Strategies for Improving Tolerance to the Combined Effect of Drought and Salinity Stress in Crops

8

Himanshu Sharma, Archana Kumari, Om Prakash Raigar,
Gaurav Augustine, Vikas Verma, Chayanika Lakhar,
Arshvir Kaur Boparai, Hitashi Aggarwal, Aman Kumar,
and Ashutosh K. Srivastava

Abstract

Abiotic variables such as water, light, nutrients, and temperature play a crucial role in optimizing growth and development of plants. The interplay of these variables results in significant yield losses in major agronomic crops, thereby putting global food security at risk. In recent times, the abiotic stress factors have been intensified by climate change, resulting in decreased crop yield and making global food security an implausible dream for agriculturists, policy makers, and researchers. Drought and salinity are two of the most important environmental factors hampering agricultural productivity worldwide. The concurrence of abiotic stress causes morphological, physiological, biochemical, and metabolic changes in plants, affecting their growth, development, and productivity. The responses of crops to this combined stress are complicated and are influenced by the severity and duration of these abiotic and other factors. In the present chapter, synergistic effects of drought and salinity stress on plant physiological processes, growth, and behaviour have been explained. Moreover, we have focused on the morphological, physiological, biochemical, and metabolic responses of plants to these combined stresses, underlying mechanisms that confer abiotic stress tolerance and key strategies for developing climate resilient crop.

H. Sharma · A. Kumari · O. P. Raigar · C. Lakhar · A. K. Boparai
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India

G. Augustine · V. Verma · H. Aggarwal · A. Kumar
School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana, India

A. K. Srivastava (✉)
Department of Basic Science, Rani Lakshmi Bai Central Agricultural University, Jhansi, Uttar Pradesh, India

A. Kumar et al. (eds.), *Salinity and Drought Tolerance in Plants*,
https://doi.org/10.1007/978-981-99-4669-3_8

Keywords

Abiotic stress · Physiology · Salinity · Drought

8.1 Introduction

Environmental factors that affect plants growing in the field include salt, drought, and extremes in temperature. Plants might be subjected to two or more stressors at any same moment (e.g., drought and salinity). Drought, which affects almost 40% of the world's geographical area, is the stress that has the greatest impact on global agriculture. According to Trenberth et al. (2014), it is anticipated that global climate change would result in high temperatures and more severe, persistent drought in several regions of the world, which will have a significant influence on agricultural growth and output. A significant factor reducing agricultural output in addition to drought is salt. According to estimates, salinity has an impact on around 7% of the planet's geographical surface. The combined areas of soils impacted by salt and drought are 10.5 million km^2 and 60 million km^2, respectively (Rozema and Flowers 2008). These territories encompass all places impacted by salt and drought across the world, including those that aren't necessarily arable. Maintaining global food supplies for the expanding population has proven to be extremely difficult due to the loss of farmable land caused by either salinity or drought. Thus, there is an urgent need to develop and apply key strategies for improving tolerance to combined effect of drought and salinity stress in crops.

8.1.1 Physiological Response of Drought and Salinity Stress

Constant exposure of plants to the fluctuating environmental conditions especially when these conditions are extreme leads to stress in plants. In many crops, these stresses affect the plant growth, biomass, ion toxicity, osmotic stress, and net photosynthetic rate. The accumulation of salt not only inhibits the plant growth but also reduces water and nutrient uptake, resulting in osmotic or water deficit stress in plants. In some crops such as wheat, it was observed that due to combined stress of drought and salinity, the plants become necrotic resulting in significant reduction of root length, plant height, chlorophyll content, and biomass. Similarly, drought stress in sorghum leads to chlorophyll content reduction and promotes leaf senescence, which further leads to the lower grain yield. The growth of panicle exertion and peduncle length were also found to be affected due to the stressed conditions. Under ambient temperature, the drought stress in plants occurs due to low soil and atmospheric humidity following deficiency of water for normal growth of plants, and in response to this, the plants adapt their water balance to improve water uptake or to reduce water losses. In response to the drought stress, plant reacts in these ways: avoidance, tolerance, and escape (Fig. 8.1) (Ngara and Ndimba 2014).

Fig. 8.1 Diverse abiotic stresses affect the plant and their physiological responses

Stress escape is the situation in which plant avoids the drought period by early maturing or completing life cycle before severe water deficient conditions, and this attribute is suitable for late-season drought stress environments. These varieties have early flowering, high photosynthetic capacity, lower total evapotranspiration, and lower yield potential. Avoidance is the plant ability to maintain higher hydration level/leaf water content under atmospheric or soil water stress conditions. These plants are characterized with small leaf area and reduce transpiration by stomatal closure, leaf rolling, and wax accumulation on leaf surface in water deficient conditions. In some cases, in response to water deficient conditions, the roots of the plant start synthesizing ABA which is transported through xylem from roots to leaves. To avoid water stress conditions, ABA plays an important role by affecting the stomata closure, leaf expansion reduction, and enhancing root growth. The stress tolerance ability of the plants means that as compared to the other plants under stress conditions, the tolerant plants will experience significantly lower level of changes. These plants attain tolerance by improving ability of osmotic adjustment and maintaining tissue turgidity by increasing cell wall elasticity.

8.1.2 Biochemical Response

These drought and salinity stresses lead to the oxidative stress in the plant cell which increases the electron leakage toward O_2 during the processes of photosynthesis and respiration resulting in enhancement of ROS such as H_2O_2, O_2, and hydroxyl radical (HO) generation (Xie et al. 2019). The salinity stress in plants which are exposed to high NaCl soils leads the accumulation of Na^+ and Cl^- ions in plant cells causing severe ion imbalance. Higher Na^+ concentration in plants during stress inhibits the K^+ ion uptake, which plays an important role in the plant growth and development leading to lower productivity and possibly plant death. Under combined (D + S) stress, the stomatal closure and leaf conductance were decreased in wheat plants which leads to the inhibition of CO_2 diffusion to carboxylation site and resulted in reduced photosynthetic uptake. The effects of salinity and drought on photosynthesis are attributed directly to the stomatal limitations for diffusion of gases which ultimately alters photosynthesis and the mesophyll metabolism (Dubey 2018).

8.1.3 Solute Accumulation

Under stress conditions, the concentration of other amino acids such as cysteine, arginine, and methionine decreases, whereas the proline concentration rises. Intracellular accumulation of proline during the salinity stress along with tolerance to the stress also serves as reservoir for organic nitrogen during the recovery under stress. For example, in rice, it was observed that the pretreated seeds with 1 mM proline produced rice seedlings which exhibited improved growth during salt stress. Glycine betaine (nontoxic cellular osmolyte) accumulation is found in large number of plants during stress (Hussain Wani et al. 2013). It plays important role under stress conditions, by raising the cell osmolarity, cell protection by osmotic adjustment, ROS reduction, and protecting photosynthetic apparatus from damages due to stress. Accumulation of glycine betaine is found in a wide variety of plants belonging to different taxonomical background.

In some plants, the accumulation of carbohydrates like sugars (fructose, sucrose, trehalose, and glucose) and starch under salt stress was also found to mitigate the stress by carbon storage, osmoprotectants, and scavenging of ROS (Goyal et al. 2023). During salt stress, accumulation of trehalose in the plant cell protects the plant from several physical and chemical damages (Sadak 2019). In rice roots, the content of starch under drought and salinity stress was observed to be low, while in the shoot, its concentration was not that much affected (Beckles and Thitisaksakul 2014).

8.1.4 Molecular Response

8.1.4.1 Genetic Basis of Drought and Salinity Stress Resistance

The traits responsible for drought and salinity stress tolerance such as yield stability, leaf rolling, root growth, ABA accumulation, osmotic adjustment, resistance to flower shedding, seedling recovery, and sustained formation of pod under stress are controlled by various major as well as minor genes. The characters of the leaf like waxy leaves and traits such as accumulation of ABA (wheat), proline accumulation (barley), and pod formation (French bean) are under the control of oligogenes (Rauf et al. 2016). On the other hand, the other remaining traits for drought or salinity stress are considered to be determined by the polygenes.

8.1.4.2 QTL Identification

There are many QTLs responsible for the abiotic stress tolerance. In many crop species, these QTLs for abiotic stress tolerance were identified and transferred to susceptible lines using linkage mapping and molecular markers linked to these QTLs through marker-assisted selection (MAS) such as QTL for osmotic adjustment in rice; for proline accumulation in *Brassica* species; for drought tolerance in rice, barley, and maize; or for salt tolerance in rice (Sahebi et al. 2018). However, due to some problems like linkage drag and the effect of environment, the transfer of marker linked QTL is limited. But new genomic approaches like next-generation sequencing (NGS), genome wide association study (GWAS), and CRISPR/Cas9 make it easier to identify and transfer these QTLs by providing genetic maps with better resolution and precisely locating the QTL position on the chromosome (Fiaz et al. 2019). The combination of genomic studies and transcriptomic analysis enhances the precision of identifying new genes and regulatory systems and their positions.

8.1.4.3 Transgenics

The transgenic plants with the overexpressing ion transporters, transformed with tissue-specific AtNHX1 gene from same species encoding for Na^+/K^+ antiporter, showed improved tolerance to NaCl and accumulated salt in leaves in many crops like *Arabidopsis thaliana* and tomato (Li et al. 2017). The manipulation of specific metabolic pathways and enhancing the cellular levels of particular osmolytes were also done in some crops to improve the abiotic stress tolerance. For example, in rice, the plants were transformed with choline oxidase gene, i.e., *codA*, resulting in higher levels of glycine betaine and simultaneously increasing tolerance to salinity (Bhowal et al. 2021). Similarly, in tobacco, the expression of 1-pyrroline-5-carboxilase synthetase leads to higher proline levels improving drought and salinity tolerance.

8.1.4.4 Activation of Antioxidant Systems

In response to abiotic stress conditions, transgenic plants with enhanced stress tolerance activates the antioxidant system by expressing different antioxidant enzymes like glutathione *S*-transferase/glutathione peroxidase in tobacco or superoxide dismutase in alfalfa and by expressing specific proteins to confer tolerance against abiotic stresses such as heat shock proteins (HSPs), LEA proteins, or transcription factors (Srivastava et al. 2019). There is another approach to increase the stress tolerance used in GM plants which involves overexpression of stress target proteins. In *A. thaliana*, two genes encoding the SR-like splicing factors were isolated from its cDNA library, and their expression in these transgenic plants of *A. thaliana* resulted in salt and drought tolerance (Naranjo et al. 2006).

8.2 Traits Which Are Crucial for Combined Salinity and Drought Stress Tolerance

Plants are frequently exposed to one or more abiotic stresses, including combined salinity and drought, which significantly lower plant growth. The two main abiotic stressors that interfere with plant growth and productivity are salinity and drought (Gull et al. 2019). Due to climate change, both salinity and drought stresses are gradually becoming more severe in many places, mainly in arid or semiarid areas (Manneh et al. 2007). Drought is frequently associated with salinity stress in coastal, arid, and semiarid regions. When the soil water evaporates, the salts become concentrated in the soil solution, resulting in combined drought and salinity (Angon et al. 2022). In general, the co-occurrence of many abiotic stresses is worse for crop output than a single stress event. For instance, the combined effects of salinity and drought on yield are more detrimental than the effects of each stress alone, as observed in barley (Yousfi et al. 2010), wheat (Yousfi et al. 2012), and potato. However, several studies to date have addressed the effects of single stresses on plant, and little is known about the physiological and molecular mechanisms underlying the acclimation of plants to a combination of salinity and drought (Zhao et al. 2020; Wu et al. 2013).

Adapting to unfavorable environment for growth and development is a common task for plants. A promising way of doing so is to identify measurable traits/parameters that are affected by combined stress conditions, which can be modified positively to improve crop productivity under combined stress conditions (Stokes and Inman-Bamber 2014). For example, a plant has evolved morphological and physiological adaptations, as well as signaling pathways that trigger biochemical and molecular mechanisms, to tolerate these extreme climatic circumstances. Some plants evolved with adapted characteristics to survive in harsh conditions including marshes, tundra, and deserts. By making morphophysiological adjustments, such as regulating stomata, reducing the number of leaves or their area, accumulating wax, improving the root system's ability to absorb available water, and using less water overall, it is possible to prevent droughts (Shelake et al. 2022). In the section below, we focus some important traits that can be used for crop improvement under combined salinity and drought stress.

8.2.1 Root System Architecture

Root system architecture has a dominant role in crop plants' response to abiotic stresses. Since roots grow underground, they are the first to sense abiotic stresses and adjust their genetic program for postembryonic development to survive the stress (Guo et al. 2009). Different abiotic stresses affect RSA in various ways. Deeper roots are associated with increased acquisition of water and mobile nutrients like N that may leach to lower soil layers (Lynch and Wojciechowski 2015). To prevent dehydration under mild or severe drought stress, the roots may alter their architecture and resource allocation (Smith and De Smet 2012; Hasibeder et al. 2015). However, under extreme dry stress, the roots shrivel, and the photosystem II in the leaf malfunctions (Fathi and Tari 2016).

