Stress Management: Sustainable Approach Towards Resilient Agriculture

5

Abstract

The improvement of crop performance by increasing osmotic potential-adjusting ability is more significant in roots than other plant parts to avert stress. The role of osmotic adjustment in root elongating zone is to maintain turgor pressure to continue root elongation and root growth in drying soils, which enable the plant to maintain its transpiration by exploiting a greater volume of soil or utilize available water in a given soil volume more efficiently. In this chapter the various tolerance mechanism and diversity among the plants to combat is documented with numerous illustrations. In this last section role of plant metabolites for abiotic stress management is detailed out.

Keywords

Stress · Metabolites · Tolerance · Abiotic · Salt · Drought

5.1 Osmotic Adjustments and Crop Improvements

Osmotic adjustment is a mechanism in plants to tolerate osmotic stress by lowering the osmotic potential by the accumulation of solutes (Radin 1983), and to maintain the volume of protoplast and turgor pressure (Santakumuri and Berkowitz 1991). Osmotic adjustment is a function of either an increase in the net osmoticum deposition rate in the growing region and/or a reduction in the rate of tissue volume expansion (Sharp et al. 1990). The former is more likely to represent an adaptive response that could contribute to growth maintenance (Sharp et al. 2004). Osmotic adjustment occurs in leaves, hypocotyls, roots, floral apex and spikelets under osmotic stress conditions (Turner and Jones 1980). In leaf mature zone, osmotic adjustment plays an important role for plant cell survival (Flower and Ludlow 1986), facilitates higher stomatal conductance (Düring and Dry 1995) and leaf expansion (Westgate and Boyer 1985) to sustain photosynthesis under water stress condition (Turner and

J. A. Parray et al., *Sustainable Agriculture: Biotechniques in Plant Biology*,
https://doi.org/10.1007/978-981-13-8840-8_5

Jones 1980). Turner and Jones (1980) stated that osmotic adjustment in the root has a different role from that in the shoot, and Serraj and Sinclair (2002) stated that osmotic adjustment in root might be important in relation to crop production. As in leaf growth, root elongation is related with the turgor pressure in root elongation zone (Westgate and Boyer 1985; Frensch and Hsiao 1994). The role of osmotic adjustment in root elongating zone is to maintain turgor pressure to continue root elongation and root growth in drying soils, which enable the plant to maintain its transpiration by exploiting a greater volume of soil or utilize available water in a given soil volume more efficiently. The significance of osmotic adjustment in the elongated zone of the root is to promote desiccation tolerance and to initiate lateral roots that are responsible for efficient absorption and transport of water (Azhiri-Sigari et al. 2000). Therefore, improving crop performance by increasing the ability to adjust osmotic potential in roots may be more important than other parts of the plant (Serraj and Sinclair 2002), although the process in roots has not been studied as extensively as in leaves. There are few reports in the root of osmotic adjustment. Sharp and Davies (1979) showed that even if osmotic potential decreased in conditions of water stress, turgor potential and root growth were maintained (Sharp and Davies 1979; Westgate and Boyer 1985). On the other hand in leaf (Sharp and Davies 1979) and stem (Westgate and Boyer 1985), extension rate and the development of leaf area were reduced by water deficit, due largely to the reduction in leaf turgor pressure. In order to reduce the osmotic potential, the accumulation of compatible solute (Voetberg and Sharp 1991) and the decrease in the rate of influx of water in the tissue and expansion of the tissue volume (Sharp et al. 1990) contributed to the seminal root of maize. Turgor was recovered faster by osmotic adjustment in the cells deep inside the tissue compared to cells near the surface of the root, which showed that the phloem was a possible source of osmotic adjustment compounds (Frensch and Hsiao 1994). The root is the first organ exposed to deficit in water. The growth of leaves is highly sensitive to water stress and can be inhibited by a slight reduction in water potential in the tissue (Hsiao and Xu 2000). Therefore, it is assumed that osmotic adjustment in the root occurs before osmotic adjustment in the leaf to increase turgor pressure for continued root growth and water and nutrient absorption. The osmotic adjustment in the root is therefore expected to delay the onset of shooting water deficit, which reduces the activity of stomatal conductance and photosynthetic activity. In order to clarify the role of root osmotic adjustment in maintaining plant growth in a water deficit condition, it is important to examine the transient changes in the concentration of solvents under stress.

5.1.1 Yield and Osmolyte Accumulation

Despite the widespread suggestion that osmotic accumulation (OA) is beneficial for increasing crop yields under conditions of water deficit, experimental data provide little support. Typically, crop yields of high osmotic-adjusting lines were compared to low osmotic-adjusting lines. The data published by Morgan on wheat (Morgan 1995) and by Ludlow on sorghum (Ludlow et al. 1990) are the ones usually cited as

the critical references for the putative benefits of OA on crop yield. Morgan (1983) worked with wheat and initiated his yield and OA studies by evaluating different wheat lines for osmotic adjustment under greenhouse conditions using estimates of relative water content (RWC) at a given water potential value (−2•5 MPa) to select high osmotic adjustment lines. Unfortunately, no direct measurements of osmotic adjustment were made either in the greenhouse or in the field, and osmotic adjustment was inferred from indirect correlations, which neglected possible variations in the elasticity module value. Babu et al. (1999) recently showed that different OA measurement methods do not necessarily yield consistent results. In the field of wheat lines selected for possible differences in osmotic adjustment (Morgan 1983), the grain yields were 44 g m^{-2} for lines identified with high OA and 29 g m^{-2} for lines with low OA. These results probably reflected an advantage during severe phase III survival in these particular experimental conditions. The difficulty is that these yield levels were so low that growers would consider even yield at 44 g m^{-2} to be a failed crop. In industrial agriculture, yields of at least 150 g m^{-2} and more likely 200–400 g m^{-2} are likely to be required for viable production under dryland conditions. Morgan (1995) also reported comparisons of the yield of wheat grain under drought for low and high osmotic adjustment lines from 5 years of field experiments. Of the nine comparisons presented, only three pairs had a significantly higher yield in high osmotic adjustment lines which was limited to severe water deficits and very low grain yield. Three other comparison pairs had a small non-significant advantage for high osmotic-adjusting lines, and three pairs had a lower but non-significant yield for the high osmotic-adjusting group. Blum, Zhang and Nguyen (1999) recently reported comparisons of OA and yield between ten spring wheat cultivars, including two Morgan lines. Ludlow et al. (1990) reported a positive association between a high capacity for osmotic adjustment and grain yield in sorghum after anthesis. Apparently the higher yield was due to more and larger grains and was associated with a higher harvest index and distribution index. Interestingly, in this study, osmotic adjustment had almost no effect on dry matter at maturity. The main physiological effect of OA was then interpreted as turgor maintenance in the panicle, which could lead to continued metabolic activity during grain filling and thus a higher harvest index. This study may have reflected the particular case in which OA may have extended physiological activity in the panicle prior to the rescue of the crop by rainfall. Results were also reported from the same sorghum lines as above for the contribution of osmotic adjustment to grain yield when subjected to severe pre-anthesis water deficits (Santamaria et al. 1990). The overall response was a higher average grain yield for high osmotic adjustment lines, mainly due to a higher number of grains and a higher harvest index. However, one pair of lines showed a non-significant yield advantage for the low osmotic-adjusting line compared to the three pairs, one pair showed that osmotic adjustment was associated with more water extraction, and the third pair showed that osmotic adjustment was associated with better panicle exertion. In a greenhouse test, the osmotic adjustment capacity of seven pea genotypes was measured and compared to the yield of grains obtained in field trials (Rodríguez-Maribona et al. 1992). Correlation between the capacity of osmotic adjustment and yield was only significant in the case of dry years, but not in a rainy year when drought was

only moderate and higher yields were achieved. The same results were obtained with chickpea (Morgan et al. 1991), in that lines produced greater yields with high osmotic-adjustment capacity only when grown in environments of greatest stress where yields were low. In addition to the frequently cited studies, which are usually used as references to illustrate the beneficial effect of OA on grain yield, numerous reports do not show any effect of osmotic adjustment or even report negative effects on crop yields. Quisenberry et al. (1984) reported a significant negative correlation between the weight of the cotton shooting and the osmotic adjustment estimated by the osmotic potential of zero turgor. They concluded that a reduced growth potential could result if selection pressure is aimed at improving osmotic adjustment during drought. Grumet et al. (1987) reported that barley lines selected for high osmotic adjustment had slower growth, lower dry matter production and grain yield than lines with low osmotic adjustment. No yield benefit was found with osmotic adjustment in four sorghum cultivars under severe drought (Flower et al. 1990). Recently, Subbarao et al. (2000) reported that OA was positively correlated with grain yields at 72 and 82 days after sowing (DAS) whereas OA at 92 DAS contributed negatively to the yield. Bolaños and Edmeades (1991) showed that correlations between osmotic adjustment and performance of tropical maize populations under drought were weak, inconsistent and non-significant. The CIMMYT maize program has apparently made the same assumption (Guei and Wassom 1993). A large amount of rice research has failed to demonstrate the benefit of OA in crop yield (Fukai and Cooper 1995). Overall, the exceptional results in the published literature show a positive correlation between osmotic adjustment and yield, which is usually achieved under severe drought stress when yields are too low to be of practical value.

5.2 Mechanism of Salt Tolerance in Plants

Depending on the severity and duration of the stress, salinity stress involves changes in different physiological and metabolic processes and ultimately inhibits crop production (Flowers 2004; Munns and Tester 2008; FAO 2009). Initially, soil salinity in the form of osmotic stress is known to suppress plant growth, followed by ion toxicity (Rahnama et al. 2010). During the initial phases of salinity stress, the ability to absorb water from root systems decreases and the loss of water from leaves is accelerated due to the osmotic stress of high salt accumulation in soil and plants, and therefore salinity stress is also considered to be hyperosmotic stress (Munns 2005). Osmotic stress in the initial phase of salinity stress causes various physiological changes, such as membrane disruption, nutrient imbalance, impairment of the ability to detoxify reactive oxygen species (ROS), differences in antioxidant enzymes and reduced photosynthetic activity, and decrease in stomatal aperture(Munns and Tester 2008; Rahnama et al. 2010). Also considered a hyperionic stress is salinity stress. The accumulation of Na^+ and Cl^- ions in tissues of plants exposed to soils with high NaCl concentrations is one of the most harmful effects of salinity stress. The entry of Na^+/Cl^- into the cells causes severe ion

imbalance and excessive absorption may cause significant physiological disorders. High concentrations of Na^+ inhibit the absorption of K^+ ions, which is an essential element for growth and development, leading to lower productivity and even death (James et al. 2011). ROS production, such as singlet oxygen, superoxide, hydroxyl radical and hydrogen peroxide, is increased in response to salinity stress (Apel and Hirt 2004; Mahajan and Ahmad et al. 2010; Ahmad and Prasad 2012). The formation of salinity-induced ROS can lead to oxidative damage in various cellular components such as proteins, lipids and DNA, which interrupts vital plant cellular functions. There are genetic variations in salt tolerance, and the degree of salt tolerance varies from species to species. Barley (*Hordeum vulgare*) is more tolerant to salt than rice (*Oryza sativa*) and wheat (*Triticum aestivum*) among the main crops. In the case of dicotyledons ranging from Arabidopsis thaliana, which is very sensitive to salinity, to halophytes such as *Mesembryanthemum crystallinum*, *Atriplex* sp., *Thellungiella salsuginea* (formerly *T. halophila*) (Abraham et al. 2011; Pang et al. 2010), the degree of variation is even more pronounced. Sumptuous research has been carried out in the last two decades to understand the mechanism of salt tolerance in model plant Arabidopsis (Zhang and Shi 2013). Genetic variations and differential responses to salinity stress in plants differing in stress tolerance enable plant biologists to identify physiological mechanisms, sets of genes, and gene products that are involved in increasing stress tolerance and to incorporate them in suitable species to yield salt tolerant varieties.

5.2.1 Physiological and Biochemical Mechanisms of Salt Tolerance

To survive in soils with high salt concentrations, plants develop various physiological and biochemical mechanisms. The main mechanisms include, but are not limited to (FAO 2009), homeostasis and compartimentation of ions (Flowers 2004), transport and absorption of ions (Munns and Tester 2008), biosynthesis of osmoprotectants and compatible solutes, (James et al. 2011), activation of antioxidant enzymes and synthesis of antioxidant compounds (Rahnama et al. 2010), synthesis of polyamines, (Munns 2005). The research progress that clarifies these mechanisms is discussed below.

5.2.2 Ion Homeostasis and Salt Tolerance

The maintenance of ion homeostasis by ion absorption and compartimentation is not only crucial for normal plant growth, but is also an essential process for salt stress growth (Xiaomu et al. 1995; Serrano et al. 1999; Hasegawa 2013). Glycophytes and halophytes cannot tolerate high concentrations of salt in their cytoplasm, regardless of their nature. The excess salt is therefore either transported to the vacuole or sequestered in older tissues, which are eventually sacrificed, protecting the plant against salinity stress (Reddy et al. 1992; Zhu 2003).

The main form of salt in the soil is NaCl, so the study of the transport mechanism of Na^+ ion and it is the main focus of research is the study about the transport mechanism of Na^+ ion and its compartmentalization. The Na^+ ion that enters the cytoplasm is then transported to the vacuole via Na^+/H^+ antiporter. Two types of H^+ pumps are present in the vacuolar membrane: vacuolar type H^+-ATPase (V-ATPase) and the vacuolar pyrophosphatase (V-PPase) (De Lourdes Oliveira Otoch et al. 2001; Wang and Ratajczak 2001; Dietz et al. 2001). Of these, V-ATPase is the most dominant H^+ pump present within the plant cell. During nonstress conditions it plays an important role in maintaining solute homeostasis, energizing secondary transport and facilitating vesicle fusion. Under stressed condition the survivability of the plant depends upon the activity of V-ATPase (Dietz et al. 2001). In a study performed by De Lourdes Oliveira Otoch et al. (2001) in hypocotyls of *Vigna unguiculata* seedlings, it was observed that the activity of VATPase pump increased when exposed to salinity stress but under similar conditions, activity of V-PPase was inhibited, whereas in the case of halophyte Suaeda salsa, V-ATPase activity was upregulated and V-PPase played a minor role (Wang and Ratajczak 2001). Increasing evidence demonstrates the roles of a Salt Overly Sensitive (SOS) stress signalling pathway in ion homeostasis and salt tolerance (Hasegawa et al. 2000; Sanders 2000). The SOS signalling pathway consists of three major proteins, SOS1, SOS2, and SOS3. SOS1, which encodes a plasma membrane Na^+/H^+ antiporter, is essential in regulating Na^+ efflux at cellular level. It also facilitates long distance transport of Na^+ from root to shoot. Overexpression of this protein confers salt tolerance in plants (Shi et al. 2000; Shi et al. 2002). SOS2 gene, which encodes a serine/threonine kinase, is activated by salt stress elicited Ca^+ signals. This protein consists of a well-developed N-terminal catalytic domain and a C-terminal regulatory domain (Liu et al. 2000). The third type of protein involved in the SOS stress signalling pathway is the SOS3 protein, which is a myristoylated Ca^+ binding protein and contains a myristoylation site at its N-terminus. This site plays an essential role in conferring salt tolerance (Ishitani et al. 2000). C-terminal regulatory domain of SOS2 protein contains a FISL motif (also known as NAF domain), which is about 21 amino acid long sequence, and serves as a site of interaction for Ca^{2+} binding SOS3 protein. This interaction between SOS2 and SOS3 protein results in the activation of the kinase (Guo et al. 2004). The activated kinase then phosphorylates SOS1 protein thereby increasing its transport activity, which was initially identified in yeast (Quintero et al. 2002). SOS1 protein is characterised by a long cytosolic C-terminal tail, about 700 amino acids long, comprising a putative nucleotide binding motif and an autoinhibitory domain. This autoinhibitory domain is the target site for SOS2 phosphorylation. Besides conferring salt tolerance it also regulates pH homeostasis, membrane vesicle trafficking, and vacuole functions (Oh et al. 2010; Quintero et al. 2011). Thus with the increase in the concentration of Na^+ there is a sharp increase in the intracellular Ca^{2+} level which in turn facilitates its binding with SOS3 protein. Ca^{2+} modulates intracellular Na^+ homeostasis along with SOS proteins. The SOS3 protein then interacts and activates SOS2 protein by releasing its

self-inhibition. The SOS3-SOS2 complex is then loaded onto plasma membrane where it phosphorylates SOS1. The phosphorylated SOS1 results in the increased Na^+ efflux, reducing Na^+ toxicity (Martínez-Atienza et al. 2007). Many plants have developed an efficient method to keep the ion concentration in the cytoplasm in a low level. Membranes along with their associated components play an integral role in maintaining ion concentration within the cytosol during the period of stress by regulating ion uptake and transport (Sairam and Tyagi 2004). Different carrier proteins, channel proteins, antiporters and symporters carry out the transport phenomenon. Maintaining cellular Na^+/K^+ homeostasis is pivotal for plant survival in saline environments. Ma et al. (2012) have reported that Arabidopsis NADPH oxidases AtrbohD and AtrbohF function in ROS-dependent regulation of Na^+/K^+ homeostasis in Arabidopsis under salt stress. Plants maintain a high level of K^+ within the cytosol of about 100 mM ideals for cytoplasmic enzyme activities. Within the vacuole K^+ concentration ranges between 10 mM and 200 mM. The vacuole serves as the largest pool of K^+ within the plant cell. K^+ plays a major role in maintaining the turgor within the cell. It is transported into the plant cell against the concentration gradient via K^+ transporter and membrane channels. K^+ transporters mediate high affinity K^+ uptake mechanisms when the extracellular K^+ concentration is low, whereas K^+ channels carry out low affinity uptake when the extracellular K^+ concentration is high. Thus uptake mechanism is primarily determined by the concentration of K+ available in the soil. On the other hand a very low concentration of Na^+ ion (about 1 mM or less) is maintained in the cytosol. During salinity stress, due to increased concentration of Na+ in the soil, Na+ ion competes with K^+ for the transporter as they both share the same transport mechanism, thereby decreasing the uptake of K^+. A large number of genes and proteins, such as HKT and NHX, encoding K^+ transporters and channels have been identified and cloned in various plant species. During salt stress expression of some low abundance transcripts is enhanced which are found to be involved in K^+ uptake. This was observed in the halophyte *Mesembryanthemum crystallinum* (Yen et al. 2000). Transporters located on the plasma membrane, belonging to the HKT (histidine kinase transporter) family, also play an essential role in salt tolerance by regulating transportation of Na^+ and K^+. Class 1 HKT transporters that have been identified in Arabidopsis protect the plant from the adverse effects of salinity by preventing excess accumulation Na^+ in leaves. Similar results were observed in the experiment which was carried out with rice where class 1 HKT transporter removes excess Na^+ from xylem, thus protecting the photosynthetic leaf tissues from the toxic effect of Na^+ (Schroeder et al. 2013). Intracellular NHX proteins are Na^+, K^+/H^+ antiporters involved in K^+ homeostasis, endosomal pH regulation, and salt tolerance. Barragan et al. (2012) showed that tonoplastlocalized NHX proteins (NHX1 and NHX2: the two major tonoplast-localized NHX isoforms) are essential for active K^+ uptake at the tonoplast, for turgor regulation, and for stomatal function. In fact more such NHX isoforms have been identified and their roles in ion (Na^+, K^+, H^+) homeostasis established from different plant species (e.g., LeNHX3 and LeNHX4 from tomato) (Galvez et al. 2012).

