Understanding Abiotic Stress Tolerance in Cereals Through Genomics and Proteomics Approaches

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Abstract

Abiotic stress severely decreases agricultural productivity worldwide. Understanding the molecular mechanism of plant defense responses using conventional methods has been a challenging task. Cereals and grain-legumes, as a primary source of vegetarian food, are quite essential in satisfying the expanding nutritional demands. The prevailing low yield of major cereals (rice, wheat, barley, etc.) has made researchers switch their focus upon enhanced abiotic stress tolerance of plants. This stands out to be rather one of the most sustainable solutions owing to the increasing nutritional demands in context to changing climate. Omics like genomics, proteomics, and metabolomics are important for better understanding, uncovering the underlying biological pathways and mechanisms in response to stress. By a rational combination of the high-throughput large-scale data of the omic approaches and bioinformatic tools, a crucial role toward the holistic understanding of the biological architecture has been established. Stress perception, signal transduction, and molecular mechanisms of defense responses are regulated by gene transcription level to cellular protein complements and metabolite profile level of stressed tissues. In this book chapter, we discuss the integration of physiological trait-based approaches with ever-evolving "omics" technology and its existing tools. These will be critical in further understanding the genetically complicated biological process of abiotic stress that could be accepted by the global omics research community. This deep understanding will thereby provide a novel insight for a great impetus to the development of crop breeding.

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5.1 Introduction

Plants are the primary producers providing approximately 80% of food for human consumption. About 50% of the global production is dominated by cereals that include rice, wheat, maize, and sorghum. The plants are exposed to harsh environmental stress conditions that impede growth and agricultural production. Biotic and abiotic stresses have an adverse effect on plant yield. Plants are frequently subjected to abiotic stresses that include water deficit, salinity stress, flooding, temperature extremities, nutrient deficiencies, and metal toxicity, considered as primary reasons to reduce crop productivity (Yadav et al. 2020). Such plants are considered more prone to weeds, insects, and pests which enhance concomitant loss (Reddy et al. 2012). Earlier, it was predicted that abiotic stress factors are involved in the loss of 70% crop yield, but later in the twenty-first century, it aggravated to 96.5%. The alarming population growth with climatic change exacerbated global food security altogether (Lesk et al. 2016). The sessile nature of plants modulates the development of various strategies. It includes transient rearrangement in the molecular level like transcription factors (TFs), heat shock protein (HSP), late embryogenesis abundant (LEA) proteins, biochemical pathways like reactive oxygen species (ROS) production and photosynthesis, physiological responses like flowering time, gene to protein level expression pattern, and modification of transport channel activities, as survival mechanisms (Soda et al. 2015).

Various omics tools and techniques have been adopted to identify the survival mechanism of plants. The hallmark of omics technology lies in its holistic approach that aims to find out novel candidate genes, proteins, and underlying pathways (Roychoudhury et al. 2011; Soda et al. 2015). The stress tolerance mechanism of plants is still not unveiled, while advancement over the technologies of genomics and proteomics has rapidly assembled data about multiple abiotic stress (Molina et al. 2008). The concept of omics has been developed to aid us with a better understanding of the genetic make-up of plants and their adaptive capacity under stressful circumstances (Soda et al. 2015).

Recent advances in research have demonstrated the idea of plant stress responses utilizing genomics and proteomics. It requires quantitative data at every stage of gene expression. Studies have deciphered the importance of post-transcriptional modifications and regulation in the translational system in plant adaptation to various abiotic challenges (Liu et al. 2012). Genomics has been tremendously advanced in the twenty-first century, with QTL (quantitative trait loci) mapping (Li et al. 2013), NGS (next-generation sequencing), WGAS (whole-genome associated sequencing), etc. Proteomics is an excellent technique for demonstrating the key proteins which recognize major pathways through 2DE (two-dimensional gel electrophoresis), SDS-PAGE (sodium dodecyl sulfate-polyacrylamide gel electrophoresis), etc.

contributing to stress (Gong et al. 2015). These approaches have been intensely discussed in the chapter. The wealth of knowledge obtained from advanced genomics and proteomics is used to explore the underpinning molecular mechanisms that make the plant stress-resilient. However, a highly synchronized perspective of systems biology with bioinformatics data is required for a complete understanding of the complex regulatory structure of plants. Substantial study on various abiotic stresses has been done to understand the regulatory processes and unravel the different stress-tolerant genes and traits in different species. The chapter outlines the proteomics and genomics approaches toward abiotic stress of crop plants and understanding the molecular mechanisms for stress tolerance. The chapter also highlights several omics techniques that have been used in unraveling notable genes and proteins of cereal crops altered under specific abiotic stress conditions. The identified novel genes, allelic variants, and traits would bring an improved degree of adaptive competence and plasticity (Gürel et al. 2016). This "upregulated" stress-tolerant variety can be further used for breeding on a large scale in field conditions.