8.2.2 Leaf Rolling and Stomatal Aperture

Leaf rolling is one of the consequences of turgor pressure adjustment observed in diverse plants when they are exposed to limited water environments. Leaf rolling during the stressful time decreases the leaf area, which in turn decreases the area that may be used for evapotranspiration and hence represents a drought acclimation response. Leaf rolling is a classic indication of soil water deficiency in wheat, as it is in other cereals. Leaf rolling is a classic indication of soil water deficiency in wheat, as it is in other cereals (Kadioglu et al. 2012). Early reactions to salinity and drought are quite similar because both cause water stress, which slows development, reduces stomatal aperture, and results in nutrient deficiencies (such K^+ and Ca^{2+}) (Pirasteh-Anosheh et al. 2016).

8.2.3 Canopy Temperature

According to Mason and Singh (2014), canopy temperature is a physiological trait that reflects crop water status, which is a recognized proxy for stomatal conductance (Deery et al. 2019). Canopy temperature has the potential to be an extremely helpful tool for the indirect selection of genotypes that are tolerant to heat and drought stress (Reynolds et al. 2010). Genotypes that retain cooler canopies are more likely to flourish in such conditions. It has been noted that canopy temperature is typically lower in deep-rooted genotypes because the crop may draw moisture from a deeper soil depth (López-Urrea et al. 2012). Canopy temperature and stomatal density may be effective measure of drought tolerance of wheat cultivars and yield improvement under drought stress conditions (Srivastava et al. 2017)

8.2.4 Osmotic Adjustment

Osmolytes or compatible solutes are small molecules sometimes known as osmoprotectants or osmolytes, have low molecular weights, and are water soluble and nontoxic at molar concentrations that enhance the cell potential to maintain turgor potential without hampering the normal physiological processes. Thus, damaging effects of drought are minimized by accumulation of solutes in cellular cytoplasm and vacuole (Taiz and Zeiger 2006). Osmotic regulation, antioxidant metabolism, and preservation of cell membrane stability are main defense strategy against abiotic stress. Plant cells enthusiastically accumulate solutes when cellular dehydration occurs as part of osmotic adjustment. Under salt, drought, and cold stresses, metabolic-compatible substances can accumulate in greater quantities and are key drivers of osmotic adjustment. They also aid in stabilizing membranes, protecting proteins' quaternary structures, and neutralizing poisonous substances which are the main tactics used by numerous creatures to overcome environmental stress (Abid et al. 2018). The most popular compatible substances are sugars (sucrose and trehalose), polyols (mannitol and sorbitol), polyamines (putrescine, spermine, and spermidine), amino acids (glutamine and proline), and quaternary amines and compatible solutes (glycine betaine and choline-O-sulfate) (Singh et al. 2015; Zulfiqar et al. 2021). Plants accumulate Osmoprotectants such proline, glycine betaine, and sugars as a result of an induced change in osmolarity. Increased proline levels in the niger showed an effective osmotic adjustment, which is consistent with findings in salt-stressed tobacco, sorghum, and *Sesuvium portulacastrum* (Çelik and Atak 2012; Kahrizi et al. 2012; Rajaravindran and Natarajan 2012; Deinlein et al. 2014).

8.3 Different Reactive Oxygen Species (ROS) Produced During Drought and Salinity Stress

The generation of ROS is a fundamental process in higher plants to transmit cellular signaling information in response to the changing environmental conditions. Different ROS are produced by the unavoidable leakage of electrons on to O_2 from the electron transport systems of chloroplasts, mitochondria, and plasma membranes or as a consequence of various metabolic pathways. Osmotic effects caused by salinity and drought change fundamental metabolic and enzymatic functions, increasing the production of reactive oxygen species (ROS). The main ROS include singlet oxygen ($^1O_2$), hydroxyl radicals (OH), superoxide anion (O_2), hydrogen peroxide (H_2O_2), and the latter two each of which have a distinct half-life and oxidizing potential (Apel and Hirt 2004; Miller et al. 2010; Hasanuzzaman et al. 2021).

Reactive $^1O_2$ can be efficiently quenched by small lipophilic compounds such as β-carotene and tocopherol or by a scavenging action of protein D1 protein present in photosystem II (Krieger-Liszkay 2005). However, minor portion of $^1O_2$ is able to diffuse to a smaller distance, where it can react with diverse biomolecules and potentially mediate its signaling pathways (Dogra et al. 2018). The superoxide radical ($O_2^{\bullet -}$) is formed mainly in the thylakoid-localized PSI during noncyclic electron transport. Its production is one of the responses to the pathogens that burst rapidly and transiently. It is mediated by NADPH oxidases, belonging to the respiratory burst oxidase homolog (RBOH) family (Sang and Macho 2017). Usually, H_2O is generated when cytochrome c oxidase interacts with O_2, and sometimes, it reacts with the different components of ETC to give $O_2^{\bullet -}$. Reactive $O_2^{\bullet -}$ often undergo further reactions to generate $_1O^2$, H_2O_2, and •OH (Janků et al. 2019). Several recent studies have demonstrated that H_2O_2 is involved in stress signaling pathways, which can activate multiple responses that strengthen resistance to various biotic and abiotic stresses (Petrov and Van Breusegem 2012; Molassiotis et al. 2016). Highly reactive •OH promotes oxidative cleavage of pectin and xyloglucans, thus causing cell elongation by loosening the cell wall. Drought stress increases Fe and Cu availability for Fenton reactions and could cause increased •OH production. There is potential of •OH for an impact on atmospheric methane levels, and after the plant's death, •OH contributes to its recycling into soil organic matter. Because cells have no enzymatic mechanism to eliminate •OH, its excess production can eventually lead to cell death (Pinto et al. 2003; Demidchik 2015; Richards et al. 2015).

8.3.1 Antioxidative Defense

If prolonged to a certain extent, drought stress or salinity stress alone or in combination inevitably resulted in oxidative damage due to the overproduction of reactive oxygen species. Reactive oxygen species (ROS), also called active oxygen species (AOS) or reactive oxygen intermediates (ROI), are the result of the partial reduction of atmospheric O_2. Both salt and drought can cause the production of reactive oxygen species (ROS) like superoxide, singlet oxygen, hydrogen peroxide, and hydroxyl radicals inside of plant cells. The overproduction of ROS causes oxidative damage to mainly cell membranes, proteins, lipids, and nucleic acids, causing oxidative stress (Gill and Tuteja 2010). The upregulation of antioxidant enzymes represents an important marker for drought stress (Laxa et al. 2019). In order to cope with the oxidative stress, plants usually rely on effective enzymatic antioxidant defense system, including catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and superoxide dismutase (SOD) as well as nonenzymatic antioxidant defense system, including ascorbate, flavonoids, glutathione, tocopherols, and phenolics, involved in removing high levels of ROS. Some plants such as *Calendula officinalis*, *Solanum lycopersicum*, *Jatropha curcas*, and *Zea mays* have been discovered to upregulate antioxidant activity under drought and salinity stresses (Chaparzadeh et al. 2004; Mittova et al. 2004; Gao et al. 2008; Anjum et al. 2017). Similarly, by strengthening the resistance of host plants to oxidative damage, maintaining a high level of antioxidative enzyme activity significantly reduces the effects of drought or salt stress.

8.4 Strategies to Improve Combined Stress Tolerance

8.4.1 Breeding Approaches for Developing Combined Stress Tolerance

Drought and salinity are major abiotic stresses that severely affect agricultural yields. Combined stress of drought and salinity severely affects physiological, biochemical, and metabolic activities/processes of plant as compared to independent either drought or salinity. Earlier breeders concern about the improvement of either drought or salinity tolerance using classical breeding techniques, due to ever changing weather climatic changes and degradation of soil and water quality by extensive use of groundwater for agriculture. Degrading soil quality and poor groundwater conditions along with uneven distribution of rainfall create salt accumulation on top most soil layer (for crop growth and development) combined with drought. Therefore, to address the negative impact of combined drought and salinity stress on crops, there is a need to adopt new classical techniques to advance breeding strategies/approaches by using wild relatives and landraces, introducing elite breeding lines, inducing mutants, transferring beneficial quantitative trait loci (QTLs) genes, and altering gene metabolites into a commercially adopted well-known cultivars/varieties of crop plants (Kaur et al. 2023). Different breeding strategies that can be utilized for combined drought stress tolerance for traits viz., earliness, lesser number of stomata per unit area on leaves, thick and small leaves, leaf and stem waxiness, deep root system, determinate growth habit with salinity stress tolerance traits viz., osmoprotectant proteins, osmolytes, metabolites, stress protein transport, stomatal conductance, cell wall modification and root architectural changes. We can develop genotypes for both stresses using evaluation of large set of germplasm through artificial intelligence with molecular markers (SSR and SNPs), mutation breeding, haploid induction, mapping of QTLs/genes, marker-assisted selection (MAS)/marker-assisted backcross selection (MABC), advanced backcross QTL mapping, gene introgression, and gene pyramiding (Fig. 8.2). Now a days recent advances in modern plant breeding that exploits for generation of targeted mutations at desired loci/genic regions in plant genomes (Shelake et al. 2019) using genome editing tools that enable fast-track introgression of novel trait of interest into crop varieties (Shelake et al. 2019, 2022) represented in Fig. 8.2.

8.4.2 Searching for Drought and Salinity Stress Tolerance Germplasm

A lot of efforts have been invested by plant breeders and geneticists after the rediscovery of Mendel's laws, for the identification of desirable germplasm for drought tolerance, salinity tolerance, and both using accessions from primary center of origin to hot spots of crop diversity, landraces, and wild relatives for different crops. Earlier breeders use large-scale screening of germplasm using morphophysiological parameters for drought and salinity separately. These are very laborious and time-consuming and require experienced personnel. With the advancement of evaluation techniques, genetic inheritance, molecular markers, modification of germplasm, and mapping techniques also facilitate the improvement in crop plants for salt and drought tolerance (Deshmukh et al. 2014). A molecular marker increases the selection intensity for a trait of interest. Nowadays, advances in artificial intelligence (AI) along with molecular data of the genotype will increase selection efficiency by reducing the environmental variation for quantitative traits (salinity and drought tolerance). So through molecular techniques along with AI, we can easily identify simultaneously tolerant germplasm for drought and salinity in large population.

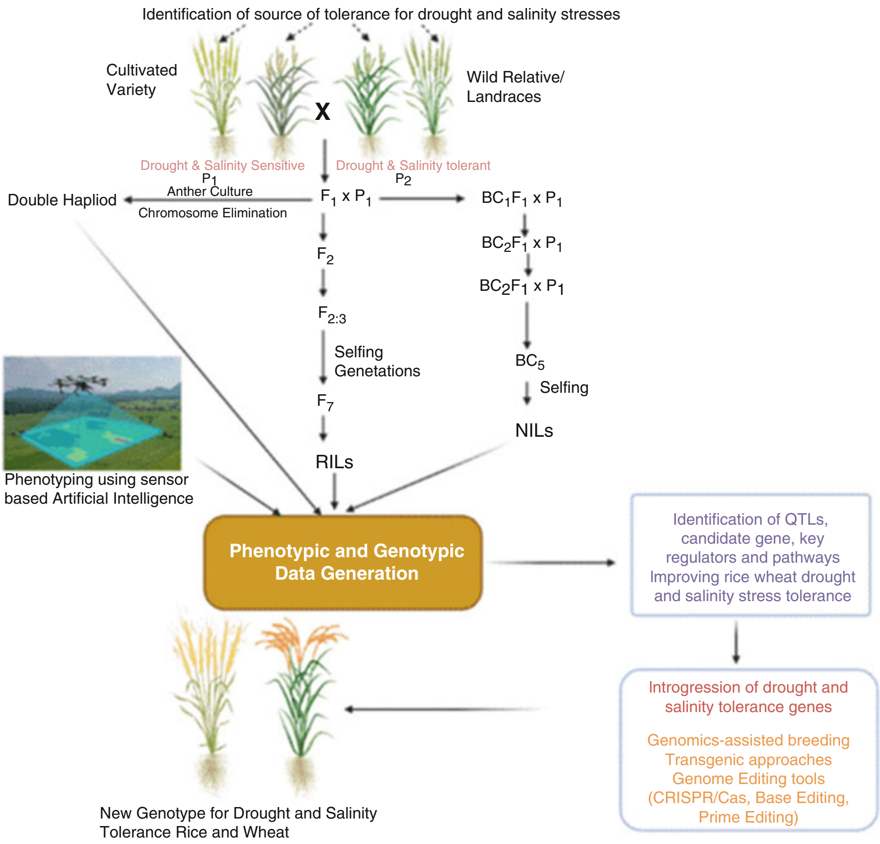

Fig. 8.2 Advanced breeding tools for development of drought and salinity tolerant genotype

8.4.3 Double Haploid

Double haploid (DH) production through anther culture, ovary culture, and chromosome elimination technique emerged as a new breeding tool having advantage by reducing the breeding cycle, homozygosity fixation, high selection efficiency, and expression of recessive alleles suitable for breeding. Guha and Maheshwari (1964) introduced the first haploid embryos and plantlets through anther culture of *Datura innoxia*. In this tool, we first developed haploid plantlets than diploidization of haploids artificially using genome doubling agents (i.e., colchicine treatment). DH technology can be utilized for fixation of desirable trait combination in an elite cultivar, and it will be used for the mapping of QTLs/genes controlling quantitative traits such as salt and drought tolerance. DH can be deployed for development of drought and salinity by using anther culture (rice, wheat, maize), ovary culture (wheat), and chromosome elimination technique, i.e., wheat × *H. bulbosum* (Inagaki 1985), wheat × maize (Laurie and Bennett 1988; Bains et al. 1998; Campbell et al.