5.2.2.1 Compatible Solute Accumulation and Osmotic Protection

Compatible solutes, also known as compatible osmolytes, are a group of uncharged, polar and soluble organic compounds that do not interfere with cellular metabolism even at high concentrations. They include mainly proline (Hoque et al. 2007; Ahmad et al. 2010; Hossain et al. 2011; Nounjan et al. 2012; Tahir et al. 2012), glycine betaine (Khan et al. 2000; Wang and Nii 2000), sugar (Bohnert et al. 1995; Kerepesi and Galiba 2000), and polyols (Ford 1984; Dopp et al. 1985; Ashraf and Foolad 2007; Saxena et al. 2013). Organic osmolytes are synthesised and accumulated in varying amounts amongst different plant species. For example, quaternary ammonium compound beta alanine betaine's accumulation is restricted among few members of Plumbaginaceae (Hanson et al. 1994), whereas accumulation of amino acid proline occurs in taxonomically diverse sets of plants (Saxena et al. 2013). The concentration of compatible solutes within the cell is maintained either by irreversible synthesis of the compounds or by a combination of synthesis and degradation. The biochemical pathways and genes involved in these processes have been thoroughly studied. As their accumulation is proportional to the external osmolarity, the major functions of these osmolytes are to protect the structure and to maintain osmotic balance within the cell via continuous water influx (Hasegawa et al. 2000). Amino acids such as cysteine, arginine and methionine, which constitute approximately 55% of total free amino acids, decrease when exposed to salinity stress, while the concentration of proline increases in response to salinity stress (El-Shintinawy and El-Shourbagy 2001). The accumulation of proline is a well-known measure for salinity stress relief (Matysik et al. 2002; Ben Ahmed et al. 2010). Intracellular proline, which accumulates during stressful salinity, not only provides stress tolerance, but also serves as an organic nitrogen reserve during stress recovery. Proline is either glutamate or ornithine synthesized. The primary function in osmotically stressed cell glutamate functions as the primary precursor. Two major enzymes are the biosynthetic pathway, pyrroline carboxylic acid synthetase and pyrroline carboxylic acid reductase. These two regulatory steps are used to overproduce plant proline (Sairam and Tyagi 2004). It works as an O_2 quencher revealing its antioxidant capability (Matysik et al. 2002). Ben Ahmed et al. (2010) observed that proline supplements increased salt tolerance in olives (Olea europaea) by improving some antioxidant enzyme activity, photosynthetic activity and plant growth and maintaining the appropriate status of plant water in salinity conditions. It has been reported that proline improves salt tolerance in *Nicotiana tabacum* by increasing the activity of enzymes involved in antioxidant defence system (Hoque et al. 2008). Deivanai et al. (2011) also showed that the growth of rice seedlings from seeds pretreated with 1 mM proline during salt stress improved. Glycine betaine is an amphoteric quaternary ammonium compound found ubiquitously in microorganisms, higher plants and animals, and is electrically neutral over a wide range of pH levels. It is highly soluble in water, but also contains non-polar moiety in 3-methyl groups. It interacts with both hydrophobic and hydrophilic domains of the macromolecules, such as enzymes and protein complexes, due to its unique structural characteristics. Glycine betaine is a non-toxic cellular osmolyte that increases the osmolarity of the cell during the stress period and therefore plays an important

role in mitigating stress. Glycine betaine also protects the cell by osmotic adjustment (Gadallah 1999), stabilizes proteins (Makela et al. 2000), and protects the photosynthetic apparatus against stress damage (Cha-Um and Kirdmanee 2010) and the reduction of ROS (Ashraf and Foolad 2007; Saxena et al. 2013). Glycine betaine accumulation occurs in a wide range of plants from different taxonomic backgrounds. Glycine betaine is either choline or glycine synthesized in the cell. Synthesis of glycine betaine from choline is a 2-step reaction involving two or more enzymes. In the first step choline is oxidised to betaine aldehyde, which is then again oxidised in the next step to form glycine betaine. In higher plants the first conversion is carried out by the enzyme choline monooxygenase (CMO), whereas the next step is catalysed by betaine aldehyde dehydrogenase (BADH) (Ahmad et al. 2013). Another pathway, which is observed in some plants, mainly halophytic, demonstrated the synthesis of glycine betaine from glycine. Here glycine betaine is synthesized by three successive N-methylation and the reactions are catalysed by two S-adenosyl methionine dependent methyl transferases, glycine sarcosine N-methyl transferase (GSMT), and sarcosine dimethylglycine N-methyl transferase (SDMT). These two enzymes have overlapping functions as GSMT catalyses the first and the second step while SDMT catalyses the second and third step (Ahmad et al. 2013). Rahman et al. (2002) reported the positive effect of glycine betaine on the ultrastructure of *Oryza sativa* seedlings when exposed to salt stress. Under stressed condition (150 mM NaCl) the ultrastructure of the seedling shows several damages such as swelling of thylakoids, disintegration of grana and intergranal lamellae, and disruption of mitochondria. However, these damages were largely prevented when seedlings were pretreated with glycine betaine. When glycine betaine is applied as a foliar spray in a plant subjected to stress, it led to pigment stabilization and increase in photosynthetic rate and growth (Cha-Um and Kirdmanee 2010; Ahmad et al. 2013). Polyols are compounds with multiple hydroxyl functional groups available for organic reactions. Sugar alcohols are a class of polyols functioning as compatible solutes, as low molecular weight chaperones, and as ROS scavenging compounds (El-Shintinawy and El-Shourbagy 2001). They can be classified into two major types, cyclic (e.g., pinitol) and acyclic (e.g., mannitol). Mannitol synthesis is induced in plants during stressed period via action of NADPH dependent mannose-6-phosphate reductase. These compatible solutes function as a protector or stabilizer of enzymes or membrane structures that are sensitive to dehydration or ionically induced damage. It was found that the transformation with bacterial mltd gene that encodes for mannitol-1-phosphate dehydrogenase in both Arabidopsis and tobacco (*Nicotiana tabacum*) plants confer salt tolerance, thereby maintaining normal growth and development when subjected to high level of salt stress (Binzel et al. 1988; Thomas et al. 1995). Pinitol is accumulated within the plant cell when the plant is subjected to salinity stress. The biosynthetic pathway consists of two major steps, methylation of myo-inositol, which results in formation of an intermediate compound, ononitol, which undergoes epimerization to form pinitol. Inositol methyl transferase enzyme encoded by imt gene plays major role in the synthesis of pinitol. Transformation of imt gene in plants shows a result similar to that observed in the case of mltd gene. Thus it can be said that pinitol also plays

a significant role in stress alleviation. Accumulation of polyols, either straight-chain metabolites such as mannitol and sorbitol or cyclic polyols such as myo-inositol and its methylated derivatives, is correlated with tolerance to drought and/or salinity, based on polyol distribution in many species, including microbes, plants, and animals (Bohnert et al. 1995). Accumulations of carbohydrates such as sugars (e.g., glucose, fructose, fructans, and trehalose) and starch occur under salt stress (Parida et al. 2004). The major role played by these carbohydrates in stress mitigation involves osmoprotection, carbon storage, and scavenging of reactive oxygen species. It was observed that salt stress increases the level of reducing sugars (sucrose and fructans) within the cell in a number of plants belonging to different species (Kerepesi and Galiba 2000). Besides being a carbohydrate reserve, trehalose accumulation protects organisms against several physical and chemical stresses including salinity stress. They play an osmoprotective role in physiological responses (Ahmad et al. 2013). Sucrose content was found to increase in tomato (*Solanum lycopersicum*) under salinity due to increased activity of sucrose phosphate synthase (Gao et al. 1998). Sugar content, during salinity stress, has been reported to both increase and decrease in various rice genotype (Alamgir and Ali 1999). In rice roots it has been observed that starch content decreased in response to salinity while it remained fairly unchanged in the shoot. Decrease in starch content and increase in reducing and non-reducing sugar content were noted in leaves of *Bruguiera parviflora* (Parida et al. 2004).

5.2.3 Antioxidant Regulation of Salinity Tolerance

Abiotic and biotic stress in living organisms, including plants, can cause chloroplasts and mitochondria to overflow, deregulate or even disrupt electron transport chains. Under these conditions, molecular oxygen (O_2) acts as an electron accepter, which results in ROS accumulation. Single oxygen (O_2), hydroxyl radical (OH^-), superoxide radical (O^{2-}) and hydrogen peroxide (H_2O_2) are all highly oxidizing compounds and thus potentially harmful to the integrity of cells (Groß et al. 2013). Antioxidant metabolism, including antioxidant enzymes and non-enzymatic compounds, play a key role in the detoxification of salinity stress-induced ROS. Salinity tolerance is positively correlated with the activity of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidise (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR) and with the accumulation of nonenzymatic antioxidant compounds (Asada 1999; Gupta et al. 2005). Gill et al. (2013) and Tuteja et al. (2013) have recently reported a couple of helicase proteins (e.g., DESD-box helicase and OsSUV3 dual helicase) functioning in plant salinity tolerance by improving/maintaining photosynthesis and antioxidant machinery. Kim et al. (2013) showed that the application of silicone (Si) to the root zone of rice influenced hormonal and antioxidant responses to salinity stress. The results showed that Si treatments increased the growth of rice plants significantly compared to salinity stress controls. Si treatments reduced the accumulation of sodium resulting in low electrolytic leakage and lipid peroxidation

compared to salinity stress control plants. In control plants, the response to enzymatic antioxidants (catalase, peroxidase and polyphenol oxidase) was more pronounced than in Si-treated plants under stress of salinity. Anthocyanin is a flavonoid whose accumulation has been largely documented in plants exposed to salt stress. Van Oosten et al. (2013) isolated the anthocyanin-impairedresponse-1 (air1) mutant that is unable to accumulate anthocyanins under salt stress. The air1 mutant showed a defect in anthocyanin production in response to salt stress but not to other stresses such as high light, low phosphorous, high temperature, or drought stress. This specificity indicated that air1 mutation did not affect anthocyanin biosynthesis but rather its regulation in response to salt stress. The discovery and characterization of AIR1 opens avenues to dissect the connections between abiotic stress and accumulation of antioxidants in the form of flavonoids and anthocyanins. Ascorbate is one of the major antioxidants present within the cell. Pea plants grown under saline (150 mM NaCl) stress showed an enhancement of both APX activity and Snitrosylated APX, as well as an increase of H2O2, NO, and S-nitrosothiol (SNO) content that can justify the induction of the APX activity. Proteomic data have shown that APX is one of the potential targets of PTMs mediated by NO^-derived molecules (Begara-Morales et al. 2014). Using recombinant pea cytosolic APX, the impact of peroxynitrite ($ONOO^-$) and S-nitrosoglutathione (GSNO), which are known to mediate protein nitration and S-nitrosylation processes, respectively, was analysed. While peroxynitrite inhibits APX activity, GSNO enhances its enzymatic activity. The results provide new insight into the molecular mechanism of the regulation of APX, which can be both inactivated by irreversible nitration and activated by reversible S-nitrosylation (Begara-Morales et al. 2014). Exogenous application of ascorbate mitigates the adverse effects of salinity stress in various plant species and promotes plant recovery from the stress (Agarwal and Shaheen 2007; Munir and Aftab 2011). Another antioxidant in stress mitigation is glutathione, which can react with superoxide radical, hydroxyl radical, and hydrogen peroxide, thereby functioning as a free radical scavenger. It can also participate in the regeneration of ascorbate via ascorbate-glutathione cycle (Foyer et al. 1997). When applied exogenously glutathione helped to maintain plasma membrane permeability and cell viability during salinity stress in Allium cepa (Aly-Salama and Al-Mutawa 2009). Application of glutathione and ascorbate was found to be effective in increasing the height of the plant, branch number, fresh and dry weight of herbs and flowers, and the content of carbohydrates, phenols, xanthophylls pigment, and mineral ion content when subjected to saline condition (Rawia Eid et al. 2011). Many studies have found differences in levels of expression or activity of antioxidant enzymes; these differences are sometimes associated with the more tolerant genotype and sometimes with the more sensitive genotype. Munns and Tester (2008) suggested that differences in antioxidant activity between genotypes may be due to genotypic differences in degrees of stomatal closure or other responses that alter the rate of CO_2 fixation and differences that lead to processes that avoid photoinhibition and for which the plant has an abundant capacity (Munns and Tester 2008). In their recent review, Roy et al. (2014) argued that plants have three main features that help them adapt to salinity stress: ion exclusion, tissue tolerance and salinity tolerance. Antioxidants appear to play a role in the mechanism of tissue and salinity tolerance.