5.2 Genomics and Proteomics for Understanding Stress Tolerance in Plants

Omics is a branch of applied biology which includes genomics, proteomics, metabolomics, transcriptomics, epigenomics, nutrigenomics, and metagenomics (Yuan et al. 2008). The "omics" approaches bring a paradigm shift for researchers toward understanding, exploring, and comprehending the behavior of plants toward biotic and abiotic stress. Omics approaches are often misinterpreted and considered relevant solely for plant adaptation associated with the signaling responses of a plant. However, it is a novel approach for paving scopes for research toward crop improvement (Bagati et al. 2018). Omics demonstrate the changes in gene expression level, causing a complex interplay with the composition of the plant proteome and the overall metabolic pathways. "Omics" study is not just limited to the terms "genomics" and "proteomics" but rather extends to both qualitative and quantitative parametrical approaches of the high-throughput techniques for detection of the identified genes, proteins, transcripts, or metabolites related to multifarious signaling pathways. Forward genetics includes observing the variation (natural or induced mutagenesis) and correlating it with genetic loci and phenotypic positional cloning of the allele. Reverse genetics comprises targeting a gene of interest and characterizing its function by studying the genetic manipulation through an experimental approach on the gene (Bowne et al. 2011).

The study of genomics is widely classified into structural, functional, mutational, and comparative genomics. Structural genomics deals with the structure of each and every protein encoded by a genome. Functional genomics, an important branch of omics, facilitates the gene function and interaction of gene products at the cellular level. The enormous information about genes, when analyzed with high-throughput genomic technologies gives data of a genome on a wide scale and validates the genomic difference between different species through “comparative genomics.” The genome sequences help in deciphering the stress-specific gene, protein profiles, and their dynamic regulation changes during stress screening. The genomic approaches enable the identification, improvement, and development of desirable genes by their over- or under-expression. Any addition or lack of information in plant genomes due to mutation is studied under “mutational genomics.” The lack of genomic information is further remunerated with the availability of expressed sequence tags (ESTs), cDNA sequence libraries, microarray, and serial analysis of gene expression (SAGE). Molecular markers enabled identification of the genes since the 1980s. Still, on a large scale, functional analysis was more promising with gene tagging. QTL mapping and designed marker-assisted selection advanced further. It further paved an effective response toward unraveling biological pathways and inheritance of the traits which might be controlled by single or multiple genes called the QTL (Micheletto et al. 2007). QTL analysis for screening can be classified under four categories: biochemical, phenological, morphological, and physiological. Recent breakthroughs implemented positional cloning that enabled multiple potential candidate genes responsive to stress conditions within cereal germplasms (Sutton et al. 2007). Resources of genome sequences of cereals (rice, maize, etc.) are invaluable for exploiting syntenic alignment and fine mapping with many other unsequenced genomes of graminaceous species. The advent of NGS is considered as a hassle-free, cost-effective, and speedy approach for annotation of the genome sequences (including introns and exons), which earlier were challenging to differentiate. NGS techniques, along with the GWAS (genome-wide association studies), have just accentuated the pace and opportunities of comparative genome sequencing of stress-related genes within and across the diversity of species (Ma et al. 2012). High-throughput NGS platforms include Roche 454, pyrosequencing, Illumina, polony sequencing, ABI SOLiD technology, Helicos, nanoball sequencing, Ion Torrent, and Oxford Nanopore. An already sequenced plant genome serves as a reference genome for genome annotation and identifies genetic discrepancies across a large number of sequences (Akpinar et al. 2013). The significant role of the MAPK (mitogen-activated protein kinase) signaling pathway in the abiotic stress has been marked. TILLING (targeting induced local lesions in genomes) is yet another recent high-throughput technology predominantly used to identify and analyze the allelic variations (mutants and SNPs) and primary phenotyping (Cordeiro et al. 2006). With the advancement of genome editing technologies, it is now feasible to introduce alterations at specific locations in the genome with genome editing techniques such as ZFNs (zinc-finger nucleases), TALENs (transcriptional activator-like effector nucleases), and clustered regularly interspaced short palindromic repeat (CRISPR)-Cas 9 (CRISPR-associated nuclease 9). It has enabled the integration of specific mutations, insertions, or deletions and precise sequence alteration using tailored nucleases in various organisms (Kumar and Jain 2015). Transcriptional level changes always do not get translated into proteins. Hence, the study of post-translation changes is significant for investigating plant mechanisms toward abiotic stress.