1998), wheat × *Imperata cylindrica* (Chaudhary et al. 2005), *Hordeum vulgare* × *H. Bulbosum* (Kasha and Kao 1970), and inducer Stock 6 in maize (Lashermes and Beckert 1988). These techniques of haploid production can be utilized for the production of haploid from the hybrids of wild relative/landraces and simultaneously produce haploids having both drought and salinity tolerance traits within a shortened time periods using cytogenetic techniques such as genomic in situ hybridization (GISH) and FISH (fluorescence in situ hybridization) (Sharma et al. 2022a).

8.4.4 Mutation

Mutation is used to create genetic variation; if such variations are not present in population, then these mutant variants can be deployment for development of new varieties. A major key point in mutation breeding is identification of desirable mutation linked with trait of interest involving two steps: first screening out the mutant and then second confirmation of mutants (Forster and Shu 2012). In mutation breeding, the seeds/plant propagating materials are treated with mutagen (X-rays, gamma rays, chemical mutagens, and fast neutrons) with desired concentration at which plant shows LD 50% than grown for segregation and recombination and selection of salinity and drought tolerance plants and further grow for next generation to stabilization of mutant alleles.

Multiyear and location trials are conducted for evaluation of stable mutant for release of a new variety with trait of interest (Oladosu et al. 2016). Salt oversensitivity is achieved through mutation in barley that enhanced salinity tolerance through ion homeostasis (i.e., M4-73-30 and its wild-type cultivar). These two genotypes showed differential expression of HVA, HvSOS3, HvSOS2, and HvSOS1 genes in the roots of barley. And there is more Na^+ accumulation in shoot tissues of wild-type than mutant because sodium ion transfer from root to shoot is in the mutant type, i.e., salt tolerant (Yousefirad et al. 2018). Lethin et al. (2020) developed a mutant of wheat variety BARI Gom-25 using EMS (ethyl methanesulfonate) that showed semi-tolerance to salinity.

8.4.5 Wild Relative Exploitation

Wild relatives of crops are utilized as a source of biotic and abiotic stress tolerance using interspecific hybridization. Hybrid from wild relatives had lot of embryo and endosperm growth and developmental associated barriers. So it requires specialized methods/techniques for embryo rescue from those hybrids. Salt tolerant wild relatives of rice, *Oryza coarctata* (halophytic relative), was identified as a source which can be exploited for transferring salt tolerance QTL/genes into elite cultivated lines through marker-assisted backcrosses (Mishra et al. 2016; Garg et al. 2013).

8.4.6 QTL Mapping

Identification of genomic regions associated with drought and salinity tolerance can be done through different types of mapping populations, molecular marker, genomic sequencing, and statistical approaches. Zang et al. (2008) identified salt tolerance QTLs at seedling and tillering stages using introgression lines derived from IR64 (indica) × Binam (japonica). Yun et al. (2012) use BC2F8 advanced backcross introgression lines derived from Teqing × Binam in Teqing background for identification of both drought and salt stress tolerance QTL governing traits, i.e., days to seedling survival, score on salt toxicity symptoms on leaves, shoot K^+ concentration, shoot Na^+ concentration at seedling stage, panicle number per plant, thousand grain weight, seed fertility, plant height, and grain yield per plant.

8.4.7 Gene Introgression and Marker-Assisted Breeding

Introgression is the transfer of genes between crop species, which is mediated primarily by backcrossing. Introgressiomics is an extensive systematic improvement of plant genomes and populations through introgressions of fragments of genome from crop wild relatives into the genetic background of prevailing crops in order to develop new cultivars having desirable traits. Due to introgression, rampant gene flow may occur between species where their distribution patterns overlap and they interact so much that introgression has been described as an “invasion of the genome” (Mallet 2005). About 25% of plant species are known to hybridize with at least one other species (Mallet 2005; Schwenk et al. 2008). Greater genomic plasticity can be obtained in a crop using exotic genetic material that was previously nonexistent within the genome through introgression. This strategy can have myriad effects, and though it is most commonly thought to be deleterious, introgression may also provide the raw genetic materials for adaptation and speciation (Arnold and Martin 2009; Suarez-Gonzalez et al. 2018). However, a major limitation when assessing introgression is the availability of genetic resources to accurately estimate interspecific gene flow.

Changes in climatic conditions led to the emergence of various biotic and abiotic stresses which are becoming a major threat limiting crop production and productivity (Gautam et al. 2013). Thus, broadening the crop genetic base will serve as armor against these rising challenges under climate change. The crop wild relatives (CWRs) are known to possess useful alien alleles and cryptic genetic variation, which are introgressed and expressed in cultivated gene pool (Pratap and Gupta 2009). Recent advances in breeding and genomic tools and techniques provide an opportunity to introgress useful alleles left behind in the secondary and tertiary gene pool into the elite background useful for breeders. For crop improvement, genetic engineering strategies are relatively faster than traditional breeding programs, as well as cloning of genes responsible for imperative traits and introgression into plants.

Drought and salinity are the major abiotic stresses that dramatically cause threat to the food security in the world. *Triticum dicoccoides* and *Hordeum spontaneum*, the progenitors of cultivated wheat and barley, have adapted to a broad range of environments and developed rich genetic diversities for drought and salt tolerances. Drought- and salt-tolerant genes and quantitative trait loci (QTLs) have been identified in *T. dicoccoides* and *H. spontaneum* and have great potential in wheat and barley improvement. Advanced backcross QTL analysis, the introgression libraries based on wild wheat and wild barley as donors, and positional cloning of natural QTLs will play critical roles in elucidating the molecular control of drought and salt tolerance. Combining tolerant genes and QTLs in crop breeding programs can be aimed at improving tolerance to drought and salinity (Nevo and Chen 2010).

Root architecture traits are an important component for improving water stress and salinity adaptation. Considerable genetic variation exists for root-related traits in major crops such as wheat, rice, and maize (*Zea mays*) in both the domesticated species and wild relatives (Ribaut et al. 2009; Gowda et al. 2011). The presence of the rye-wheat translocation (1RS) reduced central metaxylem diameter, a trait that has been associated with drought tolerance in wheat (Richards and Passioura 1989; Sharma et al. 2010). Several *Agropyron* species and wheat 3 *A. elongatum* lines have been reported to enhance tolerance to abiotic stresses, including drought, waterlogging, and salinity (Dvorák et al. 1988; McDonald et al. 2001). The physiological and molecular consequences of introgressing an alien chromosome segment (7DL) from a wild wheat relative species (*Agropyron elongatum*) into cultivated wheat (*Triticum aestivum*) were studied by Placido et al. (2013). The wheat translocation line had improved water stress adaptation and higher root and shoot biomass compared with the control genotypes. The transcriptome analysis identified candidate genes associated with root development, and two of the candidate genes mapped to the site of translocation on chromosome 7DL based on single-feature polymorphism analysis.

8.4.8 Use of High-Throughput and Automated Phenotyping Techniques

The slow pace, high costs, and inconsistencies associated with trait quantification and data management using traditional phenotyping techniques still limit the progress of drought tolerance improvement. This could, also, have been contributing to the complexities of understanding the genetic and physiological basis of drought tolerance both at the phenotypic and the genomic level (Xu and Crouch 2008). The utilization of sophisticated, nondestructive, high-throughput phenotyping technologies with automated systems for capturing, storage, and statistical analysis of large volumes of data allows for fast and precise large-scale quantification and monitoring of various phenotypic traits (Araus and Cairns 2014). Ground and remote sensing techniques based on near- or far-infrared reflectance digital sensors, thermometers, and cameras are reported to precisely measure various phenotypic traits (Araus and Cairns 2014; Honsdorf et al. 2014). These include automated camera systems which are connected to computers for monitoring complex root architectural traits through periodic image capturing. Some of these tools are graced with image processing and analysis software. These advanced phenotyping technologies may create local databases for easy management of the vast amounts of data that will be generated.

8.4.9 Omics: Genomics, Phenomics, Metabolomics, Achievements

Plant ecology is a very complicated and interconnected system. For an edge in crop development, it is crucial to comprehend the fine-tuning and integration of various signals produced by environmental interactions in the plants. Multiple biotic and abiotic environmental challenges must be overcome by a plant. The outcome of the plant-environmental interaction may be controlled by prioritizing physiological pathways in plants; many of these are similar to stress responses while others have negative effects. Multiple stress causes result in complicated defensive signals in plants. The molecular and cellular processes behind abiotic stress adaptation in cereal crops have been extensively studied. The control of genes affects a plant's response to drought, high temperatures, and salt (upregulation or downregulation). In this context, multi-omics techniques can be used to tackle the difficult issue of figuring out changes in plants at the genomic, proteomic, or metabolomic level in order to unravel the causes.

8.4.10 Genomics

Crop development projects have greatly benefited from the use of genomics-based technology. The use of molecular markers, QTL mapping, genetic mapping, comparative genomics, the intricate interactions between plants and their environment, and expression quantitative trait loci have all made genomic and systems biology methods to the discovery of stress tolerant phenotypes possible. These methods can offer a useful method for locating candidate genes implicated in the ability to withstand abiotic stress. Thus, a large number of genomic information in the form of sequenced genomes and expression profiles are driving the development of breeding techniques for stress reduction (Fig. 8.3) (Tomar et al. 2014).

The discovery of restriction fragment length polymorphisms (RFLPs) and the subsequent correlation of these variants with a number of major agronomically significant variables presaged the promises of genomics to increase genetic variation per unit time in the 1980s. Later, numerous different marker systems were employed to map quantitative trait loci, most notably microsatellite or simple sequence repeat (SSR) markers (QTLs). However, despite their excellent usage in finding the polymorphisms and in applied breeding, these methods had limited throughput and were time- and cost-inefficient. For instance, there were only 279 loci on the first SSR map of wheat (Röder et al. 1998). According to Koussevitzky et al. (2008), the cytosolic ascorbate peroxidase 1 gene Apx1 is especially needed for *Arabidopsis* to be tolerant to drought and heat stress. Ectoine, a suitable osmolyte, is in charge of *Halomonas elongata* OUT30018's ability to tolerate salt. Tobacco plant (*Nicotiana*

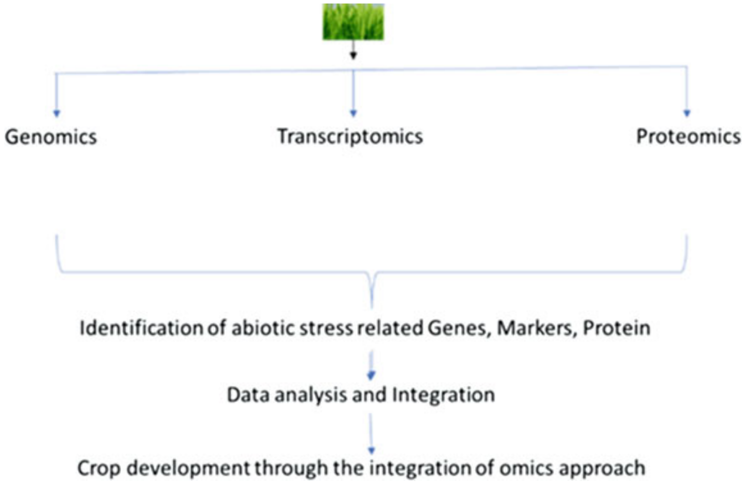

Fig. 8.3 Omics approaches for stress tolerance in plants

tabacum L.) cv. Bright Yellow 2 (BY2) was given three cloned ectoine biosynthesis genes, which increased resistance to hyperosmotic shock by accumulating ectoine and allowed it to develop normally in such circumstances (Nakayama et al. 2000). More than 15 million ha of rainfed lowland rice are under stress because of submergence in various areas of Asia (Neeraja et al. 2007). Problems with floods or anoxia affect 13% of the world's total geographical area (Cramer et al. 2011). In rice, a single main quantitative trait locus (QTL) located on chromosome 9 controls submergence tolerance (Toojinda et al. 2003). Molecular markers for the Sub1 gene were employed by Neeraja et al. (2007) in a backcross breeding effort using the recurrent parent, named Swarna. This Sub1 offers tolerance in giant varieties that are delicate. It has now been established that Sub1A is the main factor influencing submergence tolerance (Septiningsih et al. 2009). The development of submergence tolerance by marker-assisted backcrossing (MAB) has been greatly facilitated by this QTL.