5.2.4 Roles of Polyamines in Salinity Tolerance

Polyamines (PA) are small, low molecular weight, all encompassing, polycationic aliphatic molecules widely distributed throughout the plant kingdom. Polyamines play a variety of roles in normal growth and development, such as the regulation of cell proliferation, somatic embryogenesis, differentiation and morphogenesis, tubers and seed germination, flowers and fruit development, and senescence (Panicot et al. 2002; Knott et al. 2007; Gupta et al. 2013a, b). It also plays a crucial role in the tolerance of abiotic stress, including salinity, and polyamine levels are correlated with stress tolerance in plants (Kovacs et al. 2010). The PA biosynthetic pathway has been thoroughly investigated in many organisms including plants and has been reviewed in details (Rambla et al. 2010). PUT is the smallest polyamine and is synthesised from either ornithine or arginine by the action of enzyme ornithine decarboxylase (ODC) and arginine decarboxylase (ADC), respectively (Hasanuzzaman et al. 2014). N-carbamoyl-putrescine is converted to PUT by the enzyme N-carbamoyl-putrescine aminohydrolase (Alcazar et al. 2010). The PUT thus formed functions as a primary substrate for higher polyamines such as SPD and SPM biosynthesis. The triamine SPD and tetramine SPM are synthesized by successive addition of aminopropyl group to PUT and SPD, respectively, by the enzymes spermidine synthase (SPDS) and spermine synthase (SPMS) (Alcazar et al. 2006). ODC pathway is the most common pathway for synthesis of polyamine found in plants. Most of the genes involved in the ODC pathway have been identified and cloned. However there are some plants where ODC pathway is absent; for instance in Arabidopsis polyamines are synthesized via ADC pathway (Kusano et al. 2007). All the genes involved in polyamine biosynthesis pathways have been identified from different plant species including Arabidopsis (Ge et al. 2006). Polyamine biosynthesis pathway in Arabidopsisinvolves six major enzymes: ADC encoding genes (ADC1 and ADC2); SPDS (SPDS1 and SPDS2) and SAMDC (SAMDC1, SAMDC2, SAMDC3, SAMDC4) (Hanzawa et al. 2002). On the contrary SPM synthase, thermospermine synthase, agmatine iminohydrolase and N-carbamoylputrescine amidohydrolase are represented by single genes only (Urano et al. 2004). When the plant is exposed to salinity stress, an increase in endogenous polyamine levels has been reported. Polyamine catabolism regulates the level of intracellular polyamine. Polyamines are oxidatively catabolized by amine oxidases, including copper binding diamine oxidases and FAD binding polyamine oxidases. These enzymes play an important role in the tolerance of stress (Takahashi and Kakehi 2010). Changes in the level of cellular polyamine due to stress may have effects on stress, but do not demonstrate their role in counteracting stress. To understand, therefore, whether polyamines actually protect cells from damage caused by stress, the exogenous use of polyamines, which is expected to increase endogenous polyamine, has been investigated before or during stress. Application of exogenous polyamine has been found to increases the level of endogenous polyamine during stress; the positive effects of polyamines have been associated with the maintenance of membrane integrity, regulation of gene expression for the synthesis of osmotically active solutes, reduction in ROS

production, and controlling accumulation of Na^+ and Cl^- ion in different organs (Roychoudhury et al. 2011). It was observed that plant deficient in ADC1 and ADC2 is hypersensitive to stress (Hussain et al. 2011). In Arabidopsis, expression of ADC and SPMS increases when exposed to salinity stress, whereas mutants of polyamine biosynthetic genes show sensitivity to salinity (Yamaguchi et al. 2006). Overproduction of PUT, SPD, and SPM in rice, tobacco, and Arabidopsis enhances salt tolerance (Roy and Wu 2002). Salt stress regulates polyamine biosynthesis and catabolism by acting as a cellular signal in hormonal pathways thereby regulating abscisic acid (ABA) in response to stress (Shevyakova et al. 2013). Additionally, SPM and SPD are regarded as potent inducers of NO an important signaling molecule (Moschou et al. 2008a, b) and its involvement in salinity tolerance is discussed below. It has been reported that exogenous application of polyamines could alleviate salt-induced reduction in photosynthetic efficiency, but this effect depends on polyamine concentration and types and level of stress (Duan et al. 2008). When the seedling of Sorghum bicolor treated with 0.25 mM SPM is subjected to salt stress it shows improvement in growth and partial increase in the activity of peroxidase and glutathione reductase enzyme with a concomitant decrease in the level of membrane lipid peroxidation (Chai et al. 2010). Li et al. (2013) performed 2-DE gel electrophoresis and MALDITOF/TOF MS with cytosolic proteins to understand the effect of exogenous SPD on proteomic changes under normal and NaCl stress of 3 days old cucumber seedling leaves. Many changes were observed in the levels of proteins involved in energy and metabolic pathways, protein metabolic, stress defense, and other functional proteins. They observed that increased salt tolerance by exogenous SPD would contribute to higher expressions of proteins involved in the SAMs metabolism, protein biosynthesis, and defense mechanisms on antioxidant and detoxification. Li et al. (2013) also argued that the regulation of Calvin cycle, protein folding assembly, and the inhibition of protein proteolysis by SPD might play important roles in salt tolerance.

5.2.5 Roles of Nitric Oxide in Salinity Tolerance

Nitric oxide (NO) is a small volatile gaseous molecule, which is involved in the regulation of various plant growth and developmental processes, such as root growth, respiration, stomata closure, flowering, cell death, seed germination and stress responses, as well as a stress signalling molecule (Zhao et al. 2009). NO directly or indirectly triggers expression of many redox-regulated genes. NO reacts with lipid radicals thus preventing lipid oxidation, exerting a protective effect by scavenging superoxide radical and formation of peroxynitrite that can be neutralised by other cellular processes. It also helps in the activation of antioxidant enzymes (SOD, CAT, GPX, APX, and GR). Exogenous NO application has been found to play roles in stress mitigation (Hossain et al. 2010), but the effects depend on NO concentration. Exogenous application of sodium nitroprusside (SNP), a NO donor, on Lupinus luteus seedlings subjected to salt stress enhanced seed germination and root growth. Seed germination was promoted at concentrations between 0.1 and

800 μM SNP in a dose-dependent manner. The stimulation was most pronounced after 18 and 24 h and ceased after 48 h of imbibition. The promoting effect of NO on seed germination persisted even in the presence of heavy metals (Pb and Cd) and NaCl. Kopyra and Gwóźdź (2003) further showed that the pretreatment of *L. luteus* seedlings for 24 h with 10 μM SNP resulted in efficient reduction of the detrimental effect of the abiotic stressors on root growth and morphology. Pretreatment of maize seedlings with 100 μM SNP increases dry matter of roots and shoots under salinity stress; however, when the concentration of SNP was increased to 1000 μM shoot and root dry weight decreased (Zhang et al. 2006). Thus, this experiment highlighted both the protective effects of low NO concentration and the toxic effect of high NO concentration on plants. The positive effects of NO on salinity tolerance or stress mitigation have been attributed to antioxidant activities and modulation of ROS detoxification system. Improved plant growth under salinity stress by exogenous application of NO was associated with increases in antioxidant enzymes such as SOD, CAT, GPX, APX, and GR and suppression of malondialdehyde (MDA) production or lipid peroxidation. Effects of NO on salinity tolerance are also related to its regulation of plasma membrane H^+-ATPase and Na^+/K^+ ratio (Bajgu 2014). NO stimulates H^+-ATPase (H^+-PPase), thereby producing a H^+ gradient and offering the force for Na^+/H^+ exchange. Such an increase of Na^+/H^+ exchange may contribute to K^+ and Na^+ homeostasis (Zhang et al. 2006). Although NO acts as a signal molecule under salt stress and induces salt resistance by increasing PM H^+-ATPase activity, research results from Zhang et al. (2007) with calluses from *Populus euphratica* also indicated NO cannot activate purified PM H^+-ATPase activity, at least in vitro. They initially hypothesized ABA or H_2O_2 might be downstream signal molecules to regulate the activity of PM H^+-ATPase. Further results indicated H_2O_2 content increased greatly under salt stress. Since H2O2 might be the candidate downstream signal molecule, Zhang et al. (2007) tested PM H^+-ATPase activity and K to Na ratio in calluses by adding H_2O_2. The results suggested that H_2O_2inducing an increased PM H^+-ATPase activity resulted in an increased K to Na ratio leading to NaCl stress adaptation.

5.2.6 Hormone Regulation of Salinity Tolerance

ABA is an important phytohormone whose application to plant ameliorates the effect of stress condition(s). It has long been recognized as a hormone, which is unregulated due to soil water deficit around the root. Salinity stress causes osmotic stress and water deficit, increasing the production of ABA in shoots and roots (Cabot et al. 2009). The accumulation of ABA can mitigate the inhibitory effect of salinity on photosynthesis, growth, and translocation of assimilates (Jeschke et al. 1997). The positive relationship between ABA accumulation and salinity tolerance has been at least partially attributed to the accumulation of K^+, Ca^{2+} and compatible solutes, such as proline and sugars, in vacuoles of roots, which counteract with the uptake of Na^+ and Cl^- (Gurmani et al. 2011). ABA is a vital cellular signal that modulates the expression of a number of salt and water deficit-responsive genes.

Fukuda and Tanaka (2006) demonstrated the effects of ABA on the expression of two genes, HVP1 and HVP10, for vacuolar H^+-inorganic pyrophosphatase, and of HvVHA-A, for the catalytic subunit (subunit A) of vacuolar H^+-ATPase in Hordeum vulgare under salinity stress. ABA treatment in wheat induced the expression of MAPK4-like, TIP 1, and GLP 1 genes under salinity stress (Keskin et al. 2010). Some other compounds having hormonal properties, such as salicylic acid (SA) and brassinosteroids (BR), also participate in plant abiotic stress responses (Fragnire et al. 2011). Under salinity stress endogenous level of SA increased along with the increase in the activity of salicylic acid biosynthetic enzyme in rice seedling (Sawada et al. 2006). Jayakannan et al. (2013) have recently shown that SA improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing salt-induced K^+ loss via a guard cell outward rectifying K^+ (GORK) channel. Arabidopsis seedling pretreated with SA showed up regulation of H^+-ATPase activity, thereby improving K^+ retention during salt stress; SA pretreatment did not prevent accumulation of Na^+ in roots but somehow helped to reduce the concentration of accumulated Na^+ in the shoot (Jayakannan et al. 2013). The application of SA also promoted salinity tolerance in barley, as manifested by increases in the content of chlorophyll and carotenoid and maintaining membrane integrity, which was associated with more K^+ and soluble sugar accumulation in the root under saline condition (El-Tayeb, 2005). Nazar et al. (2011) have argued that SA alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in mung bean cultivars. The negative effects of salinity may also be mitigated by BR (El-Mashad and Mohamed 2012). Application of BR enhanced the activity of antioxidant enzymes (SOD, POX, APX, and GPX) and the accumulation of nonenzymatic antioxidant compounds (tocopherol, ascorbate, and reduced glutathione) (El-Mashad and Mohamed 2012). Both BRs and SA are ubiquitous in the plant kingdom, affecting plant growth and development in many different ways, and are known to improve plant stress tolerance. Ashraf et al. (2010) have reviewed and discussed the current knowledge and possible applications of BRs and SA that could be used to mitigate the harmful effects of salt stress in plants. They have also discussed the roles of exogenous applications of BRs and SA in the regulation of various biochemical and physiological processes leading to improved salt tolerance in plants.

5.3 Diversity in Germplasm Pool: Abiotic Stress Management

Producing sufficient food for the growing population is a major challenge, with climate change emerging as an additional threat to the food security and livelihood of millions of people (Abberton et al. 2016). Achieving significant yield gains in staple crops is essential because rising demand requires a twofold increase in crop production by 2050 (Tilman et al. 2011). The increasing frequency of droughts and heat stress is impacting crop productivity (Lesk et al. 2016), and the increased frequency and severity of flooding events may cause yield loss in regions such as

Asia, where prolonged flooding of rice fields already substantially reduces yields (Mackill et al. 2012). In order to meet the challenges of increasing demand in a changing climate, new and improved crop cultivars must be produced more quickly. The main components of human diet and animal feed are cereals and grain legumes. Grain legumes also enrich nitrogen soil and improve the texture of the soil for other crops (Graham and Vance 2003). The discovery of semidwarfing genes has led to a sharp increase in yields in rice and wheat production worldwide (Trethowan et al. 2007). However, dependence on a narrow range of elite cultivars has likely resulted in some negative effects on the productivity of agroecosystems (Dwivedi et al. 2016), although this assumption is present.

More recent evidence also suggests that productivity of major food crops is either stagnating or not increasing at the rate needed to ensure food security (Ortiz 2015). Accelerated progress in plant breeding is required to better harness crop genetic resources and produce higher-yielding, climate-resilient cultivars. As the methods to assess functional diversity in crops have become more sophisticated during the last 100 years, our understanding of the mechanisms underlying this diversity has grown. Functional diversity refers to a component of biodiversity related to what organisms do in communities and ecosystems (Petchey and Gaston 2006). The decreasing cost of highthroughput DNA sequencing has facilitated the recent rise of genome-wide methods such as genotyping by sequencing (Scheben et al. 2017a) for assessing functional diversity of crops using single nucleotide polymorphisms (SNPs) (Huang and Han 2014). Common targets of breeding are yield-related traits such as abiotic stress tolerance, pest resistance and flowering time. The potential yield gains are substantial, considering that abiotic stress can reduce average yields of major crops by 50% (Bray et al. 2000) and pests can cause 26–40% yield losses. The assessment and use of functional diversity in flowering time control pathways is also important for yield, especially as crop development control can improve adaptation to the predicted impact of climate change. The genomics era led to a rapid increase in sequence data capturing the genetic diversity underlying heritable target characteristics in elite cultivars, land breeds and wild relatives of crops. Although more than 100 plant genomes were already available in 2015 (Michael and VanBuren 2015), more than half of which were crops, the functions of the vast majority of plant genes remain unknown (Rhee and Mutwil 2014). Powerful and high-performance forward and reverse genetic techniques are needed to help clarify these unknown gene functions in order to support targeted breeding. Genetic mapping approaches also play an important role in the association of phenotypic genomic regions. Vast improvements in our understanding of the functional knowledge of crop genomes are an important prerequisite for targeted approaches to genome editing to access new breeding programs to diversity often limited by the natural diversity found in germplasm resources (Scheben et al. 2017b). It is necessary to understand and shape the functional diversity of crops using genomic technologies will be necessary to ensure continuing yield increases to keep pace with growing global food demand.

5.3.1 Plant Architecture and Edible Yield in Cereals

Domestication and subsequent artificial selection by humans has dramatically changed plant architecture, phenology and components of grain yield in many cereals, largely to address agronomic needs and to adapt the crops to various stress-prone environments. Candidate genes and SNPs associated with crop phenology, plant architecture, and yield-attributing traits are known in cereals. Several unique candidate gene regions related to plant growth and development and grain yield have been identified in maize (Farfan et al. 2015). Bouchet et al. (2017) found 34 and 6 QTL for individual or combinatorial trait combinations in maize, respectively. They identified a QTL cluster in a 5 Mb region around Tb1 associated with tiller number and ear row number. The latter was positively correlated with flowering (days to anthesis for male and female flowering and anthesis to silking interval measured in days) and negatively correlated to grain yield. Kn1 and ZmNIP1 have been identified as candidate genes for tillering, along with ZCN8 for leaf number and Rubisco Activase 1 for kernel weight. A more upright leaf in maize has been shown to be influenced by variation in liguleless genes (Tian et al. 2011). A large GWAS study in rice detected 42 significant genotype– phenotype associations for plant morphology, grain quality, and root architecture traits, which in most cases were co-localized with QTL and candidate genes controlling the phenotypic variation of single or multiple traits (Biscarini et al. 2016). Several SNPs in rice were associated with plant and panicle architecture, biomass and yield (Rebolledo et al. 2016), while candidate genes in pathways regulating plant architecture overlap with QTL associated with panicle architecture traits (Rebolledo et al. 2016). In wheat, candidate genes associated with SNPs were involved in carbohydrate metabolism, floral fertility, spike morphology and grain number, providing valuable targets for selection (Guo et al. 2016). Significant marker-trait associations also provided insight into genetic architecture of flowering, plant height and grain weight in barley (Pasam et al. 2012). Individual QTL accounted, however, only for a small portion of phenotypic variation. In sorghum, several SNPs were associated with plant and inflorescence architecture traits, with many located within previously mapped QTL (Zhao et al. 2016). Candidate genes KS3 (associated with seed number) and GA2ox5 (associated with plant height) were also reported (Zhao et al. 2016). A QTL with a major effect corresponded to the priori known photoperiod response gene Ppd-H1 (Maurer et al. 2015).

5.3.2 Abiotic Stress Adaptation in Soybean

Multiple SNPs are reported to be associated with tolerance to drought and heat stress in soybean. Dhanapal et al. (2015) reported 39 SNPs associated with carbon isotope ratio (δ 13C), which is a surrogate trait to measure water use efficiency. The genomic distribution of these SNPs revealed that several are co-located and likely tag the same locus, suggesting that markers for δ 13C can be identified in soybean using GWAS. Dhanapal et al. (2016) reported 52 unique SNPs for total chlorophyll

content tagged on 27 loci across 16 chromosomes. While many of these putative loci were near genes previously identified or annotated as related to chlorophyll traits (Hao et al. 2012), numerous SNPs marked chromosomal regions with unknownfunction genes. Under abiotic stress conditions, non-photochemical quenching (NPQ) protects plants from heat when more light is absorbed than photosynthesis can be used (Li et al. 2009). The reflectance of the canopy measured as a photochemical reflection index (PRI), suitable for high-performance field phenotyping, is a substitute for the measurement of NPQ (Gamon et al. 1992). Thirty-one PRI-specific SNPs may provide an opportunity to improve photosynthesis in soybean in 15 loci on 11 chromosome-harboring candidate genes associated with NPQ, photosynthesis and sugar transport (Herritt et al. 2016).