Proteomics is another interesting branch of omics that further validates the data disparity between mRNA abundance and accumulation of protein in adverse conditions. It also evaluates the gene expression level resulting in alteration of the transcriptomic, proteomic, and metabolomic make-up. The proteomic study is classified into a wide array of applications. It includes structural proteomics, functional proteomics, protein-protein interaction, proteome mining, protein expression profiling, and post-translational modification. Proteomics do not always deal with structural identification of the protein complexes, organelle composition, or sub-proteome isolation but also creates (3-D) maps for localization, signal transduction, and underlying molecular mechanisms through protein expression profiling. The presence of two proteins further elucidates the study of protein-protein interaction through yeast-two hybrid, co-precipitation, or phage display techniques. Several studies have elucidated that alteration in gene expression studies is always not proportional to protein level change. Hence, the functional aspect of proteomics is analyzed through yeast genomics, knockout systems, affinity-purified protein complexes, etc. Proteomes are direct effector molecules for plant stress response catalyzing several changes in the machinery of transcriptional and translational signaling pathways. Few modifications also occur through post-translational modification which includes the study of glycosylation, proteolysis, and phosphorylation. PTM (post-translational modification) is crucial for the investigation of proteomes by proteome mining through differential display, identification or validation, etc. Hence, proteomics deals with a wider perspective for improving crop productivity that has been opened with the advancement in omics. The aeon of "proteomic" research approach commenced through the 2D gel and DIGE (difference gel electrophoresis) (Subudhi 2011). The alternative technique of protein electrophoresis is isotope-coded affinity tags, multidimensional protein identification, and chromatographic techniques. ICAT (isotope-coded affinity tag), cation exchange, and reverse and liquid chromatography approaches convert the whole protein into peptides by enzymatic digestion. The digested peptide is identified by MS (mass spectrophotometer). MS further enables the structural information of the peptide and amino acid sequence, against the protein database (MASCOT, Expasy, PepSea, PepFrag, etc.), to predict the protein. Integration of several omics platforms includes the enormous omics data that has been generated due to computational software resources; such data are stored, analyzed, and made easy access through "databases." These databases reveal an interactome system between molecular interactions and the genotypic-phenotypic relationship network of a plant system for improving and developing novel approaches and paving scopes toward crop improvement (Bagati et al. 2018).

5.3 Plant Response Toward Abiotic Stress and Understanding Through Omics Approach

Plants have been serving as a primary renewable source of energy for the higher tropic levels since evolution. Humans have been utilizing roughly 3000 plant species as food, and 90% of our food energy intake has been served by “cereals.” It provides approximately 75% calories and 67% protein intake, which makes cereals more demanding. Stress is defined as any stimulus that exceeds the normal range of homeostatic control in any living organism (Fraire-Velázquez et al. 2011). With an exponential increase in the human growth curve, there are concomitant challenges of abiotic stress. Abiotic stress includes global warming (extreme temperature conditions); a steep decline in the availability of freshwater (drought); hypersaline conditions of the soil (salinity stress); flood and leaching of the soil (nutritional deficiency); overuse of fertilizers, pesticides, insecticides, and herbicides (heavy metals (HMs) increasing soil toxicity); and high photon irradiance (UV, blue light, high-intensity light, etc.).