Single nucleotide polymorphisms (SNPs), the smallest type of DNA variation, can be found, giving researchers the chance to examine potentially millions of DNA locations. As a result, it has become a popular site for markers. Large-scale germplasm assessments in many cereals have been made possible by high-throughput, high-efficiency, repeatability, and cheap cost per data point, which has led to the practically total replacement of RFLPs or SSR marker platforms. Both genotyping-by-sequencing and array-based genotyping are important techniques for SNP detection in grains. Both types of SNP identification may be accomplished using a variety of sequencing technologies. For the purpose of establishing the groundwork for whole-genome sequencing and determining the genetic basis of characteristics that are economically significant, high-density SNP genotyping is crucial.

Linkage mapping is the process of locating quantitative trait loci (QTLs) in segregating populations that are mostly artificially produced. Many features of economic significance are of a quantitative type, meaning that they are controlled by the coordinated action of numerous genetic loci, such as grain yield, stress tolerance, and disease resistance (Bernardo 2010). To analyze the genetic basis of a quantitative characteristic, segregating populations including practically hundreds of individuals is necessary. The development of different segregating populations, including the F2 population, recombinant inbred lines (RILs), doubled haploid (DH) population, heterogeneous inbred family (HIF), near-isogenic lines (NIL), advanced intercross recombinant inbred lines (AI-RIL), backcross inbred lines, and multiparent advanced generation intercross (MAGIC), is primarily driven by the resources available and the goals of the research. Through QTL, which can be found at the Gramene database (http://www.gramene.org/qtl/, accessed on October 5, 2022), the major cereal crops are mapped. It has QTLs for abiotic stressors such nutrient deficiency, heavy metal toxicity, salt, cold, and severe temperature. The Sorghum QTL Atlas is available online at https://aussorgm.org.au/sorghum-qtl-atlas/ containing 150 QTL and GWAS research that have been published in sorghum from 1995 to the present (accessed on October 6, 2022). It is beneficial for sorghum crop development and comparative genomics (Mace et al. 2019). The ability to identify natural differences in all recombination events that take place during the evolutionary processes of a variety of organisms makes GWAS an effective tool. SNP identification is the primary goal of the GWAS (Marees et al. 2018). To detect genetic differences based on complex variables like growth rate, blooming period, and yield, WGAS analyses complete samples using databases that contain reference plant genome sequences and genetic maps.

8.4.11 Transcriptomics

Transcriptomics is the study of gene expression patterns that can identify the genes causing abiotic stress. For abiotic stress to be managed successfully, understanding such reactions may be essential. Investigating the functional characterization of specific genes in stress tolerance systems is made possible by transcriptome profiling. For better plant genomic resources, more next-generation sequencing (NGS) and RNA sequences for short RNAs have been produced recently (Imran et al. 2021).

The high-throughput transcriptome sequencing dataset provides an efficient strategy for gene discovery, molecular marker development, and marker-assisted breeding (Munaweera et al. 2022). Typical plant responses to abiotic stress involve a network of molecules. ABA (abscisic acid) is a major phytomolecule that plays an important role in responding to a variety of stresses such as drought, heat stress, high salinity, heavy metal stress, low temperature, etc. They are also involved in various developmental processes, including seed germination, seed dormancy, and closure of stomata. ABA-dependent pathways appear to recruit antioxidant and osmoprotectant mechanisms, whereas ABA-independent pathways generally involve protective proteins (Rane et al. 2021; Khan et al. 2021).

Under abiotic conditions including drought, salt, and cold, different miRNAs in rice, *Medicago*, *Phaseolus*, *Arabidopsis*, and other plants have a regulatory function (Trindade et al. 2010). Noncoding RNAs called miRNAs, which have a length of 19–23 nucleotides, have a regulatory function in a number of biological processes (Budak et al. 2015). *Arabidopsis* overexpressing osaMIR393 exhibits tolerance to salt overload, and miR393 regulates this tolerance (Gao et al. 2011). According to Zhao et al. (2009), miR169 reduces the stress caused by salt and drought in rice via altering the expression of a nuclear transcription factor called YA (NF-YA). Drought resistance is conferred by tomato plants that overexpress the miR169c gene, which regulates the expression of the gene(s) involved in stomatal activity. WD-repeat proteins, which are essential for cucumber stress tolerance, are regulated by Bvu-miR13 (Li et al. 2015). MiRNAs target stress signaling pathways, which are involved in root development, leaf morphogenesis, and stress response, in addition to regulating TFs (Curaba et al. 2014). In silico analysis was used to identify 13 mature miRNAs in *B. vulgaris* plants (Li et al. 2015). Superoxide dismutase SOD1 and SOD2 mRNA activity is targeted by miR398 that plays a function in decreasing ROS and subsequent consequences of abiotic stress (Kantar et al. 2011). Distinct kinds of miRNAs regulate different cellular responses to stress and metabolic functions such transcriptional control, auxin homeostasis, ion transport, and apoptosis (Li et al. 2010). Additionally, it has been discovered that plants' responses to aluminum stress are regulated by miRNA (Lima et al. 2011). MiRNA expression in two distinct rice subspecies, japonica and indica, with variable levels of aluminum tolerance, was compared. The use of RT-qPCR identified 16 different types of miRNA responses, demonstrating a complicated response to aluminum stress.

The impacts of water stress, salinity stress, and combination stress were disclosed by Osthoff et al. (2019). Transcriptome sequencing was carried out in this study 6 and 24 h following the stress treatment. The gene expression responses that were shown at 6 h of stress are still present at 24 h. However, compared to a 6-h stress treatment, hundreds of genes were further altered after 24 h. Nine hundred fifty-three genes showed differential expr bHLH (basic Helix-Loop-Helix), ERF (Ethylene Response Factors), and HSF (Heat Shock Factors) transcription factors that have all been enriched at each time point under the three shocks (6 and 24 h). Additionally, the bZIP was enriched following both combined stress and water deficiencies at both time periods. After 24 h of treatment, salt stress, bZIP, G2-like, and HD-ZIP TFs were enriched, while 1802 genes did so following a 24-h salt therapy. bHLH (basic Helix-Loop-Helix), ERF (Ethylene Response Factors), and HSF (Heat Shock Factors) transcription factors have all been enriched at each time point under the three shocks (6 and 24 h). Additionally, the bZIP was enriched following both combined stress and water deficiencies at both time periods. After 24 h of treatment, salt stress, bZIP, G2-like, and HD-ZIP TFs were enriched.

The differently expressed genes in bread wheat across the salt-tolerant and sensitive cultivars were also discovered by comparative transcriptome analysis following a 150 mM salinity treatment. Five thousand one hundred and twenty-eight genes were differently expressed between salt-treated and control plants, according to the findings. One thousand nine hudred and ninety-five genes among them showed an upregulation, and 3133 genes showed a downregulation. In addition, 109 and 210 genes, respectively, were discovered to express themselves exclusively in salt-treated and control plants (Amirbakhtiar et al. 2019).

8.4.12 Proteomics

The development of genomic technologies has altered the way we study biological systems by giving us a blueprint for potential gene products. The lack of a link between mRNA and protein quantity owing to posttranslational modifications, protein function, and localization results from the static nature of the genome. Therefore, it is crucial to research protein interactions and structure in order to understand how they affect plant growth and development. A comprehensive, high-throughput method called proteomics allows for the thorough identification and study of protein expression in a cell, tissue, or organelle of an organism at a certain time and under particular circumstances (Tan et al. 2013). Proteome profile study gives in-depth understanding of many metabolic processes and how they interact with distinct regulatory pathways in a biological system. Proteomics is a potent tool that, compared to other methods, including genomics technologies, offers a robust and superior description of how a cell functions. The identification of proteins and their expression profiles, posttranslational modifications (PTMs), and protein-protein interactions under stressed and normal conditions have been made possible recently by advances in quantitative proteomics research using high-resolution and mass accuracy instruments (Agregán et al. 2021). Systematic high-throughput methods, such as 2D-PAGE (two-dimensional polyacrylamide gel electrophoresis), MALDI-TOF/MS/MS, and LC-MS/MS, are used to conduct plant proteome analyses. Utilizing protein mapping, PTM characterization, protein-protein interaction, and systems biology techniques, the elucidation of protein activities and functional protein networks is assessed in plant metabolic and signaling pathways (Holman et al. 2013).

Proteomic methodologies offer fresh research techniques for a deeper comprehension of the molecular causes of drought stress in rice. There were 900 proteins found in rice roots under drought stress. Among these, 38% had more changes than the untreated group. Tubulins and proteins linked to transport were reduced, but chitinases and redox proteins implicated in disease were elevated. The proteomes of drought resistant (IRAT109) and susceptible (Zhenshan97B) cultivars were compared. In contrast to the sensitive variety (two proteins in increased abundance; 15 proteins in decreased abundance), the tolerant variety had higher protein abundance (14 proteins in increased abundance; six proteins in decreased abundance). Proteins implicated in the action of the enzyme's superoxide dismutase and dehydroascorbate reductase shielded IRAT109 (Ji et al. 2012).

Three distinct wheat cultivars were tested for their capacity to produce grain under drought stress using an iTRAQ-based quantitative proteome analysis:

RAC875 (drought-tolerant), Excalibur (drought-tolerant), and Kukri (drought-intolerant). At various stages of drought stress, these cultivars displayed distinctive physiological reactions, with equally drought-tolerant types (RAC875, Excalibur) displaying variations in their protein responses. In contrast to Excalibur, which lacked substantial proteins, RAC875 proteins demonstrated considerably abundant proteins. The ability of a protein involved in oxidative stress metabolism and ROS scavenging to boost SOD and CAT enzyme activity was present in all three cultivars at the same time. However, by reducing the proteins necessary for photosynthesis and the Calvin cycle, both drought-tolerant cultivars are implicated in the prevention of ROS.

iTRAQ and 2-DGE investigations on the maize leaf proteome were carried out to examine the impact of drought on the proteome. This research revealed that protective and stress-related proteins were upregulated in both genotypes (chaperones and dehydrins) (Benešová et al. 2012). Out of the 220 proteins that were identified as having differential expression, it was discovered that 106 were upregulated in the tolerant genotype and downregulated in the sensitive genotype. The preventive and detoxifying proteins ascorbate peroxidase, superoxide dismutase, glutathione reductase, and catalase were upregulated in the drought-tolerant genotype CE704. Additionally, the levels of the translation initiation factor eIF3 and the mitochondrial translation elongation factor EF-TuM were both increased. Comparative proteome analysis also discovered distinct protein accumulation locations in maize between the genotypes that are resistant (YE8112) and susceptible (MO17) to drought stress (Zenda et al. 2019). They discovered 721 proteins that were differently abundant (DAPs). Among them, 107 distinct DAPs shared by drought-sensitive and drought-tolerant lines following drought treatment, 84 distinct DAPs exclusive to MO17, and 13 particular DAPs peculiar to YE8112 were found. The tolerant genotype's (YE8112) elevated proteins promoted chaperons like the ASR1 protein, photosynthesis (PSII), and lipid metabolism.

Rice's responses to salt (150 mM NaCl) stress were examined by Xu et al. (2015) utilizing a proteomic method. A total of 56 proteins were discovered to have undergone substantial alteration, 16 of which improved the photosynthesis, antioxidant, and oxidative phosphorylation pathways by upregulating peroxiredoxin Q and photosystem I subunit D. The abundances of thioredoxin x, thioredoxin peroxidase, glutathione *S*-transferase F3, PSI component H, light-harvesting antenna complex I subunits, vacuolar ATP synthase subunit H, chloroplast chaperonin, and ATP synthase delta chain were significantly decreased in response to salt exposure. The phosphor proteomic variations between a salt-tolerant and a salt sensitive maize cultivar under short-term salt stress were discovered by Zhao et al. (2016). The proteome analysis was carried out utilizing the iTRAQ technique after salt treatment with 200 mM NaCl in two different rice cultivars, Pokkali (tolerant) and IR64 (sensitive). When compared to the sensitive cultivar IR64, the tolerant cultivar Pokkali had a greater concentration of proteins. Ascorbate peroxidase, superoxide dismutase, peptidyl-prolyl cis-trans isomerases, glyoxalase II, and oxygen evolving enhancer proteins OEE1 and OEE3, as well as PsbP, are among the proteins that have been discovered as being involved in stress tolerance (Lakra et al. 2019).

8.4.13 Metabolomics

In order to comprehend complicated biological processes and decode plant metabolomes, one relatively new "-omics" method called metabolomics was developed. A cell, tissue, organ, or organism's tiny molecule (1500 Da) may be thoroughly profiled and compared using metabolomics (Deborde et al. 2017). A biological system's metabolites must be identified and quantified in order to study their compositions and interactions with the environment (Khakimov et al. 2014). Furthermore, metabolomics focuses on examining biological activity as opposed to genomes, transcriptomics, and proteomics, making it comparatively simpler to link to the phenotype (Ibarra-Estrada et al. 2016). Metabolomics has been extensively utilized to study how plants respond to stress in adaptive ways. It is crucial to study the production of certain metabolites under diverse stressors in order to comprehend how plants respond to adverse environmental conditions (Sharma et al. 2023). New substances and unique metabolic pathways that accumulate under various stress circumstances are discovered by metabolomic research (Wen et al. 2014). Additionally, metabolomic research contributes to a better knowledge of already known metabolic pathways. Numerous metabolome studies have been carried out over the past 10 years to look at how metabolite concentrations alter in response to various biotic and abiotic stress conditions.