5.3.3 Abiotic Stress Adaptation in Cereals

Cereal crops have been extensively investigated for SNPs and candidate genes associated with abiotic stress adaptation. Ethylene levels have been linked to yield penalty under heat stress in wheat, largely due to reduction in spike fertility and grain weight (Hays et al. 2007). Valluru et al. (2017) reported 5 and 32 significant SNPs associated with spike ethylene, and 22 and 142 significant SNPs associated with spike dry weight, in greenhouse and field studies, respectively. Some of these SNPs are close to SNPs associated with plant height, suggesting associations between plant height and spike related traits. This opens the possibility of gene discovery and breeding of wheat *Aegilops tauschii* has potential as an excellent source of abiotic stress tolerance. Qin et al. (2016) reported 25 SNPs and several putative candidate genes (enzyme, storage protein, and drought-induced protein) associated with drought adaptation, while Liu et al. (2015) found 13 SNPs and putative candidate genes related to P-deficiency tolerance. A major Al-tolerance gene SbMATE on chromosome 3 has been shown to be associated with grain yield in sorghum, where SbMATE specific SNPs under –P conditions contributed up to 16% genotypic variance (Leiser et al. 2014). Forty-eight genomic regions associated with Al tolerance were reported in rice, four of which co-localized with a priori known candidate genes, and two co-located with previously identified QTL (Famoso et al. 2011). In barley, a genomic region on chromosome 2H was associated with grain yield under heat stress, a region on chr 7H with grain yield, and a region on chr 4H and chr 7H with elevated CO_2 under two factor treatments (high temperature and elevated CO_2). None of the SNPs associated with single factor treatments were retrieved under two factor treatments, thus emphasizing the importance of multifactor treatments (Ingvordsen et al. 2015). Genic SNPs associated with environmental variations (but independent of geographical location) predicted genotype × environment interactions for drought stress and aluminum toxicity in sorghum (Lasky et al. 2015). Wissuwa et al. (2015) reported several SNP loci associated with phosphorus use efficiency (PUE) in rice on chromosomes 1, 4, 11, and 12. A minor indica-specific haplotype on chromosome 1 and a rare aus-specific haplotype on chromosome 11 displayed the highest PUE, and could have potential for targeted introgression while

breeding for rice under P-limited cropping systems. Emerging evidence suggests that responses to stress combinations cannot be reliably predicted from the responses to individual stresses (Makumburage et al. 2013). An integrated approach is therefore needed to model the genetics of responses to a range of single and combined stresses. For example, association analysis report QTL with contrasting and with similar responses to biotic versus abiotic stresses, and below-ground versus above-ground stresses. There is a need to conduct multi-trait GWAS to identify robust candidate genes for multiple stresses (Thoen et al. 2016). The proliferation of genome wide association analyses has led to identification of candidate loci (often co-located with major QTLs or candidate genes) associated with abiotic stress adaptation, phenology and plant architecture, and edible yield. The identification of such loci can facilitate genomics-assisted breeding in cereal and legumes.

5.4 Integrated Metabolome Analysis for Abiotic Stress Management

Environmental stresses such as stresses on biotics and abiotics are serious threats to agricultural production (Lobell et al. 2014). Abiotic stresses such as drought, salinity, cold, high light/UV-B, heat, air pollution, heavy metals, mechanical wounds and nutritional deficiencies (Vickers et al. 2009) lead to a global reduction in crops, leading to global economic costs(Suzuki et al. 2014). To understand and improve the stress responses and tolerances of crops, researchers have focused on the perception of signals, transcriptional regulation and expression of functional proteins in plants' stress response mechanisms against abiotic stress (Hirayama and Shinozaki 2010). In addition, posttranslational, posttranscriptional and epigenetic regulations have been studied. The accumulation of small molecules with antioxidative activity in vitro has often been discussed with respect to the role they play in mitigating the accumulation of reactive oxygen species (ROS) induced by abiotic stresses. This discussion has progressed under the conjecture that the reaction in vitro may occur in vivo. Integrated 'omics' analysis centered on metabolomics (integrated metabolomics) can be a powerful technique to identify the functions of genes involved in the metabolic processes of plants (Saito 2013). Analytical methodologies for narrowing down potential genes and identifying their functions are relatively mature; transcriptome coexpression analysis and (un) targeted analysis in metabolomics using mutant lines have become commonplace (Saito et al. 2008).

The development of aerobic organisms, including plants, depended on the development of effective mechanisms to mitigate the damage of highly reactive and toxic ROS caused by abiotic stress, i.e. singlet oxygen, radicals of anion superoxide, hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH) (Mittler et al. 2004). Since plant cells and organelles containing them (e.g. chloroplasts, peroxisomes, cytosol, mitochondria and vacuoles) are exposed to ROS (Miller et al. 2010), plants have developed two different biological processes to cope with ROS: Prevention or prevention of ROS formation and scavenging of ROS by enzymatic and

non-enzymatic processes, such as the accumulation of low-enzymatic processes, such as accumulation of low-enzymatic processes.

Ascorbic acid (AsA), glutathione (GSH), a-tocopherols, amino acids (e.g. proline (Signorelli et al. 2014), sugars (Nishizawa et al. 2008), carotenoids (Havaux 2014) and quinic acid derivatives (e.g. chlorogenic acid (Niggeweg et al. 2004) are antioxidants presumed to function in planta; however, it is unclear why plants produce such a wide variety of antioxidants. Along with the accumulation of metabolites exhibiting antioxidative activity, abiotic stresses also induce the production of various kinds of specialized metabolites. Of these, it has also been suggested that saponins (Okubo and Yoshiki 2000), glucosinolates (Natella et al. 2014), phenolamides (Velikova et al. 2007), phenylpropanoids (Shahidi and Chandrasekara 2010) and flavonoids (Agati et al. 2012) act as antioxidants in vivo on the basis of their in vitro antioxidative activity.

5.4.1 Integrated Metabolomics Experimentally Identifies Flavonoids as Antioxidants in Planta

Flavonoids that are common in the plant kingdom (Tohge et al. 2013) are responsive to almost all abiotic stresses. Given that flavonoid aglycones (e.g. phenylchroman-based and flavilium-based structures) generally exhibit antioxidative activity in vitro, flavonoids are assumed to function as antioxidants in vivo. It has been suggested that there is a spatio-temporal correlation between flavonoid accumulation and oxidative stress (Hernandez et al. 2009). In comparisons of natural varieties and mutant lines, integrated metabolomics is useful for identifying the functions of genes performing the biosynthesis of target specialized metabolites. The utilization of single gene knock-out/knock-down lines and overexpressing lines clarify the correlation between gene expression and metabolite accumulation, enabling the identification of the gene's function in the integrated analysis oftranscriptomic and metabolomic data Saito et al. 2013). These genetic lines can be also used in identifying the in vivo functions of target metabolites by investigating the phenotypes of plants. Recently, the antioxidative function of flavonoidsin planta was experimentally identified using a series of transgenic and mutant Arabidopsis lines (Nakabayashi et al. 2014). Wild-type Col-0 (Columbia-0), single overexpressors of MYB12/PFG1 (Production of flavonol glycosides1) or MYB75/PAP1 (Production of anthocyanin pigment1), double overexpressors of MYB12 and PAP1, and flavonoid-deficient MYB12 or PAP1 overexpressing lines — obtained by crossing tt4 (transparent testa4) and the individual MYB overexpressor — were subjected to an extensive integrated analysis using transcriptomics, hormonomics and metabolomics. This study excluded the possible effects of the overexpression of the MYBs, the expression of stress-related genes, and the alteration of phytohormones and additional metabolites other than flavonoids on enhancing stress tolerances. The enhanced stress tolerance in this report was solely due to the antioxidative chemical character of over accumulated flavonoids. It is inferred that the flavonoid

accumulation in accordance with abiotic stress exposure is a late response implemented to protect plants (Kusano et al. 2011).

5.4.2 Role of Flavonoids in the Vacuole

The hypothetical insights regarding the role of antioxidative metabolites, particularly flavonoids, may be further extended to understanding their role in the vacuole. H_2O_2 in the cytosol can easily enter into the vacuole (Bolouri-Moghaddam et al. 2010). H_2O_2-dependent class III peroxidase near the inner side of tonoplasts catalyzes the reaction that converts H_2O_2 to OH, which is known to react with almost all metabolites. AsA and GSH present in the vacuole (e.g. 4.19 mM AsA in Catharanthus roseus (Ferreres et al. 2011) and 0.03–0.70 mM GSH in Arabidopsis are general scavengers of H_2O_2 and OH (Queval et al. 2011). In addition, sugars and water-soluble specialized metabolites that are stored in the vacuole are utilized as important antioxidants in plants (Peshev et al. 2013). The in vitro research on the OH-scavenging capacity indicates that sugars and water-soluble specialized metabolites may play a role in radical reactions occurring near the inner side of the tonoplast and in the vacuolar rumen (Peshev et al. 2013). Interestingly, in Arabidopsis, the over accumulation of galactinol and raffinose, which are abiotic stress-responsive vacuole components (Obata and Fernie 2012) and display OH-scavenging activity in vitro, enhanced oxidative stress tolerance in vivo (Keunen et al. 2013). It has been hypothesized that flavonoids mediate the previously unknown key role of the vacuole in maintaining cellular H_2O_2 homeostasis despite the concentration of H2O2 in the vacuole being much lower than in other cell components (Agati et al. 2012). It is estimated that the concentration of rutin (100 mM) in the vacuole is capable of reducing H_2O_2 at a rate of 0.045 mM s^1, which is close to the rate of H_2O_2 generation. Specialized metabolites in the vacuole have been partially qualified and quantified — 1.39 mM total chlorogenic acid (caffeoyl quinic acids) and 1.57 mM total phenolics in *C. roseus* (Ferreres et al. 2011) — suggesting that these highly accumulated compounds play an ROS-mitigating role in the vacuole. Reports of the in vitro antioxidative activity of chlorogenic acid, flavonol glycosides, and anthocyanins against H_2O_2 and OH also suggest their role as antioxidants in the vacuole (Bi et al. 2014).

5.4.2.1 Chemical Challenges

Metabolomics can theoretically qualify and quantify vacuole metabolites at the same time. Recently, metabolomic profiling using gas chromatography-mass spectrometry (GC-MS) and liquid chromatography-mass spectrometry (LC-MS) enabled the simultaneous detection of 259 putative metabolites in barley vacuoles (*Hordeum vulgare*), including primary and specialized metabolites (Tohge et al. 2011). The metabolic dynamism between vacuolar and extravacuolar compartments was determined by a study using isolated vacuoles using the giant cells in algae *Chara australis* (Oikawa and Saito 2012). These research studies show that the vacuole metabolome can be characterized by combining metabolomics with

state-of - the-art technologies and gain further insights into its functionality. However, they also indicate the difficulties associated with the qualification and quantification of the metabolome, in particular with regard to specialized metabolites, since, due to the specialization of their metabolites, reference materials (i.e. standard compounds or MS/MS spectra) are often not available for chemical assignment. Metabolomic strategies are improved in order to assign putative structural information to detected metabolites using a combination of retention times, exact masses, UV spectra and MS/MS patterns of known metabolites, according to the guidelines of the alphanumeric metrics of identification (Sumner et al. 2014), the plant science community (Fernie et al. 2011) or the Metabolomics Standards Initiative (MSI) (Sumner et al. 2007). According to levels 1 and 2 of the MSI guideline, chemically assigned metabolites are often used in integrated metabolomics studies. For unknown metabolites, MS/MS, UV and isotope analysis are performed to characterize metabolite features such as substructure, metabolite group or elemental composition. Utilizing the patterns of electrospray ionization-based MS/MS spectra on known metabolites in the positive and negative ion modes allows the chemical assignment of unknown metabolites (Morreel et al. 2014). The large amount of data on flavonoid Oglycosides (Afendi et al. 2012), flavone C-glycosides (Yang et al. 2014), phenolamides (Handrick et al. 2010), saponins (Pollier et al. 2011) and glucosinolates (Bottcher et al. 2008) yield a certain pattern of MS/MS fragmentation for each group of compounds. Characteristic UV spectra distinguish these metabolite groups (Oleszek 2002). Applying the information of exact mass and natural abundance to isotopes also allows the chemical assignment of elemental composition to unknown metabolites. Using the differences in exact mass and natural abundance of 32S and 34S, S-containing metabolites were profiled in Arabidopsis (Glaser et al. 2014) and onion (*Allium cepa*) (Nakabayashi et al. 2013). The unambiguous elemental compositions determined using the sulfur and carbon numbers in stable isotope labeling is powerful information that can be utilized in further experiments on chemical assignment. The precise information concerning the generally accepted metabolites assignments can be the precursor of their isolation and structure identification/elucidation to obtain standard compounds for quantification and qualification using general or recent technologies (Nakabayashi et al. 2013). So far, metabolomics-oriented and phytochemical genomics oriented studies have revealed 78 metabolites in Arabidopsis and rice (Oryza sativa) (Yonekura-Sakakibara et al. 2014). Recently, the preparative LC–MS and LC–solid phase extraction– nuclear magnetic resonance–MS (LC–SPE–NMR–MS) systems have been made available for high-throughput analysis (Sturm and Seger 2012). The combination of empirical and computational approaches is expected to streamline the identification of metabolite structures (Nakabayashi et al. 2013).

5.4.2.2 Biological Challenge

Genome sequencing using next-generation sequencers is a great promise for the generation of biosynthesis and vacuolar metabolite roles of mutants. For the manipulation of primary and specialized metabolisms, gene expression and genome engineering technologies have recently been available. Virus-induced gene silencing

techniques (VIGS) are used for biosynthetic gene mutants that define the metabolic pathways of g-aminobutyric acid in tomatoes (*Solanum lycopersicum*) (Bao et al. 2014) and vindoline in *C. Besseau* et al. 2013). Transcription-like effector nuclease (TALEN) technology has been used to disrupt a biosynthetic cholesterol gene, sterol side chain reductase 2, in potatoes (*Solanum tuberosum*) (Sawai et al. 2014). In plants and crops, the clustered regularly interspaced short palindromic repeat (CRISPR) /CRISPR-related protein 9 (Cas9) technology (Belhaj et al. 2013) was used to edit the tt4 gene in Arabidopsis (Mao et al. 2013). In primary and specialized metabolisms, fusion proteins consisting of nuclease dead Cas9 and activator/repressor domains are expected to regulate targeted gene expression (Mahfouz et al. 2014). To identify the roles of not only flavonoids in the vacuole, but also other specialized metabolites, a series of mutants are required. Moreover, consideration of the evolution of the path would result in increasingly interesting information, especially with regard to gene clusters of certain specialized metabolites (Nutzmann and Osbourn 2014).

5.5 Plant Metabolites and Abiotic Stress Tolerance

Responses to environmental stresses alter the metabolism of plants in a variety of ways, including the production of compatible solutes (e.g., proline, raffinose and glycine betaine), which can stabilize proteins and cellular structures or maintain cell turgor by osmotic adjustment, and redox metabolism to remove excess levels of ROS and restore the balance of cell redox(Janska et al. 2010). Glycine betaine improves stress tolerance caused by chilling, frost, salt, drought and high levels of light (Chalker-Scott 2002). Under different adverse environmental conditions, non-protein amino acid c-amino butyric acid (GABA) rapidly accumulates to high levels (Kinnersley and Turano 2000). In many plant species, proline accumulates due to various environmental stresses, including drought, high salinity and heavy metals (Kavi-Kishor et al. 2005). Flavonoids are one of the largest classes of plant phenolics that carry out various functions in plant systems, including pigmentation, defense and scavenging ROS as antioxidants (Harborne and Williams 2000). In particular, the response to UV light stress tends to increase flavonoids (Lavola et al. 2000). In this section, the role of plant metabolites with particular reference to secondary compounds during abiotic stress tolerance is presented in the published literature.

5.5.1 Drought Stress

Tolerant plants initiate defense mechanisms against water shortages to deal with drought (Chaves and Oliveira 2004). Plants show a variety of physiological and biochemical responses to the prevailing drought stress at the cellular and whole organism levels (Farooq et al. 2009). These mechanisms include osmotic adjustment by accumulation of compatible solutes such as proline, betaine glycine, polyols, sugar alcohols and soluble sugars (mannitol, sorbitol, sucrose, fructans, glutamate

and oligosaccharides). Plants have also developed enzymatic antioxidant systems to cope with the stress of drought and to prevent oxidative damage. Low-molecular osmolytes, including glycine betaine, proline and other amino acids, organic acids and polyols, are essential for cellular functions under drought. Plant growth substances such as salicylic acid, auxins, gibberellins, cytokininine and ABA modulate the response to drought in plants. Polyamines, citrulline and several enzymes act as antioxidants and reduce water deficit adverse effects (Chaves and Oliveira 2004).

5.5.2 Salt Stress

Salinity is one of the most important abiotic factors in many arid and semi-arid environments around the world limiting productivity (Msanne et al. 2011). A major threat to global food security is soil salinity. Up to 20% of the irrigated land of the world, which produces a third of the world's food, is affected by salt. In addition, salinity stress is a major worldwide problem for the soil ecosystem (Sima et al. 2009). Plants respond to these stresses through various biochemical and physiological processes, including reduced stomatological performance, carbon fixation and efficiency of light harvesting mechanisms, cell growth repression, and increased respiration and accumulation of osmolytes and proteins involved in stress tolerance (Szabados and Savoure 2010). Plants must synthesize compatible organic solutes such as proline, glycine betaine, trehalose, sorbitol, mannitol, pinitol and sucrose in cytosol to combat osmotic stress imposed by high salinity (Liang et al. 2008). In order to counteract the negative effects of salinity stress, plants have developed stress management strategies involving antioxidants such as ascorbic acid, glutathione, vitamin E, flavonoids, carotenoids(Ahmed 2009) and antioxidant enzymes, such as SOD, CAT, guaiacol peroxidase, APX, monodehydroascorbate peroxidase, and dehydroascorbate peroxidase (Arora et al. 2002). Exogenous use of ascorbic acid has been reported to mitigate the effect of salinity in different crops. Proline is considered to act as an osmolyte, a ROS scavenger and a molecular chaperone that stabilizes the protein structure, thereby protecting cells against damage caused by salt stress(Hale and Orcutt 1987).

