and SOD, together with reduced MDA and O<sub>2</sub>-levels, were documented in *T. aestivum* under UV-B radiation. Selenium also increased root activity, flavonoid, and Pro contents in this plant (Yao et al. 2010). Recently, we completed a pot experiment with three rice varieties, viz., BRRI dhan45, BRRI dhan47, and Nipponbare grown under different concentration of salt water (50–150 mM). Salt stresses reduced the plant height and tillers hill<sup>-1</sup>, leaf relative water con-

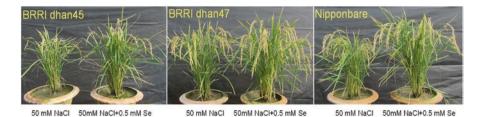


Fig. 10.5 Effect of Se supplementation in mitigating adverse effects of salt stress in different rice cultivars. Plants were subjected to 50 mM NaCl throughout its life cycles with or without 0.5 mM  $Na_2SeO_3$ 

tent, and chl content in dose-dependent manner. Salt stress also reduced the effective tillers hill<sup>-1</sup>, number of filled grains panicle<sup>-1</sup>, 1000-grain weight, grain yield, and straw yield. However, when the plants were supplemented with 0.5 mM Se (sodium selenite, Na<sub>2</sub>SeO<sub>3</sub>), these observed parameters were significantly increased compared to salt treatment alone. Importantly, the beneficial effect of Se on salt stress tolerance was prominent up to 100 mM NaCl, while it could not be more beneficial above this level of salt concentration (Naim 2015). The response of rice plant to Se and salt stress greatly varied in different cultivars (Fig. 10.5).

## **10.7** Molecular Approaches to Manipulate the Genes Associated with Trace Elements Actions in Plants

Plant cannot synthesize inorganic molecule including macronutrient, micronutrient, and heavy metals. But plant can uptake inorganic molecule from growing medium using root. To get entry into root or to be translocated, metal ions are needed to cross both cellular and organellar membranes. These membranes contain different transporter proteins which show specificity to particular inorganic elements (Guerinot 2000). For example, IRT1 is a transporter protein which shows specificity to Fe, but Mn and Zn can also be transported using this transporter. Similarly ZIP1, ZIP2, and ZIP3 act as Zn transporter in plant and AtECA1 for Ca<sup>2+</sup> and Mn<sup>2+</sup>, AtNramp3 for Mn<sup>2+</sup>, Fe<sup>2+</sup> and Cd<sup>2+</sup> in Fe-deficiency conditions, AtOPT3 for possible transport of Cu<sup>2+</sup> and Fe<sup>2+</sup> and Mn<sup>2+</sup>, and so on (Millaleo et al. 2010). Many genes already identified those encode these transporter proteins. Expression of transporter gene depends on the presence or absence of a particular ion. Regulation of genes at transcriptional and posttranscriptional level controls metal uptake as excessive accumulation metal ions cause toxicity to plants. For instance, sensing the intracellular Zn level, Zn-responsive transcriptional activator protein ZAP1 induces gene expression to uptake Zn. On the other hand, Zn uptake reduced by endocytosis of ZRT1 transporter protein (Guerinot 2000).

Abiotic stress limits ion uptake in plants. The roles of trace element in different types of abiotic stresses are well discussed in previous sections. But with the blessing of modern science, it is possible to manipulate the genes related to trace element uptake. Increasing trace element content in plant by overexpression of gene may enhance tolerance against drought, salinity, and heavy metal toxicity (Table 10.3). Very limited literatures are found in this research area. Li et al. (2011) found that overexpressed Na<sup>+</sup>/H<sup>+</sup> antiporter (AtNHX5) gene induced extreme dehydration tolerance in paper mulberry. The AtNHX5-overexpressing plants survived under drought and salinity, whereas the wild-type (WT) plants could not survive. Under salt stress, AtNHX5-overexpressed plant contained higher amounts of Na<sup>+</sup> and K<sup>+</sup> in leaves compared to WT. Higher leaf water content and leaf chl contents, Pro and soluble sugars, and less membrane damage were observed in transgenic plants than the WT plants under both drought and saline conditions. They suggested the possibility of AtNHX5 gene in improving the tolerance against abiotic stresses in paper mulberry plants. In another study, Sasaki et al. (2016) reported that overexpression of *OsHMA3* showed Cd toxicity tolerance. OsHMA3-overexpressed line alleviated the Cd-inhibited growth. Higher amount of Cd found in the roots of OsHMA3-overexpressed line than shoots of wild type and vector control line. This result suggests the role of OsHMA3 in enhancing vacuolar sequestration of Cd in the roots. Furthermore, the OsHMA3-overexpressed line constitutively upregulates five transporter genes belonging to the ZIP family. They finally proposed that overexpression of OsHMA3 is an efficient way to reduce Cd accumulation in the grain and to enhance Cd tolerance in rice.