In response to abiotic stressors, plants accumulate several metabolites such as trehalose, glycine betaine, IAA, etc. According to Allen et al. (2009), the sheer accumulation of a particular chemical does not determine stress tolerance; rather, tolerance is determined by the flux's adaptation to several routes for defense and development. Stoichiometry and metabolic modification have been described as methods for maintaining plants' optimal fitness (Rivas-Ubach et al. 2012). Time-series studies with the plant *Arabidopsis thaliana* revealed that metabolic activities react to abiotic changes more quickly than transcriptional activities (Caldana et al. 2011).

8.5 Antioxidative Enzyme-Based Approach for Combined Stress Tolerance

8.5.1 Superoxide Dismutase

Superoxide dismutase (SOD) is the first detoxification enzyme that acts as a component of first line defense system against reactive oxygen species. SODs are a class of metalloenzymes that catalyze the dismutation of two molecules of $O_2^{\bullet -}$ into O_2 and H_2O_2. In plants, there are three main groups of SODs that have been reported: Cu/Zn-SODs, Mn-SODs, and Fe-SODs. SOD removes $O_2^{\bullet -}$ and hence decreases the risk of OH formation via the metal catalyzed Haber Weiss-type reaction (Gill and Tuteja 2010). Together with other antioxidant enzymes like CAT, peroxidases (POX), and APX, SOD is able to detoxify the resultant H_2O_2 and stop the creation of additional damaging ROS like OH•. According to the previous studies, overexpression of Cu/Zn SOD and Mn-SOD in rice, sweet potato, *Arabidopsis*, alfalfa, and tobacco (Prashanth et al. 2008) improved the capacity of drought tolerance and recovery in plants.

8.5.2 Catalase (CAT)

Catalase (CAT), also known as a H_2O_2 oxidoreductase, is a heme-containing enzyme that catalyzes the dismutation of H_2O_2 into H_2O and O_2 mainly in peroxisomes (Vellosillo et al. 2010). Numerous studies demonstrated that expression abundance of CATs increased under various stresses for scavenging of ROS (Vandenabeele et al. 2004). The features that distinguish CAT from other H_2O_2 metabolizing enzymes such as ascorbate peroxidases (APX), peroxiredoxins (PRX), glutathione/thioredoxin peroxidases (GPX), and glutathione *S*-transferases (GST) are that CAT do not require a reductant. When compared to control plants, the activities of SOD, POD, and CAT in the roots of salt-stressed barley plants were greatly increased at Day 2, but they significantly decreased from Day 4 onward (Liang et al. 2003). Combined stress of high temperatures and salt resulted in a decrease of CAT activity at higher levels in durum than bread wheat genotypes, while salt stress alone significantly increased CAT activity in all genotypes under normal temperature.

8.5.3 Peroxidase

Peroxidases (POXs) are oxidoreductases that transform a variety of compounds via a free radical mechanism into oxidized or polymerized products. These POXs scavenge the H_2O_2 produced during oxidative stress. POXs are reported from all plants, animals, and microbes and are essential for living systems. POXs are involved in many physiological and biochemical processes, including the cross-linking of molecules in the cell wall and lignin and suberin formation by oxidation of cinnamyl alcohol.

8.5.4 Ascorbate Peroxidase (APX)

Ascorbic acid-glutathione (AsA-GSH) cycle is essential metabolic pathway for protection against ROS and regulation of the cellular level of H_2O_2 in plants. This pathway includes ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR) and glutathione reductase (GR), and monodehydroascorbate reductase (MDHAR) with antioxidant metabolites ascorbic acid (AsA) and reduced glutathione (GSH). It plays an important role of maintaining redox homeostasis in plants to protect them from oxidation damage (Foyer and Noctor 2016). Increased activity of APX was reported under drought stress in maize and soybean (Jiang and Zhang 2001). Under combined stress (drought and salinity), antioxidant enzymes, for example, guaiacol peroxidase activity was upregulated as compared to control (Attia et al. 2020). The drought-tolerant wheat variety's APX, CAT, and SOD activity peaked at the end of flowering, milky ripeness, and wax ripeness, respectively; the drought-sensitive cultivar, on the other hand, had the lowest SOD and GR activities at waxy maturity and the least amount of APX activity at milky ripeness (Huseynova 2012).

8.5.5 Glutathione Reductase (GR)

Glutathione reductase (GR), also known as glutathione disulfide reductase (GSR), is a flavoprotein belonging to the family of NADPH-dependent oxidoreductases. It catalyzes the reduction of GSSG to GSH and plays an important role in cell defense against ROS (Hernández et al. 2017). An increase in GR activity in plants results in the accumulation of GSH and ultimately confers stress tolerance in plants. Various studies have demonstrated that drought stress increased GR activity in tobacco, barley, maize, wheat, rice, and pea (Sharma and Dubey 2005). Liang et al. (2003) reported that GR activity in the roots of salt-stressed plants at second day was unchanged, but at Day 4 and later, it drastically decreased in barley. Under normal (24/16 °C) temperature conditions, drought stress activated GR activity, and under high temperature water stress conditions, it significantly increased in all genotypes.

8.5.6 Monodehydroascorbate Reductase (MDHAR)

Monodehydroascorbate reductase (MDHAR) is one of the key enzymes in the conversion of oxidized ascorbate back to reduced ascorbate in plants (Kavitha and Murugan 2017). The exposure of plants to environmental stress conditions like high light leads to very quick oxidation of AsA to MDHA in chloroplast. Reddy et al. (2004) found that the enzyme activity of MDHAR was significantly high in the water-stressed leaves of mulberry cultivars, while contrary to this finding, reported that the activity of MDHAR decreased significantly in the heat and drought treatments in Crofton weed. MDHAR activity was enhanced under various other stresses such as salt, high light, and UV radiations. Sharma and Dubey (2005) reported that the activities of MDHAR, DHAR, and GR were higher in drought stressed rice seedlings.

8.5.7 Dehydroascorbate Reductase (DHAR)

Dehydroascorbate reductase (DHAR) is a monomeric enzyme, which is a member of the GSHS-transferase superfamily which maintains AsA in its reduced form by catalyzing the reduction of dehydroascorbate (DHA) to AsA using GSH as a reducing substrate (Hasanuzzaman et al. 2021). AsA recycling through MDHAR or DHAR is critical for maintaining the AsA level and redox state in the adaptation of plants to environmental conditions. Knockout mutants of *Arabidopsis* DHAR were unable to show any significant differences in total AsA content until challenged with the abiotic stress, which showed the importance of DHAR in reducing the DHA under stress conditions.

8.5.8 Glutathione *S*-Transferase (GST)

Glutathione *S*-transferases (GSTs) are multigene superfamily with cytosolic, mitochondrial, and microsomal localization in plants (Kumar and Trivedi 2018). GSTs are involved in safeguard of the cells against biotic and abiotic stresses and provide tolerance by catalyzing S-conjugation between the thiol group of GSH and electrophilic moiety in the hydrophobic and toxic substrate (Nianiou-Obeidat et al. 2017). Enzymatic activity of GSTs is induced by various fungal elicitors, wounding as well as by cold, drought, oxidative stress, heavy metals, and salt (Srivastava et al. 2019). Drought-tolerant and drought-sensitive sorghum genotypes showed efficient H_2O_2 scavenging mechanisms with significantly higher activities of GSTs (Jogeswar et al. 2006). According to the Rahdari et al. (2012), the ability of antioxidant enzymes to scavenge ROS and reduce the damaging influences is closely related to plant drought or salinity stress resistance. Drought or salinity not only adversely affects numerous subcellular compartments, for instance, vacuole, cytoplasm, and nucleus, and also affects the cell organs, and whole plant level, subsequently affecting plant biomass and health.

8.6 Secondary Metabolite Enzymes and Compounds

Phenolic compounds are derived from the phenylpropanoid pathway, mainly from aromatic amino acid phenylalanine in most plants or tyrosine in few cases. Enzymes involved in the phenylpropanoid biosynthetic pathway include lyases, transferases, ligases, oxygenases, and reductases, many of which are encoded by gene superfamilies.

8.6.1 Phenylalanine Ammonia-Lyases (PAL)

In plants, phenylalanine ammonia-lyases (PAL) catalyze the first step of the phenylpropanoid pathway, i.e., conversion of L-Phe to trans-cinnamic acid, which supplies the precursors for many phenolic compounds (Sharma et al. 2022b). PALs are ubiquitous in plants and also found in fungi but have not yet been detected in animals. Studies have shown that PAL activity responds to various stresses, such as wounding, drought, salinity, heavy metals, and infection by viruses, bacteria, or fungi (MacDonald and D’Cunha 2007).

8.6.2 Tyrosine Ammonia-Lyases (TAL)

Tyrosine ammonia-lyases (TAL) convert L-tyrosine to ammonia and *p*-coumaric acid (Sharma et al. 2022b). TAL has been studied less than PAL, and it remains unclear whether TAL activity is due to a capability of PAL to accept tyrosine as a substrate or due to the activity of a specific enzyme (Jendresen et al. 2015). The rarity of TAL is likely a reflection of its specialized role in 4-coumaric acid biosynthesis, which is used as the cofactor for photoactive yellow protein (PYP) in *Rhodobacter* and initiates the conversion of tyrosine to *N*-(*m*,*p*-dihydroxy cinnamoyl) taurine moiety of Saccharomycin antibiotics.

8.6.3 Polyphenol Oxidase (PPO)

Polyphenol oxidase (PPO) is widely distributed in bacteria, animals, plants, and fungi (Boeckx et al. 2015). PPO has been involved in the formation of pigments, oxygen scavenging, defense against plant pathogens, and herbivores. During various abiotic stresses (cold, heat, and drought), there was significant increase in phenolic compounds, and oxidation of these accumulated phenolics was proposed to be inhibited by significant decreases in PPO. This decrease in PPO activity, following abiotic stress, was associated with improved antioxidant capacity of plant under stress (Sofo et al. 2005).

8.6.4 Phenolic Compounds

Phenols are plant secondary metabolites that hold an aromatic ring bearing at least one hydroxyl group which are synthesized by the shikimate-phenylpropanoid biosynthetic pathway. Secondary metabolites are generally classified into two groups: nitrogen compounds (alkaloids, nonprotein amino acids, amines, alkamides, cyanogenic glycosides, and glucosinolates) and non-nitrogen compounds (monoterpenes, diterpenes, triterpenes, tetraterpenes, sesquiterpenes, saponins, flavonoids, steroids, and coumarins). Structurally, phenolic compounds are composed of the aromatic ring bonded directly to at least one (phenol) or more (polyphenol) hydroxyl groups (-OH) and other substituents, such as methoxyl or carboxyl groups, which cause the polar character of the compounds and allow dissolution in water. Phenolic compounds are usually divided into two groups—simple phenols and more complex derivatives—often containing several aromatic rings linked together (Sharma et al. 2019). Phenolic compounds have the ability to donate electron; hence, their hydroxyl groups can directly contribute to antioxidant action by stimulating the synthesis of endogenous antioxidant molecules in the cell (Bendary et al. 2013). Phenolic compounds chelate iron and copper ions due to the presence of suitable functional groups—hydroxyl and carboxyl—while some phenolic compounds also inhibit membrane lipid peroxidation by “catching” alkoxyl radicals. These activities of phenolic compounds are dependent on the structure of molecules and the number and position of hydroxyl groups. Under drought stress, increase in the number of flavonoids and phenolic acids was reported (Akula et al. 2018).

A previous study documented that phenylpropanoid biosynthetic pathway is one of the most stimulated pathways under salinity condition. The activation of phenylpropanoid biosynthetic pathway results in the improved production of various phenolic compounds, such as hydroxybenzoic acids (e.g., gallic acid, vanillic acid, syringic acid, *p*-hydroxybenzoic acid, and ellagic acid), hydroxycinnamic acids (e.g., caffeic acid, chlorogenic acid, *p*-coumaric acid, *m*-coumaric acid, ferulic acid, sinapic acid, and trans-cinnamic acid), and flavonoids (e.g., quercetin and iso-quercetin, rutin, luteolin and luteolin-7-O-glycoside, apigenin, kaempferol, and luteolin) (Sharma et al. 2019).

8.6.5 Flavonoids

They are synthesized through the phenylpropanoid pathway. Chalcone synthase (CHS), chalcone isomerase (CHI), and flavanone 3-hydroxylase (F3H) are key enzymes in this pathway (Hodaei et al. 2018). There are different classes of flavonoids depending upon the level of oxidation and pattern of substitution of the C ring, while individual compounds within a class differ in the pattern of substitution of the A and B rings. Important flavonoids in plants are flavones, flavanones, isoflavones, flavonols, flavanonols, flavan-3-ols, chalcones, and anthocyanidins. Until now, more than 5000 different flavonoids have been described which are classified into six major subclasses, such as flavones, flavonols, flavanones, flavanols, anthocyanidins, and isoflavones (Ross and Kasum 2002). Their structural variation in each subgroup is partly due to the degree and their hydroxylation, methoxylation, prenylation, and glycosylation pattern. Flavonoids can directly scavenge ROS by donating hydrogen atom, thus inactivating ROS (Sharma et al. 2023). Flavonoids themselves get converted to phenoxyl radical which can further react with other free radicals to form stable quinone structure (Treml and Šmejkal 2016).