5.5.3 Temperature Stress

Plant temperature stress can be divided into the effects of high-temperature, chilling and freezing damage caused by temperature (Arora et al. 2002). Temperature is an important factor in the survival of living organisms, and when water, the biological solvent, freezes to ice, living species face significant challenges. High-temperature stress is often associated with reduced water availability under field conditions. Increased heat stress leads to overproduction of various organic and inorganic osmolytes and accumulation. These osmolytes protect plants against stress by cellular osmotic adjustment, ROS detoxification, biological membrane protection

and enzyme/protein stabilization (Verbruggen and Hermans 2008). The production of ROS, causing oxidative damage to cells and tissues, is one of the main effects of heat stress (Simoes-Araujo et al. 2003). The production of phenolic compounds such as flavonoids and phenylpropanoids is caused by high temperature stress (Morrison and Stewart 2002). Similarly, the accumulation of soluble sugars under heat stress in sugarcane has been reported, which has a significant impact on heat tolerance. Heat stress disturbed the relationship between leaf water and the conductivity of the root (Morales et al. 2003). HSPs are exclusively involved in the response to heat stress. The expression of stress proteins is an important adaptation to the stress of the environment. In addition, other proteins such as glycine betaine, an amphoteric quaternary amine, play an important role in high-temperature plants as compatible solutes (Sakamoto and Murata 2002). GABA acts as a compatible solution, among other osmolytes. Anthocyanins, a subclass of flavonoid compounds, are highly modulated by high temperatures in plant tissues (Shaked-Sachray et al. 2002).

5.5.4 Cold Stress

Cold stress affects plant growth and development adversely. Most temperate plants gain freezing tolerance through a cold acclimation process (Thomashow 1999). Low temperature stress causes the accumulation of phenolic compounds that protect chilled tissues from damage caused by free oxidative stress induced by radicals. Cold stress also increases the amount of water-soluble phenolics and their subsequent incorporation into the cell wall as suberin or lignin (Ippolito et al. 1997). Many researchers report the effects of low temperature on phenolic metabolism and have shown that under chill stress, phenolic metabolism is improved. The accumulation of sucrose and other simple sugars caused by cold acclimation also helps to stabilize the membrane and protects the membranes against freezing damage (Ippolito et al. 1997). Fructans reduce the freezing point during cold stress due to their high concentration in vacuoles, contributing to the change in osmotic potential and increasing plant resistance (Van den Ende et al. 2002). The accumulation of fructane in non-freezing conditions (cold acclimatization) was usually correlated with an increase in freezing tolerance (Pontis 1989). Freezing tolerance is the ability to withstand the formation of extracellular ice and prevent intracellular ice. Extracellular freezing results in freezing dehydration due to the removal of water from the cytoplasm to the growing ice crystals. As freeze-dehydration continues, the content of the cells is increasingly concentrated (Levitt 1980).

5.5.5 Chilling Stress

Chilling (low but non-freezing temperature) is one of the world's most severe abiotic stress factors that restrict plant growth and productivity. In addition to ultrastructural changes, chilling also leads to a series of physiological, biochemical and

molecular changes, such as photosystem I photo inhibition (Kudoh and Sonoike 2002) and increased accumulation of hydrogen peroxide (H2O2) in chilled leaves(Zhou et al. 2004). Endogenous phytohormones, including ABA (Anderson et al. 1994), as well as polyamines and their biosynthetic or responsive genes (Moschou et al. 2008a, b), have been modulated in order to allow plants to adapt to chilling stress. In addition, the expression of some cold-regulated genes is one of the most successful strategies developed by plants to adapt to chilling stresses. In chilling stress, polyamines are involved (Moschou et al. 2008a, b). Zhang et al. (2009) reported on the effect of treatment with chilling on cucumber polyamines. The spermidine content in leaves increased markedly in cucumber during chilling. Chilling damage in response to cold may be prevented by the accumulation of polyamine (He et al. 2002). In addition, agmantine and putrescine have also been reported in seedlings of Pringlea antiscorbutica (Hummel et al. 2004).

References

Abberton, M., Batley, J., Bentley, A., Bryant, J., Cai, H., Cockram, J., et al. (2016). Global agricultural intensification during climate change: A role for genomics. *Plant Biotechnology Journal, 14*, 1095–1098. https://doi.org/10.1111/pbi.12467.

Abraham, E., Salamo, I. P., Koncz, C., & Szabados, L. (2011). Identification of Arabidopsis and Thellungiella genes involved in salt tolerance by novel genetic system. *Acta Biologica Szegediensis, 55*(1), 53–57.

Afendi, F. M., Okada, T., Yamazaki, M., Hirai-Morita, A., Nakamura, Y., Nakamura, K., Ikeda, S., Takahashi, H., Altaf-Ul-Amin, M., Darusman, L. K., et al. (2012). KNApSAcK family databases: Integrated metabolite-plant species databases for multifaceted plant research. *Plant & Cell Physiology, 53*, e1.

Agarwal, S., & Shaheen, R. (2007). Stimulation of antioxidant system and lipid peroxidation by abiotic stresses in leaves of Momordica charantia. *Brazilian Journal of Plant Physiology, 19*(2), 149–161.

Agati, G., Azzarello, E., Pollastri, S., & Tattini, M. (2012). Flavonoids as antioxidants in plants: Location and functional significance. *Plant Science, 196*, 67–76.

Ahmad, P., & Prasad, M. N. V. (2012). *Abiotic stress responses in plants: Metabolism, productivity and sustainability*. New York: Springer.

Ahmad, C. A., Jaleel, M. A., Salem, G. N., & Sharma, S. (2010). Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. *Critical Reviews in Biotechnology, 30*(3), 161–175.

Ahmad, R., Lim, C. J., & Kwon, S.-Y. (2013). Glycine betaine: A versatile compound with great potential for gene pyramiding to improve crop plant performance against environmental stresses. *Plant Biotechnology Reports, 7*, 49–57.

Ahmed, S. (2009). Effect of soil salinity on the yield and yield components of mungbean. *Pakistan Journal of Botany, 41*, 263–268.

Alamgir, N. M., & Ali, M. Y. (1999). Effect of salinity on leaf pigments, sugar and protein concentrations and chloroplast ATPase activity of rice (Oryza sativa L.). *Bangladesh Journal of Botany, 28*(2), 145–149.

Alcazar, R., Marco, F., Cuevas, J. C., et al. (2006). Involvement of polyamines in plant response to abiotic stress. *Biotechnology Letters, 28*(23), 1867–1876.

Alcazar, R., Planas, J., Saxena, T., et al. (2010). Putrescine accumulation ´ confers drought tolerance in transgenic Arabidopsis plants overexpressing the homologous arginine decarboxylase 2 gene. *Plant Physiology and Biochemistry, 48*(7), 547–552.

Aly-Salama, K. H., & Al-Mutawa, M. M. (2009). Glutathione-triggered mitigation in salt-induced alterations in plasmalemma of onion epidermal cells. *International Journal of Agriculture and Biology, 11*(5), 639–642.

Anderson, B., Ward, J., & Schroeder, J. (1994). Evidence for an extracellular reception site for abscisic acid in Commelina guard cells. *Plant Physiology, 104*, 1177–1183.

Apel, K., & Hirt, H. (2004). Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. *Annual Review of Plant Biology, 55*, 373–399.

Arora, A., Sairam, R. K., & Srivastava, G. C. (2002). Oxidative stress and antioxidative systems in plants. *Current Science, 82*, 1227–1238.

Asada, K. (1999). The water-water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. *Annual Review of Plant Biology, 50*, 601–639.

Ashraf, M., & Foolad, M. R. (2007). Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany, 59*(2), 206–216.

Ashraf, M., Akram, N. A., Arteca, R. N., & Foolad, M. R. (2010). The physiological, biochemical and molecular roles of brassinosteroids and salicylic acid in plant processes and salt tolerance. *Critical Reviews in Plant Sciences, 29*(3), 162–190.

Azhiri-Sigari, T., Yamauchi, A., Kamoshita, A., & Wade, L. J. (2000). Genotypic variation in response of rainfed lowland rice to drought and rewatering. II. Root growth. *Plant Production Science, 3*, 180–188.

Babu, R. C., Pathan, M. S., Blum, A., & Nguyen, H. T. (1999). Comparison of measurement methods of osmotic adjustment in rice cultivars. *Crop Science, 39*, 150–158.

Bajgu. (2014). Nitric oxide: Role in plants under abiotic stress. In *Physiological mechanisms and adaptation strategies in plants under changing environment* (pp. 137–159). Springer.

Bao, H., Chen, X., Lv, S., Jiang, P., Feng, J., Fan, P., Nie, L., & Li, Y. (2014). Virus-induced gene silencing reveals control of reactive oxygen species accumulation and salt tolerance in tomato by gamma-aminobutyric acid metabolic pathway. *Plant, Cell & Environment, 38*(3), 600–613.

Barragan, V., Leidi, E. O., Andrés, Z., et al. (2012). Ion exchangers NHX1 and NHX2 mediate active potassium uptake into vacuoles to regulate cell turgor and stomatal function in Arabidopsis. *Plant Cell, 24*(3), 1127–1142.

Begara-Morales, J. C., Sanchez-Calvo, B., Chaki, M., et al. (2014). Dual regulation of cytosolic ascorbate peroxidase (APX) by tyrosine nitration and S-nitrosylation. *Journal of Experimental Botany, 65*(2), 527–538.

Belhaj, K., Chaparro-Garcia, A., Kamoun, S., & Nekrasov, V. (2013). Plant genome editing made easy: Targeted mutagenesis in model and crop plants using the CRISPR/Cas system. *Plant Methods, 9*, 1–10.

Ben Ahmed, C., Ben Rouina, B., Sensoy, S., Boukhriss, M., & Ben Abdullah, F. (2010). Exogenous proline effects on photosynthetic performance and antioxidant defense system of young olive tree. *Journal of Agricultural and Food Chemistry, 58*(7), 4216–4222.

Besseau, S., Kellner, F., Lanoue, A., Thamm, A. M., Salim, V., Schneider, B., Geu-Flores, F., Hofer, R., Guirimand, G., Guihur, A., et al. (2013). A pair of tabersonine 16-hydroxylases initiates the synthesis of vindoline in an organ-dependent manner in Catharanthus roseus. *Plant Physiology, 163*, 1792–1803.

Bi, X. L., Zhang, J. L., Chen, C. S., Zhang, D., Li, P. M., & Ma, F. W. (2014). Anthocyanin contributes more to hydrogen peroxide scavenging than other phenolics in apple peel. *Food Chemistry, 152*, 205–209.

Binzel, M. L., Hess, F. D., Bressan, R. A., & Hasegawa, P. M. (1988). Intracellular compartmentation of ions in salt adapted tobacco cells. *Plant Physiology, 86*, 607–614.

Biscarini, F., Cozzi, P., Casella, L., Riccardi, P., Vattari, A., Orasen, G., et al. (2016). Genome-wide association study for traits related to plant and grain morphology, and root architecture in temperate rice accessions. *PLoS One, 11*, e0155425. https://doi.org/10.1371/journal.pone.0155425.

Blum, A., Zhang, J., & Nguyen, H. T. (1999). Consistent differences among wheat cultivars in osmotic adjustment and their relationship to plant production. *Field Crops Research, 64*, 287–291.

Bohnert, J., Nelson, D. E., & Jensen, R. G. (1995). Adaptations to environmental stresses. *Plant Cell, 7*(7), 1099–1111.

Bolaños, J., & Edmeades, G. O. (1991). Value of selection for osmotic potential in tropical maize. *Agronomy Journal, 83*, 948–956.

Bolouri-Moghaddam, M. R., Le Roy, K., Xiang, L., Rolland, F., & Van den Ende, W. (2010). Sugar signalling and antioxidant network connections in plant cells. *The FEBS Journal, 277*, 2022–2037.

Bottcher, C., von Roepenack-Lahaye, E., Schmidt, J., Schmotz, C., Neumann, S., Scheel, D., & Clemens, S. (2008). Metabolome analysis of biosynthetic mutants reveals a diversity of metabolic changes and allows identification of a large number of new compounds in Arabidopsis. *Plant Physiology, 147*, 2107–2120.

Bouchet, S., Bertin, P., Presterl, T., Jamin, P., Coubriche, D., Gouesnard, B., et al. (2017). Association mapping for phenology and plant architecture in maize shows higher power for developmental traits compared with growth influenced traits. *Heredity, 118*, 249–259. https://doi.org/10.1038/hdy.2016.88.

Bray, E. A., Bailey-Serres, J., & Weretilnyk, E. (2000). *Responses to abiotic stresses*. Rockville: American Society of Plant Physiologists.

Cabot, C., Sibole, J. V., Barcelo, J., & Poschenrieder, C. (2009). Abscisic acid decreases leaf Na+ exclusion in salt-treated Phaseolus vulgaris L. *Journal of Plant Growth Regulation, 28*(2), 187–192.

Chai, Y. Y., Jiang, C. D., Shi, L., Shi, T. S., & Gu, W. B. (2010). Effects of exogenous spermine on sweet sorghum during germination under salinity. *Biologia Plantarum, 54*(1), 145–148.

Chalker-Scott, L. (2002). Do anthocyanins function as osmoregulators in leaf tissues? *Advances in Botanical Research, 37*, 103–106.

Cha-Um, S., & Kirdmanee, C. (2010). Effect of glycinebetaine on proline, water use, and photosynthetic efficiencies, and growth of rice seedlings under salt stress. *Turkish Journal of Agriculture and Forestry, 34*(6), 517–527.

Chaves, M. M., & Oliveira, M. M. (2004). Mechanisms underlying plant resilience to water deficits: Prospects for water-saving agriculture. *Journal of Experimental Botany, 55*, 2365–2384.

De Lourdes Oliveira Otoch, M., Menezes Sobreira, A. C., Farias De Aragao, M. E., Orellano, E. G., Da Guia Silva Lima, M., & Fernandes De Melo, ˜. D. (2001). Salt modulation of vacuolar H+-ATPase and H+-pyrophosphatase activities in Vigna unguiculata. *Journal of Plant Physiology, 158*(5), 545–551.

Deivanai, S., Xavier, R., Vinod, V., Timalata, K., & Lim, O. F. (2011). Role of exogenous proline in ameliorating salt stress at early stage in two rice cultivars. *Journal of Stress Physiology & Biochemistry, 7*, 157–174.

Dhanapal, A. P., Ray, J. D., Singh, S. K., Hoyos-Villegas, V., Smith, J. R., Purcell, L. C., et al. (2015). Genome-wide association study (GWAS) of carbon isotope ratio (δ13C) in diverse soybean (Glycine max (L.) Merr.) genotypes. *Theoretical and Applied Genetics, 128*, 73–91. https://doi.org/10.1007/s00122-014-2419-9.

Dhanapal, A. P., Ray, J. D., Singh, S. K., Hoyos-Villegas, V., Smith, J. R., Purcell, L. C., et al. (2016). Genome-wide association mapping of soybean chlorophyll traits based on canopy spectral reflectance and leaf extracts. *BMC Plant Biology, 16*, 174. https://doi.org/10.1186/s12870-016-0861-x.

Dietz, K. J., Tavakoli, N., Kluge, C., et al. (2001). Significance of the Vtype ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level. *Journal of Experimental Botany, 52*(363), 1969–1980.

Dopp, M., Larher, F., & Weigel, P. (1985). Osmotic adaption in Australian mangroves. *Vegetatio, 61*(1–3), 247–253.

Duan, J., Li, J., Guo, S., & Kang, Y. (2008). Exogenous spermidine affects polyamine metabolism in salinity-stressed Cucumis sativus roots and enhances short-term salinity tolerance. *Journal of Plant Physiology, 165*(15), 1620–1635.

Düring, H., & Dry, P. R. (1995). Osmoregulation in water stressed roots: Responses of leaf conductance and photosynthesis. *Vitis, 34*, 15–17.

Dwivedi, S. L., Salvatore, C., Blair, M. W., Upadhyaya, H. D., Are, A. K., & Ortiz, R. (2016). Landrace germplasm for improving yield and abiotic stress adaptation. *Trends in Plant Science, 21*, 31–41. https://doi.org/10.1016/j.tplants.2015.10.012.

El-Mashad, A. A., & Mohamed, H. I. (2012). Brassinolide alleviates salt stress and increases antioxidant activity of cowpea plants (Vigna sinensis). *Protoplasma, 249*(3), 625–635.

El-Shintinawy, F., & El-Shourbagy, M. N. (2001). Alleviation of changes in protein metabolism in NaCl-stressed wheat seedlings by thiamine. *Biologia Plantarum, 44*(4), 541–545.

El-Tayeb, M. A. (2005). Response of barley grains to the interactive effect of salinity and salicylic acid. *Plant Growth Regulation, 45*(3), 215–224.

Famoso, A. N., Zhao, K., Clark, R. T., Tung, C.-W., Wright, M. H., Bustamante, C., et al. (2011). Genetic architecture of aluminum tolerance in rice (Oryza sativa) determined through genome-wide association analysis and QTL mapping. *PLoS Genetics, 7*, e1002221. https://doi.org/10.1371/journal.pgen.1002221.

FAO. (2009). *High level expert forum—How to feed the world in 2050*. Economic and Social Development, Food and Agricultural Organization of the United Nations. Rome.

Farfan, I. D. B., De La Fuente, G. N., Murray, S. C., Isakeit, T., Huang, P. C., Warburton, M., et al. (2015). Genome-wide association study for drought, aflatoxin resistance, and important agronomic traits of maize hybrids in the subtropics. *PLoS One, 10*, e0117737. https://doi.org/10.1371/journal.pone.0117737.