Transporter gene	Effects	References
NcZNT1	Overexpression of <i>NcZNT1</i> conferred tolerance against high Cd and Zn in <i>A. thaliana</i>	Lin et al. (2016)
ZTP29	<i>Arabidopsis</i> zinc transporter <i>ZTP29</i> was involved in the response to salt stress, may be due to Zn-induced upregulation of the UPR pathway	Wang et al. (2010)
NIP5;1	Enhanced expression of <i>NIP5;1</i> in <i>A. thaliana</i> promoted root growth under B deficiency condition	Kato et al. (2009)
AtNHX1	Overexpression of this gene enhanced salinity stress tolerance in wheat by reducing Na <sup>+</sup>	Xue et al. (2004)
OsNHX1	Overexpressed <i>OsNHX1</i> increased K <sup>+</sup> under salinity thus contributed to salt stress tolerance and promoted growth of maize	Chen et al. (2007)
NtCBP4	This gene was responsible for Ni toxicity by reducing Ni <sup>2+</sup> uptake in transgenic tobacco plant	Arazi et al. (1999)
CAX2	Overexpression of this gene increased Cd and Mn toxicity though transgenic tobacco plant accumulated more Cd and Mn	Hirschi et al. (2000)
CsMTP8	High or low amount of Mn-induced upregulation or downregulation improved Mn homeostasis in cucumber	Migocka et al. (2014)

 Table 10.3
 Overexpressed transporters that enhance abiotic stress tolerance

## 10.8 Conclusions and Outlooks

The trace elements are not critical for all plants but may improve plant growth and vield through their different beneficial influences on plants' physiological and morphological mechanisms. Essential trace elements or micronutrients are elements necessary for maintaining the life processes in plants. The continous hammering on soil for producing more foods without allowing time for natural replenishment of the nutrients uptaken by plants from the same piece of land has led to evolution of newer elements essential for plants. Trace elements present at very low concentrations in agroecosystems are essential to plant growth and development. Both deficiency and toxicity of trace elements occur in agroecosystems. However, the range of essential to lethal for these elements is rather thin. Application of trace elements in fertilizers is effective in correcting micronutrient deficiencies for crop production, whereas, though costlier, remediation of soils contaminated with metals through phytoremediation appears promising as a cost-effective approach. Stressed plant suffering from due by far but not limited to climatic change/aberrations, seasonal rotations, or geographical positions around the globe are galore (Hasanuzzaman et al. 2014b). Plants also develop physiological and morphological mechanisms for adaptations with the stressful conditions. On reflection of the research works have been conducted so far, it can be said that participation of trace elements in mechanisms of stress tolerance in plants is very vital (Hasanuzzaman et al. 2011b). To be more specific, under adverse environmental conditions, supplementing trace elements have mostly beneficial effects in plant survival, vegetative growth, and reproductive growth and productivity (yield), unless they are in toxic concentration in soil-plant systems. As for example, 50 mg B L<sup>-1</sup> foliar spray at booting and anthesis stage of Triticum aestivum reduces drought stress effects on plants through increasing chl and Car and decreasing H<sub>2</sub>O<sub>2</sub> and Pro content (Abdel-Motagally and El-Zohri 2016). Abiotic stress-induced oxidative stress is another phenomena that plants experienced under different stress conditions such as waterlogging, drought, salinity, heat, ozone, UV-B radiation, redox-active metals, etc. but trace elements can mitigate through different ways, for example, by reducing the production of ROS and other radicals. Besides these, the actions of trace elements on a wide range of crops (Euglena gracilis to Oryza sativa) have been tested in terms of tolerance or avoidance of abiotic stresses, and the results were positive to a great extent.

Trace elements are indispensable part for either physiological, biochemical or molecular approach of stress tolerant mechanism development in plants. To exemplify, *Arabidopsis* zinc transporter *ZTP29* was involved in the response to salt stress through Zn-induced upregulation of the unfolded protein response (UPR) pathway, and overexpression of *AtNHX1* gene reduced Na<sup>+</sup> content in plant and enhanced salinity stress tolerance in wheat. The reviewed research results on role of trace elements on abiotic stress tolerance in plants predict that trace elements are only trace for their presence, but they are huge for their actions and overlooking them as trace elements will results in failure of developing tolerance in plants to abiotic stresses.

However, thorough actions of trace elements on abiotic stress avoidance, tolerance, or resistance mechanisms by plants are still poorly understood for drawing out a full panorama. Foolproof researches focusing on the equilibrium of trace elements in an agroecosystem and elaboration of soil biochemical and molecular approaches that can be used to diagnose trace elements responsible for stress control and to use for future use are urgently needed. Besides these, most of the experiments conducted around the world on actions of beneficial trace elements on plant tolerance of abiotic stresses are confined mostly to laboratory conditions and short-term studies only. Field performances of the biochemical, molecular approaches along with agronomic management practices are also needed to strengthen the science of plants tolerance to abiotic stresses.

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