8.7 Photosynthetic Machinery

8.7.1 Metabolism (Photosynthesis and Respiration)

The green leaves of plants indicate its capability for photosynthetic activity and offers important clues about agricultural productivity, as well as the physiological and phenological state of the plant. One of the primary processes impacted by salinity and drought is photosynthesis (Chaves et al. 2009). However, long-term salt stress exposure also causes plants to experience ionic stress, which impairs photosynthesis and causes leaf senescence, both of which have a detrimental impact on growth (Chaves et al. 2009). When plants are stressed by prolonged drought stress, their roots continue to elongate, which may be explained by the demand for groundwater on the part of the plant (Brunner et al. 2015). Long-term salinity stress might cause heavier roots to store more chloride. The photosynthetic components are negatively impacted by an excessive accumulation of ions, primarily Na^{2+}, which lowers enzyme activity and pigment synthesis.

Plants use stomata for two crucial processes: controlling CO_2 entry into the leaf and regulating transpiration, which supplies plants with nutrients and regulates leaf temperature. These stressful circumstances reduce the rate of CO_2 assimilation, and the excess light received that is not utilized by the plant may increase the generation of reactive oxygen species (ROS), which in turn causes oxidative stress. The reduction of the stomata aperture width (stomatal closure) prevents the loss of water to the atmosphere, and this protection mechanism is considered an adaptation response of plants to the onset of drought conditions (Saradadevi et al. 2017). Plants with salt exclusion mechanisms can either prevent salt from entering plant cells or reduce the amount of salt present in the cytoplasm by compartmentalizing salt in the vacuoles. In addition to lowering water potential and stomatal conductance, the combined stress also decreased plant photosynthetic efficiency.

8.8 Accumulation of Stress Protein

During water deficit and salt stress conditions, plants not only unregulated the production of osmoprotectants (e.g., proline and glycine betaine), antioxidant enzymes, but also enhance the expression of several drought- and salt stress-responsive genes and proteins such as late embryogenesis abundant proteins (LEA) and dehydrins (Fahad et al. 2015; Wani et al. 2016; Ullah et al. 2018).

8.9 Conclusion

Various studies regarding the drought and salinity stress response in plants have suggested the diverse adaptation mechanism to combat such conditions. These studies have improved our knowledge regarding the strategies and mechanisms involved to improve the tolerance in plants. Plants mitigate the combined stresses by regulating the genomic, proteomic, and metabolic responses. Plants have built-in adaptation mechanism to tackle complex abiotic conditions. Technological advancements can help to develop plant species with resistance toward the combined drought and salinity stresses. These advancements include breeding strategies, omics approaches, enzyme engineering, and other metabolic adjustments. These strategies further may be helpful to tackle the stress conditions for plant by maintaining the stress-responsive signaling. In this way, these approaches can be the coordinated efforts to develop resistance plants/varieties which can be helpful in maintaining food and nutritional security.

References

Abid M, Tian Z, Zahoor R, Ata-Ul-Karim ST, Daryl C, Snider JL, Dai T (2018) Pre-drought priming: a key drought tolerance engine in support of grain development in wheat. Adv Agron 152:51–85.4

Agregán R, Echegaray N, López-Pedrouso M, Aadil RM, Hano C, Franco D, Lorenzo JM (2021) Proteomic advances in cereal and vegetable crops. Molecules 26:4924

Akula R, Gill SS, Ravishankar GA (2018) Protective role of Indoleamines (Serotonin and Melatonin) during abiotic stress in plants. In: Metabolic adaptations in plants during abiotic stress. CRC Press, pp 221–228

Allen DK, Libourel IG, Shachar-Hill Y (2009) Metabolic flux analysis in plants: coping with complexity. Plant Cell Environ 32:1241–1257. https://doi.org/10.1111/j.1365-3040.2009.01992.x

Amirbakhtiar N, Ismaili A, Ghaffari MR, Firouzabadi FN, Shobbar ZS (2019) Transcriptome response of roots to salt stress in a salinity-tolerant bread wheat cultivar. PLoS One 14:e0213305

Angon PB, Tahjib-Ul-Arif M, Samin SI, Habiba U, Hossain MA, Brestic M (2022) How do plants respond to combined drought and salinity stress?—a systematic review. Plants 11(21):2884

Anjum SA, Ashraf U, Tanveer M, Khan I, Hussain S, Shahzad B, Wang LC (2017) Drought induced changes in growth, osmolyte accumulation and antioxidant metabolism of three maize hybrids. Front Plant Sci 8:69

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signaling transduction. Annu Rev Plant Biol 55:373

Araus JL, Cairns JE (2014) Field high-throughput phenotyping: the new crop breeding frontier. Trend Plant Sci 19(1):52–61

Arnold ML, Martin NH (2009) Adaptation by introgression. J Biol 8:82

Attia EA, Singh BP, Dashora K, Abdel-Azeem AM (2020) A potential antimicrobial, extracellular enzymes, and antioxidants resource: endophytic fungi associated with medicinal plants. Int J Biosci 17(1):119–132

Bains NS, Mangat GS, Singh K, Nanda GS (1998) A simple technique for the identification of embryo carrying seeds from wheat 9 maize crosses prior to dissection. Plant Breed 117:191–192

Beckles DM, Thitisaksakul M (2014) How environmental stress affects starch composition and functionality in cereal endosperm. Starch 66(1–2):58–71

Bendary E, Francis RR, Ali HMG, Sarwat MI, El Hady S (2013) Antioxidant and structure–activity relationships (SARs) of some phenolic and anilines compounds. Ann Agric Sci 58(2):173–181

Benešová M, Hola D, Fischer L, Jedelský PL, Hnilička F, Wilhelmová N, Rothova O, Kočová M, Prochazkova D, Honnerova J (2012) The physiology and proteomics of drought tolerance in maize: early stomatal closure as a cause of lower tolerance to short-term dehydration? PLoS One 7:e38017

Bernardo R (2010) Breeding for quantitative traits in plants. Stemma Press, Woodbury

Bhowal B, Chandra P, Saxena SC (2021) Engineering glycine betaine biosynthesis in alleviating abiotic stress effects in plants. In: Compatible solutes engineering for crop plants facing climate change. Springer, Cham, pp 97–127

Boeckx T, Winters AL, Webb KJ, Kingston-Smith AH (2015) Polyphenol oxidase in leaves: is there any significance to the chloroplastic localization? J Exp Bot 66(12):3571–3579

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C (2015) How tree roots respond to drought. Front Plant Sci 6:547

Budak H, Kantar M, Bulut R, Akpinar BA (2015) Stress responsive miRNAs and isomiRs in cereals. Plant Sci 235:1–13. https://doi.org/10.1016/j.plantsci.2015.02.008

Caldana C, Degenkolbe T, Cuadros-Inostroza A, Klie S, Sulpice R, Leisse A et al (2011) High-density kinetic analysis of the metabolomic and transcriptomic response of *Arabidopsis* to eight environmental conditions. Plant J 67:869–884. https://doi.org/10.1111/j.1365-313X.2011.04640.x

Campbell AW, Griffin WB, Conner AJ, Rowarth JS, Burritt DJ (1998) The effects of temperature and light intensity on embryo numbers in wheat doubled haploid production through wheat 9 maize crosses. Ann Bot 82:29–33

Çelik Ö, Atak C (2012) The effect of salt stress on antioxidative enzymes and proline content of two Turkish tobacco varieties. Turk J Biol 36(3):339–356

Chaparzadeh N, D'Amico ML, Khavari-Nejad RA, Izzo R, Navari-Izzo F (2004) Antioxidative responses of Calendula officinalis under salinity conditions. Plant Physiol Biochem 42(9): 695–701

Chaudhary HK, Sethi GS, Singh S, Pratap A, Sharma S (2005) Efficient haploid induction in wheat by using pollen of Imperata cylindrica. Plant Breed 124:96–98

Chaves MM, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103(4):551–560

Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. BMC Plant Biol 11:163. https://doi.org/10.1186/1471-2229-11-163

Curaba J, Singh MB, Bhalla PL (2014) miRNAs in the crosstalk between phytohormone signalling pathways. J Exp Bot 65:1425–1438. https://doi.org/10.1093/jxb/eru002

Deborde C, Moing A, Roch L, Jacob D, Rolin D, Giraudeau P (2017) Plant metabolism as studied by NMR spectroscopy. Prog Nucl Magn Reson Spectrosc 102:61–97

Deery DM, Rebetzke GJ, Jimenez-Berni JA, Bovill WD, James RA, Condon AG et al (2019) Evaluation of the phenotypic repeatability of canopy temperature in wheat using continuous-terrestrial and airborne measurements. Front Plant Sci 10:875

Deinlein U, Stephan AB, Horie T, Luo W, Xu G, Schroeder JI (2014) Plant salt-tolerance mechanisms. Trends Plant Sci 19(6):371–379

Demidchik V (2015) Mechanisms of oxidative stress in plants: from classical chemistry to cell biology. Environ Exp Bot 109:212–228

Deshmukh R, Sonah H, Patil G, Chen W, Prince S, Mutava R, Vuong T, Valliyodan B, Nguyen HT (2014) Integrating omic approaches for abiotic stress tolerance in soybean. Front Plant Sci 5:244

Dogra V, Rochaix JD, Kim C (2018) Singlet oxygen-triggered chloroplast-to-nucleus retrograde signalling pathways: an emerging perspective. Plant Cell Environ 41(8):1727–1738

Dubey RS (2018) Photosynthesis in plants under stressful conditions. In: Handbook of photosynthesis. CRC Press, Boca Raton, FL, pp 629–649

Dvorák J, Edge M, Ross K (1988) On the evolution of the adaptation of Lophopyrum elongatum to growth in saline environments. Proc Natl Acad Sci U S A 85:3805–3809

Fahad S, Hussain S, Matloob A, Khan FA, Khaliq A, Saud S, Hassan S, Shan D, Khan F, Ullah N, Faiq M (2015) Phytohormones and plant responses to salinity stress: a review. Plant Growth Regul 75:391–404

Fathi A, Tari DB (2016) Effect of drought stress and its mechanism in plants. Int J Life Sci 10(1): 1–6

Fiaz S, Ahmad S, Noor MA, Wang X, Younas A, Riaz A et al (2019) Applications of the CRISPR/Cas9 system for rice grain quality improvement: perspectives and opportunities. Int J Mol Sci 20(4):888

Forster BP, Shu QY (2012) Plant mutagenesis in crop improvement: basic terms and applications. In: Shu QY, Forster BP, Nakagawa H (eds) Plant mutation breeding and biotechnology. CABI, Wallingford, pp 9–20

Foyer CH, Noctor G (2016) Stress-triggered redox signalling: what's in pROSpect? Plant Cell Environ 39(5):951–964

Gao X, Starmer J, Martin ER (2008) A multiple testing correction method for genetic association studies using correlated single nucleotide polymorphisms. Genet Epidemiol 32(4):361–369

Gao P, Bai X, Yang L, Lv D, Pan X, Li Y et al (2011) osa-MIR393: a salinity and alkaline stress-related microRNA gene. Mol Biol Rep 38:237–242. https://doi.org/10.1007/s11033-010-0100-8

Garg R, Verma M, Agrawal S, Shankar R, Majee M, Jain M (2013) Deep transcriptome sequencing of wild halophyte rice, Porteresia coarctata, provides novel insights into the salinity and submergence tolerance factors. DNA Res 21:69–84

Gautam HR, Bhardwaj ML, Kumar R (2013) Climate change and its impact on plant diseases. Curr Sci 105:1685–1691

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48(12):909–930

Gowda VRP, Henry A, Yamauchi A, Shashidhar HE, Serraj R (2011) Root biology and genetic improvement for drought avoidance in rice. Field Crop Res 122:1–13

Goyal M, Kumari A, Kumari A, Sharma H, Vasmatkar P, Gupta N (2023) Oxidative stress and antioxidant defense in mitigating abiotic stresses in forage crops: a physiological and biochemical perspective. In: Molecular interventions for developing climate-smart crops: a forage perspective. Springer Nature Singapore, Singapore, pp 109–135

Guha S, Maheshwari SC (1964) In vitro production of embryos from anthers of Datura. Nature 204: 497

Gull A, Lone AA, Wani NUI (2019) Biotic and abiotic stresses in plants. In: Abiotic and biotic stress in plants. IntechOpen, London, pp 1–19

Guo D, Liang J, Li L (2009) Abscisic acid (ABA) inhibition of lateral root formation involves endogenous ABA biosynthesis in Arachis hypogaea L. Plant Growth Regul 58(2):173–179