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development, 29*, 185–212.

Fernie, A. R., Aharoni, A., Willmitzer, L., Stitt, M., Tohge, T., Kopka, J., Carroll, A. J., Saito, K., Fraser, P. D., & DeLuca, V. (2011). Recommendations for reporting metabolite data. *Plant Cell, 23*, 2477–2482.

Ferreres, F., Figueiredo, R., Bettencourt, S., Carqueijeiro, I., Oliveira, J., Gil-Izquierdo, A., Pereira, D. M., Valentao, P., Andrade, P. B., Duarte, P., et al. (2011). Identification of phenolic compounds in isolated vacuoles of the medicinal plant Catharanthus roseus and their interaction with vacuolar class III peroxidase: An H2O2 affair? *Journal of Experimental Botany, 62*, 2841–2854.

Flower, D. J., & Ludlow, M. M. (1986). Conbination of osmotic adjustment to the dehydration tolerance of water-stressed pigeonpea (Cajanus cajan (L.) mill sp) leaves. *Plant, Cell & Environment, 13*, 33–40.

Flower, D. J., Rani, A. U., & Peacock, J. M. (1990). Influence of osmotic adjustment on the growth, stomatal conductance and light interception of contrasting sorghum lines in a harsh environment. *Australian Journal of Plant Physiology, 17*, 91–105.

Flowers, J. (2004). Improving crop salt tolerance. *Journal of Experimental Botany, 55*(396), 307–319.

Ford, W. (1984). Accumulation of low molecular weight solutes in water-stressed tropical legumes. *Phytochemistry, 23*(5), 1007–1015.

Foyer, H., Lopez-Delgado, H., Dat, J. F., & Scott, I. M. (1997). Hydrogen peroxide- and glutathione-associated mechanisms of acclimatory stress tolerance and signalling. *Physiologia Plantarum, 100*(2), 241–254.

Fragnire, C., Serrano, M., Abou-Mansour, E., Metraux, J.-P., & L'Haridon, F. (2011). Salicylic acid and its location in response to biotic and abiotic stress. *FEBS Letters, 585*(12), 1847–1852.

Frensch, J., & Hsiao, T. C. (1994). Transient responses of cell turgor and growth of maize roots as affected by changes in water potential. *Plant Physiology, 104*, 246–254.

Fukai, S., & Cooper, M. (1995). Development of drought-resistant cultivars using physiomorphological traits in rice. *Field Crops Research, 40*, 67–86.

Fukuda, A., & Tanaka, Y. (2006). Effects of ABA, auxin, and gibberellin on the expression of genes for vacuolar H+- inorganic pyrophosphatase, H+-ATPase subunit A, and Na+/H+ antiporter in barley. *Plant Physiology and Biochemistry, 44*(5–6), 351–358.

Gadallah, A. (1999). Effects of proline and glycinebetaine on Vicia faba responses to salt stress. *Biologia Plantarum, 42*(2), 249–257.

Galvez, J., Baghour, M., Hao, G., Cagnac, O., Rodríguez-Rosales, M. P., & Venema, K. (2012). Expression of LeNHX isoforms in response to salt stress in salt sensitive and salt tolerant tomato species. *Plant Physiology and Biochemistry, 51*, 109–115.

Gamon, J., Penuelas, J., & Field, C. (1992). A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment, 41*, 35–44. https://doi.org/10.1016/0034-4257(92)90059-s.

Gao, Z., Sagi, M., & Lips, S. H. (1998). Carbohydrate metabolism in leaves and assimilate partitioning in fruits of tomato (Lycopersicon esculentum L.) as affected by salinity. *Plant Science, 135*(2), 149–159.

Ge, C., Cui, X., Wang, Y., et al. (2006). BUD2, encoding an Sadenosylmethionine decarboxylase, is required for Arabidopsis growth and development. *Cell Research, 16*(5), 446–456.

Gill, S. S., Tajrishi, M., Madan, M., & Tuteja, N. (2013). A DESDbox helicase functions in salinity stress tolerance by improving photosynthesis and antioxidant machinery in rice (Oryza sativa L. cv. PB1). *Plant Molecular Biology, 82*(1–2), 1–22.

Glaser, K., Kanawati, B., Kubo, T., Schmitt-Kopplin, P., & Grill, E. (2014). Exploring the Arabidopsis sulfur metabolome. *The Plant Journal, 77*, 31–45.

Graham, P. H., & Vance, C. P. (2003). Legumes: Importance and constraints to greater use. *Plant Physiology, 131*, 872–877. https://doi.org/10.1104/pp.017004.

Groß, F., Durner, J., & Gaupels, F. (2013). Nitric oxide, antioxidants and prooxidants in plant defence responses. *Frontiers in Plant Science, 4*, 419.

Grumet, R., Albrechtsen, R. S., & Handon, A. D. (1987). Growth and yield of barley isopopulations differing in solute potential. *Crop Science, 27*, 991–995.

Guei, R. G., & Wassom, C. E. (1993). Genetics of osmotic adjustment in breeding maize for drought tolerance. *Heredity, 71*, 436–441.

Guo, Y., Qiu, Q.-S., Quintero, F. J., et al. (2004). Transgenic evaluation of activated mutant alleles of SOS2 reveals a critical requirement for its kinase activity and C-terminal regulatory domain for salt tolerance in Arabidopsis thaliana. *Plant Cell, 16*(2), 435–449.

Guo, Z., Chen, D., Alqudah, A. M., Röder, M. S., Ganal, M. W., & Schnurbusch, T. (2016). Genome-wide association analyses of 54 traits identified multiple loci for the determination of floral fertility in wheat. *The New Phytologist, 214*, 257–270. https://doi.org/10.1111/nph.14342.

Gupta, K. J., Stoimenova, M., & Kaiser, W. M. (2005). In higher plants, only root mitochondria, but not leaf mitochondria reduce nitrite to NO, in vitro and in situ. *Journal of Experimental Botany, 56*(420), 2601–2609.

Gupta, K., Dey, A., & Gupta, B. (2013a). Plant polyamines in abiotic stress responses. *Acta Physiologiae Plantarum, 35*(7), 2015–2036.

Gupta, K., Dey, A., & Gupta, B. (2013b). Polyamines and their role in plant osmotic stress tolerance. In N. Tuteja & S. S. Gill (Eds.), *Climate change and plant abiotic stress tolerance* (pp. 1053–1072). Weinheim: Wiley-VCH.

Gurmani, R., Bano, A., Khan, S. U., Din, J., & Zhang, J. L. (2011). Alleviation of salt stress by seed treatment with abscisic acid (ABA), 6-benzylaminopurine (BA) and chlormequat chloride (CCC) optimizes ion and organic matter accumulation and increases yield of rice (Oryza sativa L.). *Australian Journal of Crop Science, 5*(10), 1278–1285.

Hale, M. G., & Orcutt, D. M. (1987). *The physiology of plants under stress*. New York: Wiley.

Handrick, V., Vogt, T., & Frolov, A. (2010). Profiling of hydroxycinnamic acid amides in Arabidopsis thaliana pollen by tandem mass spectrometry. *Analytical and Bioanalytical Chemistry, 398*, 2789–2801.

Hanson, A. D., Rathinasabapathi, B., Rivoal, J., Burnet, M., Dillon, M. O., & Gage, D. A. (1994). Osmoprotective compounds in the Plumbaginaceae: A natural experiment in metabolic engineering of stress tolerance. *Proceedings of the National Academy of Sciences of the United States of America, 91*(1), 306–310.

Hanzawa, Y., Imai, A., Michael, A. J., Komeda, Y., & Takahashi, T. (2002). Characterization of the spermidine synthase-related gene family in Arabidopsis thaliana. *FEBS Letters, 527*(1–3), 176–180.

Hao, D., Cheng, H., Yin, Z., Cui, S., Zhang, D., Wang, H., et al. (2012). Identification of single nucleotide polymorphisms and haplotypes associated with yield and yield components in soybean (Glycne max) landraces across multiple environments. *Theoretical and Applied Genetics, 124*, 447–458. https://doi.org/10.1007/s00122-011-1719-0.

Harborne, J. B., & Williams, C. A. (2000). Advances in flavonoid research since 1992. *Phytochemistry, 55*, 481–504.

Hasanuzzaman, M., Nahar, K., & Fujita, M. (2014). Regulatory role of polyamines in growth, development and abiotic stress tolerance in plants. In *Plant adaptation to environmental change: Significance of amino acids and their derivatives* (pp. 157–193).

Hasegawa, P. M. (2013). Sodium (Na+) homeostasis and salt tolerance of plants. *Environmental and Experimental Botany, 92*, 19–31.

Hasegawa, P. M., Bressan, R. A., Zhu, J.-K., & Bohnert, H. J. (2000). Plant cellular and molecular responses to high salinity. *Annual Review of Plant Biology, 51*, 463–499.

Havaux, M. (2014). Carotenoid oxidation products as stress signals in plants. *The Plant Journal, 79*, 597–606.

Hays, D. B., Do, J. H., Mason, R. E., Morgan, G., & Finlayson, S. A. (2007). Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation in a susceptible cultivar. *Plant Science, 172*, 1113–1123. https://doi.org/10.1016/j.plantsci.2007.03.004.

He, L., Nada, K., & Tachibana, S. (2002). Effects of Spd pretreatment through the roots on growth and photosynthesis of chilled cucumber plants (Cucumis sativus L.). *Journal of the Japanese Society for Horticultural Science, 71*, 490–498.

Hernandez, I., Alegre, L., Van Breusegem, F., & Munne-Bosch, S. (2009). How relevant are flavonoids as antioxidants in plants? *Trends in Plant Science, 14*, 125–132.

Herritt, M., Dhanapal, A. P., & Fritschi, F. B. (2016). Identification of genomic loci associated with the photochemical reflectance index by genome-wide association study in soybean. *Plant Genome, 9*. https://doi.org/10.3835/plantgenome2015.08.0072.

Hirayama, T., & Shinozaki, K. (2010). Research on plant abiotic stress responses in the post-genome era: Past, present and future. *The Plant Journal, 61*, 1041–1052.

Hoque, M. A., Banu, M. N. A., Okuma, E., et al. (2007). Exogenous proline and glycinebetaine increase NaCl-induced ascorbateglutathione cycle enzyme activities, and proline improves salt tolerance more than glycinebetaine in tobacco Bright Yellow-2 suspension-cultured cells. *Journal of Plant Physiology, 164*(11), 1457–1468.

Hoque, M. A., Banu, M. N. A., Nakamura, Y., Shimoishi, Y., & Murata, Y. (2008). Proline and glycinebetaine enhance antioxidant defense and methylglyoxal detoxification systems and reduce NaCl-induced damage in cultured tobacco cells. *Journal of Plant Physiology, 165*(8), 813–824.

Hossain, K. K., Itoh, R. D., Yoshimura, G., et al. (2010). Effects of nitric oxide scavengers on thermoinhibition of seed germination in Arabidopsis thaliana. *Russian Journal of Plant Physiology, 57*(2), 222–232.

Hossain, M. A., Munemasa, S., Uraji, M., Nakamura, Y., Mori, I. C., & Murata, Y. (2011). Involvement of endogenous abscisic acid in methyl jasmonate-induced stomatal closure in Arabidopsis. *Plant Physiology, 156*(1), 430–438.

Hsiao, T. C., & Xu, L. K. (2000). Sensitivity of growth of root versus leaves to water stress: Biophysical analysis and relation to water transport. *Journal of Experimental Botany, 51*, 1595–1616.

Huang, X., & Han, B. (2014). Natural variations and genome-wide association studies in crop plants. *Annual Review of Plant Biology, 65*, 531–551. https://doi.org/10.1146/annurev-arplant-050213-035715.

Hummel, I., El-Amrani, A., Gouesbet, G., Hennion, F., & Couee, I. (2004). Involvement of polyamines in the interacting effects of low temperature and mineral supply on Pringlea antiscorbutica (Kerguelen cabbage) seedlings. *Journal of Experimental Botany, 55*, 1125–1134.

Hussain, K., Nawaz, K., Majeed, A., et al. (2011). Role of exogenous salicylic acid applications for salt tolerance in violet (Viola Odorata L.). *Sarhad Journal of Agriculture, 27*, 171–175.

Ingvordsen, C. H., Backes, G., Lyngkjaer, M. F., Peltonen-Sainio, P., Jahoor, A., Mikkelsen, T. N., et al. (2015). Genome-wide association study of production and stability traits in barley cultivated under future climate scenarios. *Molecular Breeding, 35*, 84. https://doi.org/10.1007/s11032-015-0283-8.

Ippolito, A., Nigro, F., Lima, G., et al. (1997). Mechanism of resistance to Botrytis cinerea in wound of cured kiwifruits. *Acta Horticulturae, 444*, 719–724.

Ishitani, M., Liu, J., Halfter, U., Kim, C.-S., Shi, W., Zhu, J.- K. (2000). SOS3 function in plant salt tolerance requires Nmyristoylation and calcium binding. *Plant Cell,* 12(9), 1667–1677.

James, R. A., Blake, C., Byrt, C. S., & Munns, R. (2011). Major genes for Na+ exclusion, Nax1 and Nax2 (wheat HKT1;4 and HKT1;5), decrease Na+ accumulation in bread wheat leaves under saline and waterlogged conditions. *Journal of Experimental Botany, 62*(8), 2939–2947.

Janska, A., Marsik, P., Zelenkova, S., & Odessa, J. (2010). Cold stress and acclimation – What is important for metabolic adjustment? *Plant Biology, 12*, 395–405.

Jayakannan, M., Bose, J., Babourina, O., et al. (2013). Salicylic acid improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing salt-induced K+ loss via a GORK channel. *Journal of Experimental Botany, 64*(8), 2255–2268.

Jeschke, W. D., Peuke, A. D., Pate, J. S., & Hartung, W. (1997). Transport, synthesis and catabolism of abscisic acid (ABA) in intact plants of castor bean (Ricinus communis L.) under phosphate deficiency and moderate salinity. *Journal of Experimental Botany, 48*(314), 1737–1747.

Kavi-Kishor, P. B., Sangam, S., Amrutha, R. N., Sri-Laxmi, P., Naidu, K. R., Rao, K. R. S. S., Sreenath, R., Reddy, K. J., Theriappan, P., & Sreenivasulu, N. (2005). Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: Its implications in plant growth and abiotic stress tolerance. *Current Science, 88*, 424–438.

Kerepesi, I., & Galiba, G. (2000). Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. *Crop Science, 40*(2), 482–487.

Keskin, B. C., Sarikaya, A. T., Yuksel, B., & Memon, A. R. (2010). Abscisic acid regulated gene expression in bread wheat (Triticum aestivum L.). *Australian Journal of Crop Science, 4*(8), 617–625.

Keunen, E., Peshev, D., Vangronsveld, J., Van den Ende, W., & Cuypers, A. (2013). Plant sugars are crucial players in the oxidative challenge during abiotic stress: Extending the traditional concept. *Plant, Cell & Environment, 36*, 1242–1255.

Khan, M. A., Ungar, I. A., & Showalter, A. M. (2000). Effects of sodium chloride treatments on growth and ion accumulation of the halophyte haloxylon recurvum. *Communications in Soil Science and Plant Analysis, 31*(17–18), 2763–2774.

Kim, H., Latif Khan, A., Waqas, M., et al. (2013). Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress. *Journal of Plant Growth Regulation, 33*, 137–149.

Kinnersley, A. M., & Turano, F. J. (2000). Gamma aminobutyric acid (GABA) and plant responses to stress. *Critical Reviews in Plant Sciences, 19*, 479–509.

Knott, J. M., Romer, P., & Sumper, M. (2007). Putative spermine syn- ¨ thases from Thalassiosira pseudonana and Arabidopsis thaliana synthesize thermospermine rather than spermine. *FEBS Letters, 581*(16), 3081–3086.

Kopyra, M., & Gwóźdź, E. A. (2003). Nitric oxide stimulates seed ´ germination and counteracts the inhibitory effect of heavy metals and salinity on root growth of Lupinus luteus. *Plant Physiology and Biochemistry, 41*(11–12), 1011–1017.

Kovacs, Z., Simon-Sarkadi, L., Szucs, A., & Kocsy, G. (2010). Differential effects of cold, osmotic stress and abscisic acid on polyamine accumulation in wheat. *Amino Acids, 38*(2), 623–631.

Kudoh, H., & Sonoike, K. (2002). Irreversible damage to photo system I by chilling in the light: Cause of the degradation of chlorophyll after returning to normal growth temperature. *Planta, 215*, 541–548.

Kusano, T., Yamaguchi, K., Berberich, T., & Takahashi, Y. (2007). Advances in polyamine research in 2007. *Journal of Plant Research, 120*(3), 345–350.

Kusano, M., Tohge, T., Fukushima, A., Kobayashi, M., Hayashi, N., Otsuki, H., Kondou, Y., Goto, H., Kawashima, M., Matsuda, F., et al. (2011). Metabolomics reveals comprehensive repro-

gramming involving two independent metabolic responses of Arabidopsis to UV-B light. *The Plant Journal, 67*, 354–369.