Additionally, biotic stress reduces crop yield by 4.1% and 2.6% for being infected with pests and weeds. Around 69.1% of loss is attributed to abiotic stress conditions with a lack of management practices, economic hurdles, and training (Godfray et al. 2010). 70 million hectares and 100 million hectares of cereal crop-growing land have been affected solely by drought and salt stress worldwide, respectively, rendering the land uncultivable and retarding its nutritional benefits (Ahmad et al. 2014). With such substantial loss of annual productivity due to abiotic stress, food security is one of the critical issues, particularly in rural areas. With the concomitant loss of agricultural land to urbanization, industrialization has tightened the availability of crop land owing to the ever-increasing population. Crop breeding with abiotic resilience through traditional approaches has met limited success. The population explosion challenges to fulfill the enormous demand toward maintaining quality and supply of the agricultural productivity to satiate hunger parallelly (Bowne et al. 2011). When a plant suffers from abiotic stress, the response of the plant toward abiotic stress ranges from the molecular level to whole-plant physiological level depending upon the duration of exposure, age, developmental stage, species, and genotype of the plant. Plants change their “omics” profiles to adapt to changing environments. Hence, integrating the phenotypic, genotypic, and omics approaches will aid in identifying genes and their underlying mechanisms for the selection and development of stress-resilient and high-yielding cereal plants (Takeda and Matsuoka 2008). Abiotic stress targets the vegetative phase, yet it initiates many responses in the various level of cell types. Plants, over a period of time, generate responses to acclimatize to the prevailing stress conditions. Throughout evolution, this acclimatization leads to adaptation, which is generally established by acquiring mechanisms and metabolic alterations.

Plants have been divided into two categories based on their sensitivity to stress: (a) glycophytes (stress-susceptible) and halophytes (stress-tolerant). The majority of plants come under glycophytes for their tolerance, avoidance, and resistance mechanisms from damage. Various physiological processes by which plants function at the cellular level to adapt to abiotic stress are an accumulation of osmoprotectants (glycerol, sorbitol, polyols), amino acids and its compounds (proline, phenylpropanoid from phenylalanine and tyrosine), terpenes (squalene, lycopene), sulfur-containing compounds (dimethylsulphoniopropionate, defensins, glutathione), phenolic compounds (coumarins, flavonoids, isoflavonoids, lignin, ferulic acid), and ammonium compounds (glycine betaine, alkaloids, cyanogenic glycosides). The production of secondary metabolites confers protection of the protein structure from getting disaggregated and maintains osmoregulation and membrane integrity during environmental stress conditions. Accumulation of proline is a marked response defense mechanism (Roychoudhury et al. 2015). It regulates cellular potential, membrane stabilization, protein solvation, cell-proliferative mechanisms, and autophagy, altering the mitochondrial activity during adverse conditions (Ashraf and Foolad 2007). ROS is detrimental to the plants. Hence, plants produce ROS-scavenging antioxidant enzymes like ascorbate peroxidase (APX), superoxide dismutase (SOD), and peroxidase and catalase (CAT), conferring tolerance and protection to stress conditions by maintaining homeostasis (Horváth et al. 2007; Das and Roychoudhury 2014). Abscisic acid (ABA) signaling shows an evident molecular cross-talk in pathways that induce both abiotic stress resilience and pathogen resistance (Roychoudhury et al. 2013). Plants trigger multiple signal transduction cascades, activating the stress-responsive genes (Ge et al. 2009). Therefore, screening and selecting well-adapted germplasm with high-throughput omics technologies is a challenging job. "Omics" approaches have been quite persuasive for elucidating the molecular mechanisms controlling stress response in plants (Fraire-Velázquez et al. 2011). Generating improved lines of cereal crops for abiotic stress conditions has followed a continuous application of molecular breeding.

5.3.1 Drought Stress

Drought is one of the most devastating factors affecting world agriculture among all the abiotic stress conditions. One-third of the total agricultural land suffers from inadequate water supply triggering dehydration stress conditions impacting the overall growth and yield of a plant (Araus et al. 2003). Irrigation utilizes 80% of the usable water resource. The plant prevails in drought conditions by improving its water usage capacity. The first noticeable impact is the hardening of the soil due to dryness. Physiologically, it impacts plant growth and yield by harnessing mechanical stress on the roots, accompanied with removal of extracellular water content, the decline in photosynthetic activity, and loss of pigment. It leads to the accumulation of compatible solutes, amino acids, polyols, amines, ions, and organic acids. Osmotic adjustment is an inherited trait to counter ROS that stimulates oxidative stress and activates chaperonins and signaling pathways for dehydration−/drought-responsive genes in plants. The development of stress tolerance in crops by traditional approach is a very time-consuming and labor-intensive process (Manavalan et al. 2009). Hence, the focus has been shifted on improving the genetic make-up of the high-demanded cereal crops through modern transcriptomic techniques associated with in vitro genomic studies for verifying the response of the stress and efficacy of the construct of the identified potential gene (Roychoudhury and Banerjee 2015). Abiotic stress induces the transcription factors in rice (*Oryza sativa)* like DREBs (dehydration responsive element-binding protein), CBFs (C-repeat-binding factor), NACs (NAM, ATAF, and CUC), members of gene family 14.3.3 (GF14b and GF14c), and mitogen-activated protein kinase (MAPK) signaling pathway (Pitzschke et al. 2009). G14 genes possess cis-elements in their promoter responsible for tolerance toward abiotic stress and pathogen attack in rice.