Hasanuzzaman M, Raihan MRH, Masud AAC, Rahman K, Nowroz F, Rahman M et al (2021) Regulation of reactive oxygen species and antioxidant defense in plants under salinity. Int J Mol Sci 22(17):9326

Hasibeder R, Fuchslueger L, Richter A, Bahn M (2015) Summer drought alters carbon allocation to roots and root respiration in mountain grassland. New Phytol 205(3):1117–1127

Hernández JA, Barba-Espín G, Diaz-Vivancos P (2017) Glutathione-mediated biotic stress tolerance in plants. In: Glutathione in plant growth, development, and stress tolerance, pp 309–329

Hodaei M, Rahimmalek M, Arzani A, Talebi M (2018) The effect of water stress on phytochemical accumulation, bioactive compounds and expression of key genes involved in flavonoid biosynthesis in Chrysanthemum morifolium L. Ind Crops Prod 120:295–304

Holman JD, Dasari S, Tabb DL (2013) Informatics of protein and posttranslational modification detection via shotgun proteomics. In: Proteomics for biomarker discovery. Springer, Berlin, pp 167–179

Honsdorf N, March TJ, Berger B, Tester M, Pillen K (2014) High-throughput phenotyping to detect drought tolerance QTL in wild barley introgression lines. PLoS One 9(5):e97047

Huseynova IM (2012) Photosynthetic characteristics and enzymatic antioxidant capacity of leaves from wheat cultivars exposed to drought. Biochimica et Biophysica Acta (BBA)-Bioenergetics 1817(8):1516–1523

Hussain Wani S, Brajendra Singh N, Haribhushan A, Iqbal Mir J (2013) Compatible solute engineering in plants for abiotic stress tolerance-role of glycine betaine. Curr Genom 14(3): 157–165

Ibarra-Estrada E, Soto-Hernández RM, Palma-Tenango M (2016) Metabolomics as a tool in agriculture. In: Metabolomics - fundamentals and applications. IntechOpen, London, pp 148–168

Imran QM, Falak N, Hussain A, Mun B-G, Yun B-W (2021) Abiotic stress in plants; stress perception to molecular response and role of biotechnological tools in stress resistance. Agronomy 11:1579

Inagaki M (1985) Chromosome doubling of the wheat haploids obtained from crosses with Hordeum bulbosom L. Jpn J Breed 35:193–195

Janků M, Luhová L, Petřivalský M (2019) On the origin and fate of reactive oxygen species in plant cell compartments. Antioxidants 8(4):105

Jendresen CB, Stahlhut SG, Li M, Gaspar P, Siedler S, Förster J, Maury J, Borodina I, Nielsen AT (2015) Highly active and specific tyrosine ammonia-lyases from diverse origins enable enhanced production of aromatic compounds in bacteria and Saccharomyces cerevisiae. Appl Environ Microbiol 81(13):4458–4476

Ji K, Wang Y, Sun W, Lou Q, Mei H, Shen S, Chen H (2012) Drought-responsive mechanisms in rice genotypes with contrasting drought tolerance during reproductive stage. J Plant Physiol 169:336–344

Jiang M, Zhang J (2001) Effect of abscisic acid on active oxygen species, antioxidative defence system and oxidative damage in leaves of maize seedlings. Plant Cell Physiol 42(11):1265–1273

Jogeswar G, Pallela R, Jakka NM, Reddy PS, Venkateswara Rao J, Sreenivasulu N, Kavi Kishor PB (2006) Antioxidative response in different sorghum species under short-term salinity stress. Acta Physiol Plant 28:465–475

Kadioglu A, Terzi R, Saruhan N, Saglam A (2012) Current advances in the investigation of leaf rolling caused by biotic and abiotic stress factors. Plant Sci 182:42–48

Kahrizi S, Sedighi M, Sofalian O (2012) Effect of salt stress on proline and activity of antioxidant enzymes in ten durum wheat cultivars. Ann Biol Res 3(8):3870–3874

Kantar M, Lucas SJ, Budak H (2011) miRNA expression patterns of Triticum dicoccoides in response to shock drought stress. Planta 233:471–484. https://doi.org/10.1007/s00425-010-1309-4

Kasha KJ, Kao KN (1970) High frequency haploid production in barley (Hordeum vulgare L.). Nature 225:874–876

Kaur M, Malik P, Devi U, Mukta A, Kaur A, Dhillon GS, Padhy AK, Sharma H, Sharma A, Kaur S (2023) Wheat biofortification: a molecular breeding outlook. In: QTL mapping in crop improvement. Academic Press, pp 163–201

Kavitha CH, Murugan K (2017) Modulating role for antioxidant system in desiccation tolerance of Dicranopteris linearis. Indian J Sci Res:1–13

Khakimov B, Bak S, Engelsen SB (2014) High-throughput cereal metabolomics: current analytical technologies, challenges and perspectives. J Cereal Sci 59:393–418

Khan MIR, Palakolanu SR, Chopra P, Rajurkar AB, Gupta R, Iqbal N, Maheshwari C (2021) Improving drought tolerance in rice: ensuring food security through multi-dimensional approaches. Physiol Plant 172:645–668

Koussevitzky S, Suzuki N, Huntington S, Armijo L, Sha W, Cortes D et al (2008) Ascorbate peroxidase 1 plays a key role in the response of *Arabidopsis thaliana* to stress combination. J Biol Chem 283:34197–34203. https://doi.org/10.1074/jbc.M806337200

Krieger-Liszkay A (2005) Singlet oxygen production in photosynthesis. J Exp Bot 56(411): 337–346

Kumar S, Trivedi PK (2018) Glutathione S-transferases: role in combating abiotic stresses including arsenic detoxification in plants. Front Plant Sci 9:751

Lakra N, Kaur C, Singla-Pareek SL, Pareek A (2019) Mapping the 'Early Salinity Response' triggered proteome adaptation in contrasting rice genotypes using ITRAQ approach. Rice 12:3

Lashermes P, Beckert M (1988) Genetic control of maternal haploidy in maize (Zea mays L.) and selection of haploid inducing lines. Theor Appl Genet 76:405–410

Laurie DA, Bennett MD (1988) The production of haploid plants from wheat 9 maize crosses. Theor Appl Genet 76:393–397

Laxa M, Liebthal M, Telman W, Chibani K, Dietz KJ (2019) The role of the plant antioxidant system in drought tolerance. Antioxidants 8(4):94

Lethin J, Shakil SS, Hassan S, Sirijovski N, Töpel M, Olsson O, Aronsson H (2020) Development and characterization of an EMS-mutagenized wheat population and identification of salt-tolerant wheat lines. BMC Plant Biol 20:18

Li YF, Zheng Y, Addo-Quaye C, Zhang L, Saini A, Jagadeeswaran G et al (2010) Transcriptome-wide identification of microRNA targets in rice. Plant J 62:742–759. https://doi.org/10.1111/j.1365-313X.2010.04187.x

Li JL, Cui J, Cheng DY (2015) Computational identification and characterization of conserved miRNAs and their target genes in beet (*Beta vulgaris*). Genet Mol Res 14:9103–9108. https://doi.org/10.4238/2015.August.7.19

Li N, Wang X, Ma B, Du C, Zheng L, Wang Y (2017) Expression of a Na+/H+ antiporter RtNHX1 from a recretohalophyte Reaumuria trigyna improved salt tolerance of transgenic Arabidopsis thaliana. J Plant Physiol 218:109–120

Liang Y, Chen QIN, Liu Q, Zhang W, Ding R (2003) Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (Hordeum vulgareL.). J Plant Physiol 160(10):1157–1164

Lima JC, Arenhart RA, Margis-Pinheiro M, Margis R (2011) Aluminum triggers broad changes in microRNA expression in rice roots. Genet Mol Res 10:2817–2832. https://doi.org/10.4238/2011.November.10.4

López-Urrea R, Montoro A, Mañas F, López-Fuster P, Fereres E (2012) Evapotranspiration and crop coefficients from lysimeter measurements of mature 'Tempranillo' wine grapes. Agric Water Manag 112:13–20

Lynch JP, Wojciechowski T (2015) Opportunities and challenges in the subsoil: pathways to deeper rooted crops. J Exp Bot 66(8):2199–2210

MacDonald MJ, D'Cunha GB (2007) A modern view of phenylalanine ammonia lyase. Biochem Cell Biol 85(3):273–282

Mace E, Innes D, Hunt C, Wang X, Tao Y, Baxter J, Hassall M, Hathorn A, Jordan D (2019) The sorghum QTL atlas: a powerful tool for trait dissection, comparative genomics and crop improvement. Theor Appl Genet 132:751–766

Mallet J (2005) Hybridization as an invasion of the genome. Trends Ecol Evol 20:229–237

Manneh B, Kiepe P, Sie M, Ndjiondjop M, Drame NK, Traore K et al (2007) Exploiting partnerships in research and development to help African rice farmers cope with climate variability. SAT eJournal 4:1

Marees AT, de Kluiver H, Stringer S, Vorspan F, Curis E, Marie-Claire C, Derks EM (2018) A tutorial on conducting Genome Wide Association studies: quality control and statistical analysis. Int J Methods Psychiatr Res 27:e1

Mason RE, Singh RP (2014) Considerations when deploying canopy temperature to select high yielding wheat breeding lines under drought and heat stress. Agronomy 4(2):191–201

McDonald MP, Galwey NW, Ellneskog-Staam P, Colmer TD (2001) Evaluation of Lophopyrum elongatum as a source of genetic diversity to increase the waterlogging tolerance of hexaploid wheat (Triticum aestivum). New Phytol 151:369–380

Miller GAD, Suzuki N, Ciftci-Yilmaz SULTAN, Mittler RON (2010) Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environ 33(4): 453–467

Mishra S, Singh B, Misra P, Rai V, Singh NK (2016) Haplotype distribution and association of candidate genes with salt tolerance in Indian wild rice germplasm. Plant Cell Rep 35:2295

Mittova V, Guy M, Tal M, Volokita M (2004) Salinity up-regulates the antioxidative system in root mitochondria and peroxisomes of the wild salt-tolerant tomato species Lycopersicon pennellii. J Exp Bot 55(399):1105–1113

Molassiotis A, Job D, Ziogas V, Tanou G (2016) Citrus plants: a model system for unlocking the secrets of NO and ROS-inspired priming against salinity and drought. Front Plant Sci 7:229

Munaweera TIK, Jayawardana NU, Rajaratnam R, Dissanayake N (2022) Modern plant biotechnology as a strategy in addressing climate change and attaining food security. Agric Food Secur 11:26

Nakayama H, Yoshida K, Ono H (2000) Ectoine, the compatible solute of *Halomonas elongata*, confers hyperosmotic tolerance in cultured tobacco cells. Plant Physiol 122:1239–1247. https://doi.org/10.1104/pp.122.4.1239

Naranjo MA, Forment J, Roldan M, Serrano R, Vicente O (2006) Overexpression of Arabidopsis thaliana LTL1, a salt-induced gene encoding a GDSL-motif lipase, increases salt tolerance in yeast and transgenic plants. Plant Cell Environ 29(10):1890–1900

Neeraja CN, Maghirang-Rodriguez R, Pamplona A, Heuer S, Collard BCY, Septiningsih EM et al (2007) A marker-assisted backcross approach for developing submergence-tolerant rice cultivars. Theor Appl Genet 115:767–776. https://doi.org/10.1007/s00122-007-0607-0

Nevo E, Chen G (2010) Drought and salt tolerances in wild relatives for wheat and barley improvement. Plant Cell Environ 33(4):670–685

Ngara R, Ndimba BK (2014) Understanding the complex nature of salinity and drought-stress response in cereals using proteomics technologies. Proteomics 14(4–5):611–621

Nianiou-Obeidat I, Madesis P, Kissoudis C, Voulgari G, Chronopoulou E, Tsaftaris A, Labrou NE (2017) Plant glutathione transferase-mediated stress tolerance: functions and biotechnological applications. Plant Cell Rep 36:791–805

Oladosu Y, Rafii MY, Abdullah N, Hussin G, Ramli A, Rahim HA, Usman M (2016) Principle and application of plant mutagenesis in crop improvement: a review. Biotech Equip 30(1):1–16

Osthoff A, Donà dalle Rose P, Baldauf JA, Piepho HP, Hochholdinger F (2019) Transcriptomic reprogramming of barley seminal roots by combined water deficit and salt stress. BMC Genomics 20:1–14

Petrov VD, Van Breusegem F (2012) Hydrogen peroxide—a central hub for information flow in plant cells. AoB Plants 2012:pls014

Pinto E, Sigaud-kutner TC, Leitao MA, Okamoto OK, Morse D, Colepicolo P (2003) Heavy metal–induced oxidative stress in algae 1. J Phycol 39(6):1008–1018

Pirasteh-Anosheh H, Saed-Moucheshi A, Pakniyat H, Pessarakli M (2016) Stomatal responses to drought stress. Water Stress Crop Plant Sustain Appr 1:24–40