Lasky, J. R., Upadhyaya, H. D., Ramu, P., Deshpande, S., Hash, C. T., Bonnette, J., et al. (2015). Genome-environment associations in sorghum landraces predict adaptive traits. *Science Advances, 1*, e1400218. https://doi.org/10.1126/sciadv.1400218.

Lavola, A., Julkunen-Tiitto, R., de laRosa, T. M., Lehto, T., & Aphalo, P. J. (2000). Allocation of carbon to growth and secondary metabolites in birch seedlings under UV-B radiation and CO2 exposure. *Physiologia Plantarum, 109*, 260–267.

Leiser, W. L., Rattunde, H. F. W., Weltzein, E., Cisse, N., Abdou, M., Diallo, A., et al. (2014). Two in one sweep: Aluminum tolerance and grain yield in P-limited soils are associated to the same genomic region in West African Sorghum. *BMC Plant Biology, 14*, 206. https://doi.org/10.1186/s12870-014-0206-6.

Lesk, C., Rowhami, P., & Ramankutty, N. (2016). Influence of extreme weather disasters on global crop production. *Nature, 529*, 84–87. https://doi.org/10.1038/nature16467.

Levitt, J. (1980). *Responses of plants to environmental stress: Chilling, freezing, and high temperature stresses* (2nd ed.). New York: Academic.

Li, Z., Wakao, S., Fischer, B. B., & Niyogi, K. K. (2009). Sensing and responding to excess light. *Annual Review of Plant Biology, 60*, 391–395. https://doi.org/10.1146/annurev.arplant.58.032806.103844.

Li, B., He, L., Guo, S., et al. (2013). Proteomics reveal cucumber Spd-responses under normal condition and salt stress. *Plant Physiology and Biochemistry, 67*, 7–14.

Liang, S., Zhou, R., Dong, S., & Shil, S. (2008). Adaptation to salinity in mangroves: Implication on the evolution of salt tolerance. *Chinese Science Bulletin, 53*, 1708–1715.

Liu, J., Ishitani, M., Halfter, U., Kim, C.-S., & Zhu, J.-K. (2000). The Arabidopsis thaliana SOS2 gene encodes a protein kinase that is required for salt tolerance. *Proceedings of the National Academy of Sciences of the United States of America, 97*(7), 3730–3734.

Liu, W., Li, R.-J., Han, T.-T., Cai, W., Fu, Z.-W., & Lu, Y.-T. (2015). Salt stress reduces root meristem size by nitric oxide-mediated modulation of Auxin accumulation and Signaling in Arabidopsis. *Plant Physiology, 168*(1), 343–356.

Lobell, D. B., Roberts, M. J., Schlenker, W., Braun, N., Little, B. B., Rejesus, R. M., & Hammer, G. L. (2014). Greater sensitivity to drought accompanies maize yield increase in the U.S. Midwest. *Science, 344*, 516–519.

Ludlow, M. M., Santamaria, J. M., & Fukai, S. (1990). Contribution of osmotic adjustment to grain yield in Sorghum bicolor (L.) Moench under water-limited conditions. II. Water stress after anthesis. *Australian Journal of Agricultural Research, 41*, 67–78.

Ma, L., Zhang, H., Sun, L., et al. (2012). NADPH oxidase AtrbohD and AtrbohF function in ROS-dependent regulation of Na+/K+ homeostasis in Arabidopsis under salt stress. *Journal of Experimental Botany, 63*(1), 305–317.

Mackill, D. J., Ismail, A. M., Singh, U. S., Labios, R. V., & Paris, T. R. (2012). Development and rapid adoption of sub-mergence-tolerant (Sub1) rice varieties. *Advances in Agronomy, 155*, 299–352. https://doi.org/10.1016/B978-0-12-394276-0.00006-8.

Mahfouz, M. M., Piatek, A., & Stewart, C. N., Jr. (2014). Genome engineering via TALENs and CRISPR/Cas9 systems: Challenges and perspectives. *Plant Biotechnology Journal, 12*, 1006–1014.

Makela, P., Karkkainen, J., & Somersalo, S. (2000). Effect of glycinebetaine on chloroplast ultrastructure, chlorophyll and protein content, and RuBPCO activities in tomato grown under drought or salinity. *Biologia Plantarum, 43*(3), 471–475.

Makumburage, G. B., Richbourg, H. L., La Torre, K. D., Capps, A., Chen, C. X., & Stapleton, A. E. (2013). Genotype to phenotype maps: Multiple input abiotic signals combine to produce growth effects via attenuating signaling interactions in maize. G3. *Bethesda, 3*, 2195–2204. https://doi.org/10.1534/g3.113.008573.

Mao, Y., Zhang, H., Xu, N., Zhang, B., Gou, F., & Zhu, J. K. (2013). Application of the CRISPR-Cas system for efficient genome engineering in plants. *Molecular Plant, 6*, 2008–2011.

Martínez-Atienza, J., Jiang, X., Garciadeblas, B., et al. (2007). Conservation of the salt overly sensitive pathway in rice. *Plant Physiology, 143*(2), 1001–1012.
Matysik, J., Alia, A., Bhalu, B., & Mohanty, P. (2002). Molecular mechanisms of quenching of reactive oxygen species by proline under stress in plants. *Current Science, 82*(5), 525–532.
Maurer, A., Draba, V., Jiang, Y., Schnaithmann, F., Sharma, R., Schumann, E., et al. (2015). Modelling the genetic architecture of flowering time in barley through nested association mapping. *BMC Genomics, 16*, 290. https://doi.org/10.1186/s12864-015-1459-7.
Michael, T. P., & VanBuren, R. (2015). Progress, challenges and the future of crop genomes. *Current Opinion in Plant Biology, 24*, 71–81. https://doi.org/10.1016/j.pbi.2015.02.002.
Miller, G., Suzuki, N., Ciftci-Yilmaz, S., & Mittler, R. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, Cell & Environment, 33*, 453–467.
Mittler, R., Vanderauwera, S., Gollery, M., & Van Breusegem, F. (2004). Reactive oxygen gene network of plants. *Trends in Plant Science, 9*, 490–498.
Morales, D., Rodriguez, P., Dellamico, J., Nicolas, E., Torrecillas, A., & Sanchez-Blanco, M. J. (2003). Hightemperature preconditioning and thermal shock imposition affects water relations, gas exchange and root hydraulic conductivity in tomato. *Biologia Plantarum, 47*, 203–208.
Morgan, J. M. (1983). Osmoregulation as a selection criterion for drought tolerance in wheat. *Australian Journal of Agricultural Research, 34*, 607–614.
Morgan, J. M. (1995). Growth and yield of wheat lines with differing osmoregulative capacity at high soil water deficit in seasons of varying evaporative demand. *Field Crops Research, 40*, 143–152.
Morgan, J. M., Rodríguez-Maribona, B., & Knights, E. J. (1991). Adaptation to water-deficit in chickpea breeding lines by osmoregulation: Relationship to grain-yields in the field. *Field Crops Research, 27*, 61–70.
Morreel, K., Saeys, Y., Dima, O., Lu, F., Van de Peer, Y., Vanholme, R., Ralph, J., Vanholme, B., & Boerjan, W. (2014). Systematic structural characterization of metabolites in Arabidopsis via candidate substrate–product pair networks. *Plant Cell, 26*, 929–945.
Morrison, M. J., & Stewart, D. W. (2002). Heat stress during flowering in summer rape. *Crop Science, 42*, 797–803.
Moschou, P. N., Delis, I. D., Paschalidis, K. A., & Roubelakis-Angelakis, K. A. (2008a). Transgenic tobacco plants over expressing polyamine oxidase are not able to cope with oxidative burst generated by abiotic factors. *Physiologia Plantarum, 133*, 140–156.
Moschou, P. N., Paschalidis, K. A., & RoubelakisAngelakis, K. A. (2008b). Plant polyamine catabolism: The state of the art. *Plant Signaling and Behavior, 3*(12), 1061–1066.
Msanne, J., Lin, J., Stone, J., & Awada, T. (2011). Characterization of abiotic stress responsive Arabidopsis thaliana RD29A and RD29B genes and evaluation of transgenes. *Planta, 234*, 97–107.
Munir, N., & Aftab, F. (2011). Enhancement of salt tolerance in sugarcane by ascorbic acid pretreatment. *African Journal of Biotechnology, 10*(80), 18362–18370.
Munns, R. (2005). Genes and salt tolerance: Bringing them together. *New Phytologist, 167*(3), 645–663.
Munns, R., & Tester, M. (2008). Mechanisms of salinity tolerance. *Annual Review of Plant Biology, 59*, 651–681.
Nakabayashi, R., Sawada, Y., Yamada, Y., Suzuki, M., Hirai, M. Y., Sakurai, T., & Saito, K. (2013). Combination of liquid chromatography– Fourier transform ion cyclotron resonance-mass spectrometry with 13C-labeling for chemical assignment of sulfur-containing metabolites in onion bulbs. *Analytical Chemistry, 85*, 1310–1315.
Nakabayashi, R., Yonekura-Sakakibara, K., Urano, K., Suzuki, M., Yamada, Y., Nishizawa, T., Matsuda, F., Kojima, M., Sakakibara, H., Shinozaki, K., et al. (2014). Enhancement of oxidative and drought tolerance in Arabidopsis by overaccumulation of antioxidant flavonoids. *The Plant Journal, 77*, 367–379.
Natella, F., Maldini, M., Leoni, G., & Scaccini, C. (2014). Glucosinolates redox activities: Can they act as antioxidants? *Food Chemistry, 149*, 226–232.

Nazar, R., Iqbal, N., Syeed, S., & Khan, N. A. (2011). Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars. *Journal of Plant Physiology, 168*(8), 807–815.

Niggeweg, R., Michael, A. J., & Martin, C. (2004). Engineering plants with increased levels of the antioxidant chlorogenic acid. *Nature Biotechnology, 22*, 746–754.

Nishizawa, A., Yabuta, Y., & Shigeoka, S. (2008). Galactinol and raffinose constitute a novel function to protect plants from oxidative damage. *Plant Physiology, 147*, 1251–1263.

Nounjan, N., Nghia, P. T., & Theerakulpisut, P. (2012). Exogenous proline and trehalose promote recovery of rice seedlings from salt-stress and differentially modulate antioxidant enzymes and expression of related genes. *Journal of Plant Physiology, 169*(6), 596–604.

Nutzmann, H. W., & Osbourn, A. (2014). Gene clustering in plant specialized metabolism. *Current Opinion in Biotechnology, 26*, 91–99.

Obata, T., & Fernie, A. R. (2012). The use of metabolomics to dissect plant responses to abiotic stresses. *Cellular and Molecular Life Sciences, 69*, 3225–3243.

Oh, D.-H., Lee, S. Y., Bressan, R. A., Yun, D.-J., & Bohnert, H. J. (2010). Intracellular consequences of SOS1 deficiency during salt stress. *Journal of Experimental Botany, 61*(4), 1205–1213.

Oikawa, A., & Saito, K. (2012). Metabolite analyses of single cells. *The Plant Journal, 70*, 30–38.

Okubo, K., & Yoshiki, Y. (2000). The role of triterpenoid on reactive oxygen scavenging system: Approach from the new chemiluminescence system (XYZ system). *BioFactors, 13*, 219–223.

Oleszek, W. A. (2002). Chromatographic determination of plant saponins. *Journal of Chromatography. A, 967*, 147–162.

Ortiz, R. (2015). *Plant breeding in the Omics era* (p. 249). New York: Springer. https://doi.org/10.1007/978-3-319-20532-8.

Pang, S., Chen, S., Dai, Y., Chen, Y. W., & Yan, X. (2010). Comparative proteomics of salt tolerance inArabidopsis thaliana and Thellungiella halophila. *Journal of Proteome Research, 9*(5), 2584–2599.

Panicot, M., Minguet, E. G., Ferrando, A., et al. (2002). A polyamine metabolon involving aminopropyl transferase complexes in Arabidopsis. *Plant Cell, 14*(10), 2539–2551.

Parida, K., Das, A. B., & Mohanty, P. (2004). Investigations on the antioxidative defence responses to NaCl stress in a mangrove, Bruguiera parviflora: Differential regulations of isoforms of some antioxidative enzymes. *Plant Growth Regulation, 42*(3), 213–226.

Pasam, R. K., Sharma, R., Malosetti, M., van Eeuwijk, F. A., Haseneyer, G., Kilian, B., et al. (2012). Genome-wide association studies for agronomical traits in a worldwide spring barley collection. *BMC Plant Biology, 12*, 16. https://doi.org/10.1186/1471-2229-12-16.

Peshev, D., Vergauwen, R., Moglia, A., Hideg, E., & Van den Ende, W. (2013). Towards understanding vacuolar antioxidant mechanisms: A role for fructans? *Journal of Experimental Botany, 64*, 1025–1038.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters, 9*, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.

Pollier, J., Morreel, K., Geelen, D., & Goossens, A. (2011). Metabolite profiling of triterpene saponins in Medicago truncatula hairy roots by liquid chromatography Fourier transform ion cyclotron resonance mass spectrometry. *Journal of Natural Products, 74*, 1462–1476.

Pontis, H. G. (1989). Fructans and cold stress. *Journal of Plant Physiology, 134*, 148–150.

Qin, P., Lin, Y., Hu, Y., Liu, K., Mao, S., Li, Z., et al. (2016). Genome-wide association study of drought-related resistance traits in Aegilops tauschii. *Genetics and Molecular Biology, 39*, 398–407. https://doi.org/10.1590/1678-4685-GMB-2015-0232.

Queval, G., Jaillard, D., Zechmann, B., & Noctor, G. (2011). Increased intracellular H_2O_2 availability preferentially drives glutathione accumulation in vacuoles and chloroplasts. *Plant, Cell & Environment, 34*, 21–32.

Quintero, J., Ohta, M., Shi, H., Zhu, J.-K., & Pardo, J. M. (2002). Reconstitution in yeast of the Arabidopsis SOS signaling pathway for Na+ homeostasis. *Proceedings of the National Academy of Sciences of the United States of America, 99*(13), 9061–9066.

Quintero, J., Martinez-Atienza, J., Villalta, I., et al. (2011). Activation of the plasma membrane Na/H antiporter salt-overly-sensitive 1 (SOS1) by phosphorylation of an auto-inhibitory C-terminal domain. *Proceedings of the National Academy of Sciences of the United States of America, 108*(6), 2611–2616.

Quisenberry, J. E., Cartwright, G. B., & McMichael, B. L. (1984). Genetic relationship between turgor maintenance and growth in cotton germplasm. *Crop Science, 24*, 479–482.

Radin, J. W. (1983). Physiological consequences of cellular water defi cit: Osmotic adjustment. In H. M. Taylor, W. R. Jordan, & T. R. Sinclair (Eds.), *Limitations to efficient water use in crop production* (pp. 267–276). Madison: American Society of Agronomy.

Rahman, S., Miyake, H., & Takeoka, Y. (2002). Effects of exogenous glycinebetaine on growth and ultrastructure of salt-stressed rice seedlings (Oryza sativa L.). *Plant Production Science, 5*(1), 33–44.

Rahnama, A., James, R. A., Poustini, K., & Munns, R. (2010). Stomatal conductance as a screen for osmotic stress tolerance in durum wheat growing in saline soil. *Functional Plant Biology, 37*(3), 255–263.

Rambla, J. L., Vera-Sirera, F., Blazquez, M. A., Carbonell, J., & Granell, A. ´. (2010). Quantitation of biogenic tetraamines in Arabidopsis thaliana. *Analytical Biochemistry, 397*(2), 208–211.

Rawia Eid, A., Taha, L. S., & Ibrahiem, S. M. M. (2011). Alleviation of adverse effects of salinity on growth, and chemical constituents of marigold plants by using glutathione and ascorbate. *Journal of Applied Sciences Research, 7*, 714–721.

Rebolledo, M. G., Peña, A. L., Duitama, J., Cruz, D. F., Dingkuhn, M., Grenier, C., et al. (2016). Combining image analysis, genome wide association studies and different field trials to reveal stable genetic regions related to panicle architecture and the number of spikelets per panicle in rice. *Frontiers in Plant Science, 7*, 1384. https://doi.org/10.3389/fpls.2016.01384.

Reddy, M. P., Sanish, S., & Iyengar, E. R. R. (1992). Photosynthetic studies and compartmentation of ions in different tissues of Salicornia brachiata Roxb. under saline conditions. *Photosynthetica, 26*, 173–179.

Rhee, S. Y., & Mutwil, M. (2014). Towards revealing the functions of all genes in plants. *Trends in Plant Science, 19*, 212–221. https://doi.org/10.1016/j.tplants.2013.10.006.

Rodríguez-Maribona, B., Tenorio, J. L., Conde, J. R., & Ayerbe, L. (1992). Correlation between yield and osmotic adjustment of peas (Pisum sativum L.) under drought stress. *Field Crops Research, 29*, 15–22.

Roy, M., & Wu, R. (2002). Overexpression of S-adenosylmethionine decarboxylase gene in rice increases polyamine level and enhances sodium chloride-stress tolerance. *Plant Science, 163*(5), 987–992.

Roy, S. J., Negrao, S., & Tester, M. (2014). Salt resistant crop plants. *Current Opinion in Biotechnology, 26*, 115–124.