Various stress-related and developmental pathways have been marked for expanding understanding of the interactome processes which play a crucial role in selecting beneficial candidates for molecular breeding (Budak et al. 2015). The genomic approaches include molecular breeding techniques, which dissect quantitative traits of a genetic compartment through techniques like QTLs. Progeny lines of extreme phenotypic characters are crossed for segregation and screened with molecular marker-assisted techniques like RAPD, AFLP, and RFLP for verifying genetic polymorphism. Molecular markers associated with drought-tolerant sub-traits are further used for segregation maps analyzed by computer software like ArcMap, MadMapper, RECORD, and JoinMap (Cheema and Dicks 2009). Transfer of the drought-resilient traits into cereal crops is only possible if there is a linkage of the sub-traits of drought-tolerance to the QTLs of the molecular markers. Drought-resilient QTLs associated with the cloning of gene/DNA sequences have marked a vital approach in molecular breeding.

5.3.2 Salinity Stress

About 20% of the available irrigated land suffers from salinity. It affects key metabolic processes, leading to genomic instability, cell wall destruction, and cytoplasmic lysis. Salinity stress alters membrane trafficking, photosynthesis, transcription level, energy metabolism, signal transduction, and protein biosynthesis pathway (Roychoudhury and Chakraborty 2013). Salt-tolerant genes are categorized based on salt uptake, transport, homeostasis, and osmoprotectants. Ion imbalance leads to the accumulation of Na^+ over a long period having a two-phase response to salinity. Osmotic stresses affect the root and shoot elongation and Na^+ toxicity of the plant (Roychoudhury et al. 2008). Salt stress is highly regulated by ion homeostasis (Witcombe et al. 2008). Sulfates and chlorides also contribute to enhancing the toxicity levels of saline soil. Salt stress results in calcium deficiency because the calcium uptake is reduced due to enhanced toxicity levels of other minerals. Hyposalinity (concentration of 80 mM NaCl or below) can also exacerbate stress. It suppresses vegetative growth, seed germination, and root weight causes decline in leaf area and reduces yield (Kanayama and Kochetov 2015). The salt tolerance of plants has been improved by metabolic readjustment (Na^+ exclusion or regulation).

Traditional breeding approaches to enhance salt tolerance included hybridization, wide hybridization, and ideotype breeding. The success rate is not ample for the development of stress-resilient varieties. Modern genomic approaches like QTLs have marked an improvement in the screening efficiency for selecting polygenic traits in the hypersaline environment. Plant transformation methods that include callus induction and tissue regeneration of the explants served crucially for developing salt-tolerant transgenics of model cereal crops. Genetic engineering by introducing cloned genes has also proved highly promising (Verulkar and Verma 2014). Expression profiling of a single gene under varying salt concentrations with differential sensitivity has been explored (Basu and Roychoudhury 2014) with the roles of miRNA. Thorough proteome analysis of rice anthers, wheat root seedlings, and rice plasma membranes has been conducted as part of tissue-specific proteomic research of salinity stress. The wheat chloroplast proteins were linked to a variety of physiological factors responsive to salinity. However, in most of these investigations, only a few salt-responsive proteins were discovered (Sarhadi et al. 2012). Omics analysis reported that sorghum undergoes moderate tolerance under salinity stress, and the most affected cereal includes maize. Rice, barley, and wheat (glycophytes) are the most salt-sensitive cereal, yet rice serves as the best model crop for studying salt tolerance. A few limitations to salinity stress include screening complications due to the expression of salt-tolerant polygenes in several cereal crops (Ashraf et al. 2008).