Placido DF, Campbell MT, Folsom JJ, Cui X, Kruger GR, Baenziger PS, Walia H (2013) Introgression of novel traits from a wild wheat relative improves drought adaptation in wheat. Plant Physiol 161(4):1806–1819

Prashanth SR, Sadhasivam V, Parida A (2008) Over expression of cytosolic copper/zinc superoxide dismutase from a mangrove plant Avicennia marina in indica rice var Pusa Basmati-1 confers abiotic stress tolerance. Transgenic Res 17:281–291

Pratap A, Gupta SK (2009) Biotechnological interventions in host plant resistance. In: Peshin R, Dhawan AK (eds) Integrated pest management: innovation, dissemination and impact. Springer, Dordrecht, pp 183–207

Rahdari P, Hosseini SM, Tavakoli S (2012) The studying effect of drought stress on germination, proline, sugar, lipid, protein and chlorophyll content in purslane (Portulaca oleracea L.) leaves. J Med Plants Res 6(9):1539–1547

Rajaravindran M, Natarajan S (2012) Effects of salinity stress on growth and biochemical constituents of the halophyte Sesuvium portulacastrum. Int J Res Biol Sci 2(1):18–25

Rane J, Singh AK, Tiwari M, Prasad PVV, Jagadish SVK (2021) Effective use of water in crop plants in dryland agriculture: implications of reactive oxygen species and antioxidative system. Front Plant Sci 12:778270

Rauf S, Al-Khayri JM, Zaharieva M, Monneveux P, Khalil F (2016) Breeding strategies to enhance drought tolerance in crops. In: Advances in plant breeding strategies: agronomic, abiotic and biotic stress traits. Springer, Cham, pp 397–445

Reddy AR, Chaitanya KV, Vivekanandan M (2004) Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J Plant Physiol 161(11):1189–1202

Reynolds MP, Hays D, Chapman S (2010) Breeding for adaptation to heat and drought stress. Clim Change Crop Prod 1:71–91

Ribaut JM, Betran J, Monneveux P, Setter T (2009) Handbook of maize: its biology. Springer, New York, NY

Richards R, Passioura J (1989) A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. Aust J Agric Res 40:943–950

Richards S, Aziz N, Bale S, Bick D, Das S, Gastier-Foster J et al (2015) Standards and guidelines for the interpretation of sequence variants: a joint consensus recommendation of the American

College of Medical Genetics and Genomics and the Association for Molecular Pathology. Genet Med 17(5):405–423

Rivas-Ubach A, Sardans J, Perez-Trujillo M, Estiarte M, Penuelas J (2012) Strong relationship between elemental stoichiometry and metabolome in plants. Proc Natl Acad Sci U S A 109: 4181–4186. https://doi.org/10.1073/pnas.1116092109

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier M-H, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Ross JA, Kasum CM (2002) Dietary flavonoids: bioavailability, metabolic effects, and safety. Annu Rev Nutr 22(1):19–34

Rozema J, Flowers T (2008) Crops for a salinized world. Science 322:1478–1480

Sadak MS (2019) Physiological role of trehalose on enhancing salinity tolerance of wheat plant. Bull Natl Res Cent 43(1):1–10

Sahebi M, Hanafi MM, Rafii MY, Mahmud TMM, Azizi P, Osman M et al (2018) Improvement of drought tolerance in rice (Oryza sativa L.): genetics, genomic tools, and the WRKY gene family. Biomed Res Int 2018:3158474

Sang Y, Macho AP (2017) Analysis of PAMP-triggered ROS burst in plant immunity. In: Plant pattern recognition receptors. Humana Press, New York, NY, pp 143–153

Saradadevi R, Palta JA, Siddique KH (2017) ABA-mediated stomatal response in regulating water use during the development of terminal drought in wheat. Front Plant Sci 8:1251

Schwenk K, Brede N, Streit B (2008) Introduction. Extent, processes and evolutionary impact of interspecific hybridization in animals. Philos Trans R Soc Lond Ser B Biol Sci 363:2805–2811

Septiningsih EM, Pamplona AM, Sanchez DL, Neeraja CN, Vergara GV, Heuer S et al (2009) Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. Ann Bot 103: 151–160. https://doi.org/10.1093/aob/mcn206

Sharma P, Dubey RS (2005) Modulation of nitrate reductase activity in rice seedlings under aluminium toxicity and water stress: role of osmolytes as enzyme protectant. J Plant Physiol 162(8):854–864

Sharma S, Demason DA, Ehdaie B, Lukaszewski AJ, Waines JG (2010) Dosage effect of the short arm of chromosome 1 of rye on root morphology and anatomy in bread wheat. J Exp Bot 61: 2623–2633

Sharma H, Chawla N, Dhatt AS (2019) Nutraceutical content and free radical scavenging capacity of brinjal (Solanum melongena L.) genotypes. Sci Hort 244:294–303

Sharma P, Chaudhary HK, Kapoor C, Manoj NV, Singh K, Sood VK (2022a) Molecular cytogenetic analysis of novel wheat-rye translocation lines and their characterization for drought tolerance and yellow rust resistance. Cereal Res Commun 50(4):655–665

Sharma H, Chawla N, Dhatt AS (2022b) Role of phenylalanine/tyrosine ammonia lyase and anthocyanidin synthase enzymes for anthocyanin biosynthesis in developing Solanum melongena L. genotypes. Physiol Plant 174(5):e13756

Sharma H, Singh S, Shamshad M, Padhy AK, Kaur R, Kashyap L, Srivastava P, Mavi GS, Kaur S, Sharma A, Sohu VS (2023) Variability in iron, zinc, phytic acid and protein content in prebreeding wheat germplasm under different water regimes. Plant Growth Regul 100:531–543. https://doi.org/10.1007/s10725-022-00943-5

Shelake RM, Pramanik D, Kim JY (2019) Evolution of plant mutagenesis tools: a shifting paradigm from random to targeted genome editing. Plant Biotechnol Rep 13:423–445

Shelake RM, Kadam US, Kumar R, Pramanik D, Singh AK, Kim JY (2022) Engineering drought and salinity tolerance traits in crops through CRISPR-mediated genome editing: targets, tools, challenges, and perspectives. Plant Commun 3:100417

Singh A, Meena M, Kumar D, Dubey AK, Hassan MI (2015) Structural and functional analysis of various globulin proteins from soy seed. Crit Rev Food Sci Nutr 55(11):1491–1502

Smith S, De Smet I (2012) Root system architecture: insights from Arabidopsis and cereal crops. Phil Trans R Soc B Biol Sci 367(1595):1441–1452

Sofo A, Dichio B, Xiloyannis C, Masia A (2005) Antioxidant defences in olive trees during drought stress: changes in activity of some antioxidant enzymes. Funct Plant Biol 32(1):45–53

Srivastava A, Srivastava P, Sharma A, Sarlach RS (2017) Canopy temperature an effective measure of drought stress tolerance in RIL population of wheat. Vegetos 30:1. https://doi.org/10.4172/2229-4473.1000212

Srivastava D, Verma G, Chauhan AS, Pande V, Chakrabarty D (2019) Rice (Oryza sativa L.) tau class glutathione S-transferase (OsGSTU30) overexpression in Arabidopsis thaliana modulates a regulatory network leading to heavy metal and drought stress tolerance. Metallomics 11(2): 375–389

Stokes CJ, Inman-Bamber NG (2014) Climate ready sugarcane: traits for adaptation to high CO2 levels. CSIRO, Townsville, QLD

Suarez-Gonzalez A, Lexer C, Cronk QCB (2018) Adaptive introgression: a plant perspective. Biol Lett 14:20170688

Taiz L, Zeiger E (2006) Secondary metabolites and plant defense. Plant Physiol 4:315–334

Tan L, Chen S, Wang T, Dai S (2013) Proteomic insights into seed germination in response to environmental factors. Proteomics 13:1850–1870

Tomar RSS, Deshmukh RK, Naik K, Tomar SMS (2014) Development of chloroplast-specific microsatellite markers for molecular characterization of alloplasmic lines and phylogenetic analysis in wheat. Plant Breed 133:12–18. https://doi.org/10.1111/pbr.12116

Toojinda T, Siangliw M, Tragroonrung S, Vanavichit A (2003) Molecular genetics of submergence tolerance in rice: QTL analysis of key traits. Ann Bot 91:243–253. https://doi.org/10.1093/aob/mcf072

Treml J, Šmejkal K (2016) Flavonoids as potent scavengers of hydroxyl radicals. Compr Rev Food Sci Food Saf 15(4):720–738

Trenberth KE, Dai A, Van der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J (2014) Global warming and changes in drought. Nat Clim Chang 4:17–22

Trindade I, Capitao C, Dalmay T, Fevereiro MP, Santos DM (2010) miR398 and miR408 are up-regulated in response to water deficit in Medicago truncatula. Planta 231:705–716. https://doi.org/10.1007/s00425-009-1078-0

Ullah A, Manghwar H, Shaban M, Khan AH, Akbar A, Ali U, Ali E, Fahad S (2018) Phytohormones enhanced drought tolerance in plants: a coping strategy. Environ Sci Pollut Res 25:33103–33118

Vandenabeele S, Vanderauwera S, Vuylsteke M, Rombauts S, Langebartels C, Seidlitz HK, Zabeau M, Van Montagu M, Inzé D, Van Breusegem F (2004) Catalase deficiency drastically affects gene expression induced by high light in Arabidopsis thaliana. Plant J 39(1):45–58

Vellosillo T, Vicente J, Kulasekaran S, Hamberg M, Castresana C (2010) Emerging complexity in reactive oxygen species production and signaling during the response of plants to pathogens. Plant Physiol 154(2):444–448

Wani SH, Kumar V, Shriram V, Sah SK (2016) Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. Crop J 4(3):162–176

Wen W, Li D, Li X, Gao Y, Li W, Li H, Liu J, Liu H, Chen W, Luo J (2014) Metabolome-based genome-wide association study of maize kernel leads to novel biochemical insights. Nat Commun 5:1–10

Wu QS, Srivastava AK, Zou YN (2013) AMF-induced tolerance to drought stress in citrus: a review. Sci Hortic 164:77–87

Xie X, He Z, Chen N, Tang Z, Wang Q, Cai Y (2019) The roles of environmental factors in regulation of oxidative stress in plant. Biomed Res Int 2019:9732325

Xu J, Lan H, Fang H, Huang X, Zhang H, Huang J (2015) Quantitative proteomic analysis of the rice (Oryza sativa L.) salt response. PLoS One 10:e0120978

Xu Y, Crouch JH (2008) Marker-assisted selection in plant breeding: from publications to practice. Crop Sci 48(2):391–407

Yousefirad S, Soltanloo H, Ramezanpour SS, Zaynalinezhad K, Shariati V (2018) Salt oversensitivity derived from mutation breeding improves salinity tolerance in barley via ion homeostasis. Biol Plant 62:775–785

Yousfi N, Slama I, Ghnaya T, Savouré A, Abdelly C (2010) Effects of water deficit stress on growth, water relations and osmolyte accumulation in Medicago truncatula and M. laciniata populations. Comptes Rendus Biologies 333(3):205–213

Yousfi M, Eichwald O, Merbahi N, Jomaa N (2012) Analysis of ionization wave dynamics in low-temperature plasma jets from fluid modeling supported by experimental investigations. Plasma Sources Sci Technol 21(4):045003

Yun W, Jinping Z, Yong S, Jauhar A, Jianlong X, Zhikang L (2012) Identification of genetic overlaps for salt and drought tolerance using simple sequence repeat markers on an advanced backcross population in rice. Crop Sci 52(4):1583–1592

Zang J, Sun Y, Wang Y et al (2008) Dissection of genetic overlap of salt tolerance QTLs at the seedling and tillering stages using backcross introgression lines in rice. Sci China Ser C 51:583–591. https://doi.org/10.1007/s11427-008-0081-1

Zenda T, Liu S, Wang X, Liu G, Jin H, Dong A, Yang Y, Duan H (2019) Key maize drought-responsive genes and pathways revealed by comparative transcriptome and physiological analyses of contrasting inbred lines. Int J Mol Sci 20:1268

Zhao MG, Chen L, Zhang LL, Zhang WH (2009) Nitric reductase-dependent nitric oxide production is involved in cold acclimation and freezing tolerance in *Arabidopsis*. Plant Physiol 151: 755–767. https://doi.org/10.1104/pp.109.140996

Zhao F, Zhang D, Zhao Y, Wang W, Yang H, Ta F, Li C, Hu X (2016) The difference of physiological and proteomic changes in maize leaves adaptation to drought, heat, and combined both stresses. Front Plant Sci 7:1471

Zhao A, Yu Q, Feng L, Zhang A, Pei T (2020) Evaluating the cumulative and time-lag effects of drought on grassland vegetation: a case study in the Chinese Loess Plateau. J Environ Manag 261:110214

Zulfiqar F, Chen J, Younis A, Abideen Z, Naveed M, Koyro HW, Siddique KH (2021) Biochar, compost, and biochar–compost blend applications modulate growth, photosynthesis, osmolytes, and antioxidant system of medicinal plant Alpinia zerumbet. Front Plant Sci 12:707061