Roychoudhury, A., Basu, S., & Sengupta, D. N. (2011). Amelioration of salinity stress by exogenously applied spermidine or spermine in three varieties of indica rice differing in their level of salt tolerance. *Journal of Plant Physiology, 168*(4), 317–328.

Sairam, R. K., & Tyagi, A. (2004). Physiology and molecular biology of salinity stress tolerance in plants. *Current Science, 86*(3), 407–421.

Saito, K. (2013). Phytochemical genomics — A new trend. *Current Opinion in Plant Biology, 16*, 373–380.

Saito, K., Hirai, M. Y., & Yonekura-Sakakibara, K. (2008). Decoding genes with coexpression networks and metabolomics — 'Majority report by precogs'. *Trends in Plant Science, 13*, 36–43.

Saito, K., Yonekura-Sakakibara, K., Nakabayashi, R., Higashi, Y., Yamazaki, M., Tohge, T., & Fernie, A. R. (2013). The flavonoid biosynthetic pathway in Arabidopsis: Structural and genetic diversity. *Plant Physiology and Biochemistry, 72*, 21–34.

Sakamoto, A., & Murata, N. (2002). The role of glycine betaine in the protection of plants from stress: Clues from transgenic plants. *Plant, Cell & Environment, 25*, 163–171.

Sanders, D. (2000). Plant biology: The salty tale of Arabidopsis. *Current Biology, 10*(13), R486–R488.

Santakumari, M., & Berkowitz, G. A. (1991). Chloroplast volume: Cell water potential relationships and acclimation of photosynthesis to leaf water deficits. *Photosynthesis Research, 28*, 9–20.

Santamaria, J. M., Ludlow, M. M., & Fukai, S. (1990). Contribution of osmotic adjustment to grain yield in Sorghum bicolor (L.) Moench under water-limited conditions. I. Water stress before anthesis. *Australian Journal of Agricultural Research, 41*, 51–65.

Sawada, H., Shim, I.-S., & Usui, K. (2006). Induction of benzoic acid 2-hydroxylase and salicylic acid biosynthesis-modulation by salt stress in rice seedlings. *Plant Science, 171*(2), 263–270.

Sawai, S., Ohyama, K., Yasumoto, S., Seki, H., Sakuma, T., Yamamoto, T., Takebayashi, Y., Kojima, M., Sakakibara, H., Aoki, T., et al. (2014). Sterol side chain reductase 2 is a key enzyme in the biosynthesis of cholesterol, the common precursor of toxic steroidal glycoalkaloids in potato. *Plant Cell, 26*, 3763–3774.

Saxena, S. C., Kaur, H., Verma, P., et al. (2013). Osmoprotectants: Potential for crop improvement under adverse conditions. In *Plant acclimation to environmental stress* (pp. 197–232). New York: Springer.

Scheben, A., Batley, J., & Edwards, D. (2017a). Genotyping-by-sequencing approaches to characterize crop genomes: Choosing the right tool for the right application. *Plant Biotechnology Journal, 15*, 149–161. https://doi.org/10.1111/pbi.12645.

Scheben, A., Wolter, F., Batley, J., Puchta, H., & Edwards, D. (2017b). Towards CRISPR/Cas crops – Bringing together genomics and genome editing. *The New Phytologist*. https://doi.org/10.1111/nph.14702. Epub ahead of print.

Schroeder, J. I., Delhaize, E., Frommer, W. B., et al. (2013). Using membrane transporters to improve crops for sustainable food production. *Nature, 497*, 60–66.

Serraj, R., & Sinclair, T. R. (2002). Osmolyte accumulation: Can it really help increase crop yield under drought conditions? *Plant, Cell & Environment, 25*, 333–341.

Serrano, R., Mulet, J. M., Rios, G., et al. (1999). A glimpse of the mechanisms of ion homeostasis during salt stress. *Journal of Experimental Botany, 50*, 1023–1036.

Shahidi, F., & Chandrasekara, A. (2010). Hydroxycinnamates and their in vitro and in vivo antioxidant activities. *Phytochemistry Reviews, 9*, 147–170.

Shaked-Sachray, L., Weiss, D., Reuveni, M., Nissim-Levi, A., & Oren-Shamir, M. (2002). Increased anthocyanin accumulation in aster flowers at elevated temperatures due to magnesium treatment. *Physiologia Plantarum, 114*, 559–565.

Sharp, R. E., & Davies, W. J. (1979). Solute regulation and growth by roots and shoots of water-stressed maize plants. *Planta, 147*, 43–49.

Sharp, R. E., Hsiao, C. T., & Silk, W. K. (1990). Growth of the maize primary root at low water potentials. II role of growth and deposition of hexose and potassium in osmotic adjustment. *Plant Physiology, 93*, 1337–1346.

Sharp, R. E., Poroyko, V., Hejlek, L. G., Spollen, W. G., Springer, G. K., Bohnert, H. J., & Nguyen, H. T. (2004). Root growth maintenance during water defi cits: Physiology to functional genomics. *Journal of Experimental Botany, 55*, 2343–2351.

Shevyakova, I., Musatenko, L. I., Stetsenko, L. A., et al. (2013). Effects of abscisic acid on the contents of polyamines and proline in common bean plants under salt stress. *Russian Journal of Plant Physiology, 60*, 200–211.

Shi, H., Ishitani, M., Kim, C., & Zhu, J.-K. (2000). The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter. *Proceedings of the National Academy of Sciences of the United States of America, 97*(12), 6896–6901.

Shi, Quintero, F. J., Pardo, J. M., & Zhu, J.-K. (2002). The putative plasma membrane Na+/H+ antiporter SOS1 controls longdistance Na+ transport in plants. *Plant Cell, 14*(2), 465–477.

Signorelli, S., Coitiño, E. L., Borsani, O., & Monza, J. (2014). Molecular mechanisms for the reaction between (_)OH radicals and proline: Insights on the role as reactive oxygen species scavenger in plant stress. *The Journal of Physical Chemistry. B, 118*, 37–47.

Sima, N. A. K. K., Askari, H., Mirzaei, H. H., & Pessarakli, M. (2009). Genotype-dependent differential responses of three forage species to calcium supplement in saline conditions. *Journal of Plant Nutrition, 32*, 579–597.

Simoes-Araujo, J. L., Rumjanek, N. G., & Margis-Pinheiro, M. (2003). Small heat shock proteins genes are differentially expressed in distinct varieties of common bean. *Brazilian Journal of Plant Physiology, 15*, 33–41.

Sturm, S., & Seger, C. (2012). Liquid chromatography–nuclear magnetic resonance coupling as alternative to liquid chromatography– Mass spectrometry hyphenations: Curious option or powerful and complementary routine tool? *Journal of Chromatography. A, 1259*, 50–61.

Subbarao, G. V., Chauhan, Y. S., & Johansen, C. (2000). Patterns of osmotic adjustment in pigeonpea – Its importance as a mechanism of drought resistance. *European Journal of Agronomy, 12*, 239–249.

Sumner, L. W., Amberg, A., Barrett, D., Beale, M. H., Beger, R., Daykin, C. A., Fan, T. W., Fiehn, O., Goodacre, R., Griffin, J. L., et al. (2007). Proposed minimum reporting standards for chemical analysis chemical analysis working group (CAWG) metabolomics standards initiative (MSI). *Metabolomics, 3*, 211–221.

Sumner, L. W., Lei, Z., Nikolau, B. J., Saito, K., Roessner, U., & Trengove, R. (2014). Proposed quantitative and alphanumeric metabolite identification metrics. *Metabolomics, 10*, 1047–1049.

Suzuki, N., Rivero, R. M., Shulaev, V., Blumwald, E., & Mittler, R. (2014). Abiotic and biotic stress combinations. *The New Phytologist, 203*, 32–43.

Szabados, L., & Savoure, A. (2010). Proline: A multifunctional amino acid. *Trends in Plant Science, 15*, 89–97.

Tahir, M. A., Aziz, T., Farooq, M., & Sarwar, G. (2012). Siliconinduced changes in growth, ionic composition, water relations, chlorophyll contents and membrane permeability in two salt-stressed wheat genotypes. *Archives of Agronomy and Soil Science, 58*(3), 247–256.

Takahashi, T., & Kakehi, J.-I. (2010). Polyamines: Ubiquitous polycations with unique roles in growth and stress responses. *Annals of Botany, 105*(1), 1–6.

Thoen, M. P. M., Olivas, N. H. D., Kloth, K. J., Coolen, S., Huang, P.-P., Aarts, M. G., et al. (2016). Genetic architecture of plant stress resistance: Multi-trait genome-wide association mapping. *The New Phytologist, 213*, 1346–1362. https://doi.org/10.1111/nph.14220.

Thomas, J. C., Sepahi, M., Arendall, B., & Bohnert, H. J. (1995). Enhancement of seed germination in high salinity by engineering mannitol expression inArabidopsis thaliana. *Plant, Cell and Environment, 18*(7), 801–806.

Thomashow, M. F. (1999). Plant cold acclimation: Freezing tolerance genes and regulatory mechanisms. *Annual Review of Plant Physiology and Plant Molecular Biology, 50*, 571–599.

Tian, F., Bradbury, P. J., Brown, P. J., Hung, H., Sun, Q., Flint-Garcia, S., et al. (2011). Genome-wide association study of leaf architecture in the maize nested association mapping population. *Nature Genetics, 43*, 159–162. https://doi.org/10.1038/ng.746.

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 20260–20264. https://doi.org/10.1073/pnas.1116437108.

Tohge, T., Ramos, M. S., Nunes-Nesi, A., Mutwil, M., Giavalisco, P., Steinhauser, D., Schellenberg, M., Willmitzer, L., Persson, S., Martinoia, E., et al. (2011). Toward the storage metabolome: Profiling the barley vacuole. *Plant Physiology, 157*, 1469–1482.

Tohge, T., Watanabe, M., Hoefgen, R., & Fernie, A. R. (2013). The evolution of phenylpropanoid metabolism in the green lineage. *Critical Reviews in Biochemistry and Molecular Biology, 48*, 123–152.

Trethowan, R. M., Reynolds, M. P., Ortiz-Monasterio, I., & Ortiz, R. (2007). The genetic basis of the green revolution in wheat production. *Plant Breeding Reviews, 28*, 39–58. https://doi.org/10.1002/9780470168028.ch2.

Turner, N. C., & Jones, M. M. (1980). Turgor maintenance by osmotic adjustment: A review and evaluation. In N. C. Turner & P. J. Kramer (Eds.), *Adaptation of plant to water and high temperature stress* (pp. 87–103). New York: Wiley.

Tuteja, N., Sahoo, R. K., Garg, B., & Tuteja, R. (2013). OsSUV3 dual helicase functions in salinity stress tolerance by maintaining photosynthesis and antioxidant machinery in rice (Oryza sativa L. cv. IR64). *The Plant Journal, 76*(1), 115–127.

Urano, K., Yoshiba, Y., Nanjo, T., Ito, T., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2004). Arabidopsis stress-inducible gene for arginine decarboxylase AtADC2 is required for accumulation of putrescine in salt tolerance. *Biochemical and Biophysical Research Communications, 313*(2), 369–375.

Valluru, R., Reynolds, M. P., Davies, W. J., & Sukumaran, S. (2017). Phenotypic and genome-wide association analysis of spike ethylene in diverse wheat genotypes under heat stress. *The New Phytologist, 214*, 271–283. https://doi.org/10.1111/nph.14367.

Van den Ende, W., Michiels, A., DeRoover, J., & VanLaere, A. (2002). Fructan biosynthetic and breakdown enzymes in dicots evolved from different invertases: Expression of fructan genes throughout chicory development. *Scientific World Journal, 2*, 1273–1287.

Van Oosten, M. J., Sharkhuu, A., Batelli, G., Bressan, R. A., & Maggio, A. (2013). The Arabidopsis thaliana mutant air1 implicates SOS3 in the regulation of anthocyanins under salt stress. *Plant Molecular Biology, 83*, 405–415.

Velikova, V. B., Edreva, A. M., Tsonev, T. D., & Jones, H. G. (2007). Singlet oxygen quenching by phenylamides and their parent compounds. *Zeitschrift für Naturforschung. Section C, 62*, 833–838.

Verbruggen, N., & Hermans, C. (2008). Proline accumulation in plants: A review. *Amino Acids, 35*, 753–759.

Vickers, C. E., Gershenzon, J., Lerdau, M. T., & Loreto, F. (2009). A unified mechanism of action for volatile isoprenoids in plant abiotic stress. *Nature Chemical Biology, 5*, 283–291.

Voetberg, G. S., & Sharp, R. E. (1991). Growth of the maize primary root at low water potentials. III. Role of increased proline deposition in osmotic adjustment. *Plant Physiology, 96*, 1125–1130.

Wang, Y., & Nii, N. (2000). Changes in chlorophyll, ribulose bisphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in Amaranthus tricolor leaves during salt stress. *Journal of Horticultural Science and Biotechnology, 75*(6), 623–627.

Wang, B., Luttge, U., & Ratajczak, R. (2001). Effects of salt treatment ¨ and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte Suaeda salsa. *Journal of Experimental Botany, 52*(365), 2355–2365.

Westgate, M. E., & Boyer, J. S. (1985). Osmotic adjustment and the inhibition of leaf, root, stem, and silk growth at low water potentials in maize. *Planta, 164*, 540–549.

Wissuwa, M., Kondo, K., Fukuda, T., Mori, A., Rose, M. T., Pariasca-Tanaka, J., et al. (2015). Unmasking novel loci for internal phosphorus utilization efficiency in rice germplasm through genome-wide association analysis. *PLoS One, 10*, e0124215. https://doi.org/10.1371/journal.pone.0124215.

Xiaomu, N. X. N., Bressan, R. A., Hasegawa, P. M., & Pardo, J. M. (1995). Ion homeostasis in NaCl stress environments. *Plant Physiology, 109*(3), 735–742.

Yamaguchi, K., Takahashi, Y., Berberich, T., et al. (2006). The polyamine spermine protects against high salt stress in Arabidopsis thaliana. *FEBS Letters, 580*(30), 6783–6788.

Yang, Z., Nakabayashi, R., Okazaki, Y., Mori, T., Takamatsu, S., Kitanaka, S., Kikuchi, J., & Saito, K. (2014). Toward better annotation in plant metabolomics: Isolation and structure elucidation of 36 specialized metabolites from Oryza sativa (rice) by using MS/MS and NMR analyses. *Metabolomics, 10*, 543–555.

Yen, H. E., Wu, S.-M., Hung, Y.-H., & Yen, S.-K. (2000). Isolation of 3 salt-induced low-abundance cDNAs from light-grown callus of Mesembryanthemum crystallinum by suppression subtractive hybridization. *Physiologia Plantarum, 110*(3), 402–409.

Yonekura-Sakakibara, K., Nakabayashi, R., Sugawara, S., Tohge, T., Ito, T., Koyanagi, M., Kitajima, M., Takayama, H., & Saito, K. (2014). A flavonoid 3-O-glucoside:200-O-glucosyltransferase responsible for terminal modification of pollen-specific flavonols in Arabidopsis thaliana. *The Plant Journal, 79*, 769–782.

Zhang, J. L., & Shi, H. (2013). Physiological and molecular mechanisms of plant salt tolerance. *Photosynthesis Research, 115*, 1–22.

Zhang, Y., Wang, L., Liu, Y., Zhang, Q., Wei, Q., & Zhang, W. (2006). Nitric oxide enhances salt tolerance in maize seedlings through increasing activities of proton-pump and Na+/H+ antiport in the tonoplast. *Planta, 224*(3), 545–555.

Zhang, Y., Wang, Y., Yang, H. W., Wang, D., & Liu, J. (2007). Involvement of hydrogen peroxide and nitric oxide in salt resistance in the calluses from Populus euphratica. *Plant, Cell and Environment, 30*(7), 775–785.

Zhang, W., Jiang, B., Li, W., Song, H., Yu, Y., & Chen, J. (2009). Polyamines enhance chilling tolerance of cucumber (Cucumis sativus L.). through modulating antioxidative system. *Scientia Horticulturae, 122*, 200–208.

Zhao, M.-G., Chen, L., Zhang, L.-L., & Zhang, W.-H. (2009). Nitric reductase-dependent nitric oxide production is involved in cold acclimation and freezing tolerance in Arabidopsis. *Plant Physiology, 151*(2), 755–767.

Zhao, C., Takeshima, R., Zhu, J., Xu, M., Sato, M., Watanabe, S., et al. (2016). A recessive allele for delayed flowering at the soybean maturity locus E9 is a leaky allele of F2a, a FLOWERING LOCUS T ortholog. *BMC Plant Biology, 16*, 20. https://doi.org/10.1186/s12870-016-0704-9.

Zhou, Y. H., Yu, J. Q., Huang, L. F., & Nogues, S. (2004). The relationship between CO_2 assimilation, photosynthetic electron transport and water–water cycle in chill-exposed cucumber leaves under low light and subsequent recovery. *Plant, Cell & Environment, 27*, 1503–1514.

Zhu, J.-K. (2003). Regulation of ion homeostasis under salt stress. *Current Opinion in Plant Biology, 6*(5), 441–445.