5.3.3 High-Temperature Stress

Climate change and global warming have been accompanied by an unprecedented rise in temperature by 2–4 °C. High temperature hampers nutrient security by escalating the loss in agricultural productivity in the tropical and subtropical regions. The natural tolerance mechanism of plants includes activating a cascade of events that activates stress-responsive genes, TFs and proteins (HSP), etc. Heat-tolerant genes (HT) are vital for the breeding program (Cossani and Reynolds 2012). High temperature interferes with a variety of important physiological activities in plants, including photosynthesis, respiration, and transpiration, by limiting carbon absorption and obstructing overall reproductive processes, resulting in significant yield loss (Zinn et al. 2010).

Temperature above 40 °C has detrimental impacts on the development of the warm season crops (rice, sorghum) (Akman 2009). It includes impairment in plant height, dry weight, tillers, reproductive traits, fertility, kernel development, seed viability, and fruit formation (Manigbas et al. 2014). Cool-season crops (wheat) are more vulnerable to damage by high temperatures. A temperature difference of 2 °C causes 50% retardation in grain growth and number (Rane et al. 2007). Morphological abnormalities of the damage include unusual ovary, tapetum degradation, and ultimate sterility (Zinn et al. 2010).

The productivity of major cereal crops (wheat, rice, maize, soybean, barley, etc.) is lost by almost 0.45 tons/ha by just 1 °C rise of temperature. The morphological and physiological characteristics for assessing crop diversity via the traditional breeding approaches could not cope with the loss. Hence, researchers shifted their focus to modern omics techniques (You et al. 2009) that included the screening of heat-tolerant genes or QTLs. The molecular study integrates the signaling pathway as a response generated by the activated receptors on the plasma membrane of cells undergoing heat stress. The pathway activates secondary messengers that include calcium sensors like calmodulins (Wu and Jinn 2010), calcium ions, CNL (calcium neurin like), CDPKs (calcium-dependent protein kinases), etc. It further activates the MAPK, TFs, and the concerned *HSP* genes. Stress-responsive genes are regulated via the TFs (Mizoi et al. 2012). *HSP* genes confer survival to the plant under heat stress conditions by maintaining the conformation of the protein structure (Saidi et al. 2010). The identified QTLs gave impressive genetic variation data between the wild type and the HT species. Heat-tolerant wheat genotypes "WH1021 and WH730" (Dhanda and Munjal 2012), soybean genotype "DG 5630RR," and maize genotype "AZ100" were developed. Apart from creating hybrids, researchers have also exploited certain defense traits (heat escape) to create genetic variability and stabilize yield. Genotypes of heat escape developed included "Waha-1" and "Omrabi-5" of wheat (Al-Karaki 2012). These varieties aimed for enhanced photosynthetic efficiency, harvest index, reproductive traits, a decline in respiratory rate, delayed senescence, etc. (Cossani and Reynolds 2012). The intervention of molecular markers for trait mapping of the identified QTLs has been deployed extensively for studying *HT* genes and their mechanisms which assisted in a better and faster breeding strategy (Shirasawa et al. 2013). Proteomic and functional genomic analyses have made progress by elucidating the role of the *HT* genes. The differential expression analysis of tolerance and regulation has been studied in HT plants (Urano et al. 2010). Several up/downregulated proteins were observed and identified at varying temperatures with their role in plant metabolism. To combat heat stress, several omics techniques have been refined for developing "transgenics." Omics technology, paired with systems biology approaches, might substantially boost traditional breeding to reduce HS problems and simplify the future of sustainable agriculture (Ahuja et al. 2010).

5.3.4 Cold Stress

The human population explosion has doubled the need for agricultural yield. However, low temperature is an intimidating stress factor affecting plant growth with unpredictable duration and intensity (Sinha et al. 2015). Cold-/low-temperature stress, disrupting metabolic homeostasis, can be classified based on its intensity into chilling (0 to 20 °C) and freezing (<0 °C). Freezing results in ice formation in plant tissues (inter and intracellular spaces) causing cellular dehydration that restricts plant metabolism and hampers growth and development with concomitant loss to global agricultural productivity (Chinnusamy et al. 2007). The severity of cold stress damage shows detrimental symptoms affecting both vegetative and reproductive phase that includes poor germination rate, arrested growth of seedlings, surface lesions on the plant (below −10 °C), waterlogged condition, dehydration, discoloration, osmotic changes (−2 to −4 °C), lamellar phase transitions (−4 to −10 °C), tissue disintegration, protein denaturation, hastened senescence with abscission, floral sterility, and deformation in the pollen tube and ovule growth with decreased fruit yield. Tropical and subtropical belt has chilling-sensitive cereals including rice and maize. Temperate belt grows chilling-tolerant cereals (Chinnusamy et al. 2007).

The cold acclimation of a plant is related to the metabolic pathway in both ABA-dependent and ABA-independent signaling. It induces a change in numerous gene expressions, membrane fluidity, lipid composition, and proteins at molecular levels (Lin et al. 2016). In cold stress circumstances, cytosolic calcium, which is maintained by chelators and channel blockers, plays a crucial role during signal transduction by altering conformations of the Ca^{2+} sensor proteins, including CaM (calmodulins), CDPK, etc. (Tuteja and Mahajan 2007). The alteration in expression levels is associated with the induction of several antifreeze proteins (AFPs). It includes LEA, DMSO (dimethyl sulfoxide)-induced COR (cold-regulated) proteins, HSPs, CSDPs (cold shock domain proteins), chaperones, PR (pathogenesis-related) proteins, etc. (Heidarvand et al. 2010). Apart from this, there is also an accumulation of several amino acids, antioxidants, sugars, pigments, and secondary metabolites that act as a protective shield from membrane desiccation, cell disruption, injury, and unbalanced hydrophobic interaction, promoting membrane rigidity and homeostasis (Janská et al. 2010). Enhanced membrane lipid unsaturation and bilayer fluidity are the significant adaptations for successful cold acclimation, as evident from knockout mutation studies in *Arabidopsis* (model plant) toward sensitivity to low temperature (Chen and Thelen 2013).

The stress-responsive gene expression has been studied enormously (through QTL identification, GWAS, marker-assisted breeding) in various species of cereals (Fig. 5.1). Protein expression level and interaction network are directly affected by stress and were hence investigated with advanced proteomic approaches (such as 2 DE, LC-MS, MALDI-TOF/MS, etc.), providing a complete overview during stress responses (Agrawal and Rakwal 2011) (Table 5.1). The differentially expressed cold-responsive proteins are involved in the regulatory and functional network. Few of them include photosynthetic and photorespiratory proteins, which are very susceptible to damage by proteases induced by ROS.

Genomic and proteomic analysis aided in the deciphering of freezing-inducible/ freezing-tolerant genes and proteins and understanding of molecular networks. It generated a shift toward a metabolomic approach to link and uncover the physiological and adaptive stress responses in cereal crops. To understand the phenotype of plants under cold stress, a collaborative approach toward understanding physiological and metabolic components of cold stress is required. Nonetheless, integrating these “Omic”-based methods in diverse cereal crop plants through a holistic approach to address the problem of cold- and freezing-related plant damage remains a major challenge.

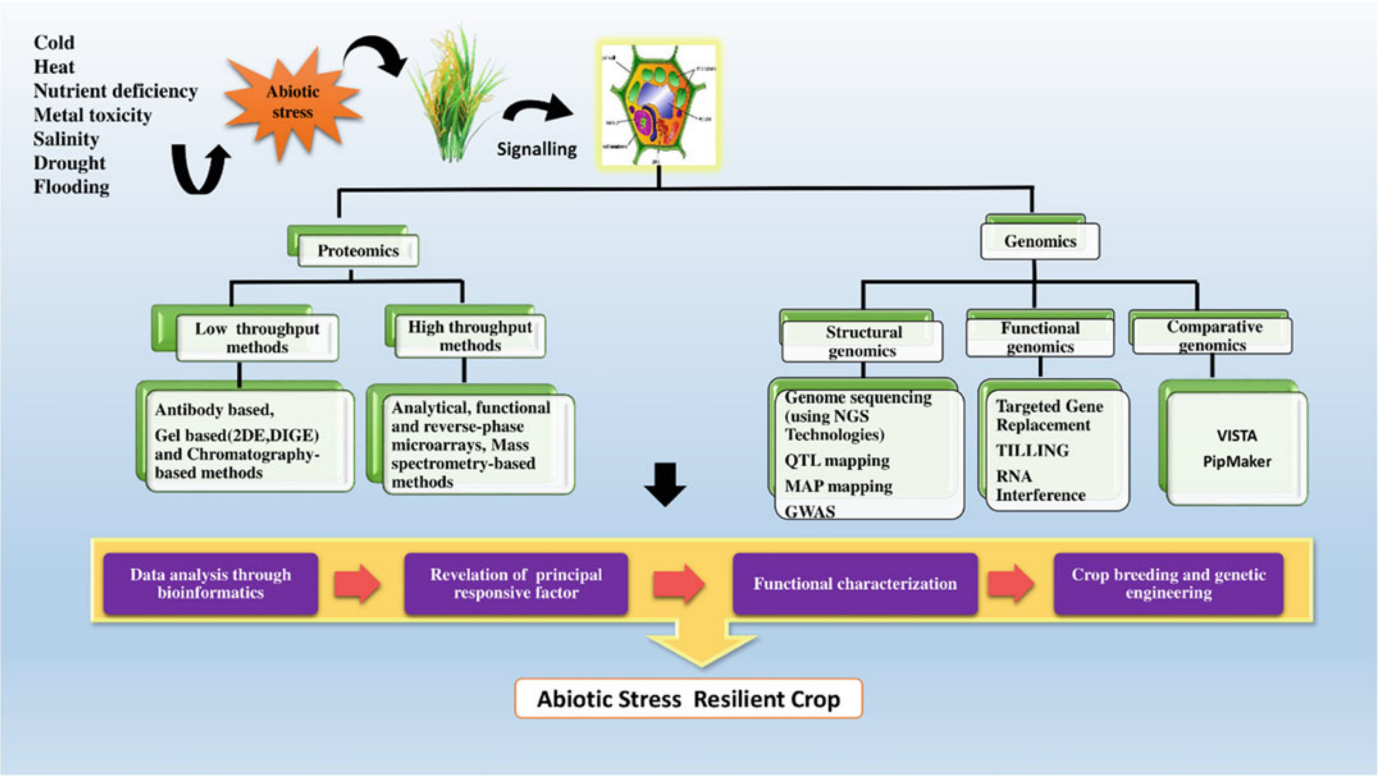

Fig. 5.1 Integrated omics approaches for the development of abiotic stress-resilient crop

Table 5.1 Application of omics tools in various cereal crops under abiotic stress

Crops	Genomic/proteomic tools	Stress conditions	Genes/proteins identified	References
Rice	QTL identified	Anoxia submergence and drought	*QTL9* and *Sub1A*, *Sub1B* and *Sub1C* on chromosome 9, *QTL2,11*, *12.1*- on chromosome 2, 11, 12	Ahmad et al. (2014)
	Genes identified	Drought	OsDREB1A, OsDREB2A, SNAC1, OsERD1, OsNAC6	Ahmad et al. (2014) and Ohnishi et al. (2005)
	QTL identified	Salinity	OsDREB2A, OsERD1, OsNAC6upregulated	Ohnishi et al. (2005)
	GWAS, QTL	Cold	42 QTLs in seedling, 29 QTLs in response to metabolism pathway	Shakiba et al. (2017) and Borjas et al. (2016)
	2-DE, MS, MALDI-TOF MS, label-free and iTRAQ	Cold	Several up- and downregulated unique protein spots identified	Neilson et al. (2011)
	2DE, MS, and MALDI TOF-MS analysis	Heavy metal (Cd, As)	Upregulated proteins and DEP found in roots and leaves	Lee et al. (2010) and Liu et al. (2013)
	GWAS, QTL, Genetic mapping	Heavy metal (As, Cd, Cu, Zn, Fe, and Hg)	QTL identified on Chr 2, 3, 5, 6, 7, 8 DEP, candidate genes for Fe and Zn identified	Gautam et al. (2012), Wang J et al. (2018), Zhu et al. (2020) and Zhang et al. (2017a, b)
	2-DE-MS, QTL GWAS. Linkage mapping	Nutrient deficiency (P, K, N, S, Fe)	Protein spot, OTL (*qRST9.14*), gene and QTL were identified related to survival in stress	Torabi et al. (2009), Kim et al. (2011), Fang et al. (2015), Pariasca-Tanaka et al. (2020), Jewel et al. (2019), Chen et al. (2015) and Hakeem et al. (2013)
	QTL, genotyping, RAPD, and RFLP linkage	Flooding	QTL on Chr. 1,2,5,7,10,11 SNP-mapped on Chr. 9,d	Toojinda et al. (2003) and Singh et al. (2017)
Wheat	2 DE, LC-MS/MS	Drought	Proteasomal factors and protease inhibitors, LEA proteins	Alvarez et al. (2014), Wang et al. (2016a, b), Zhang et al. (2014) and Li et al. (2014, 2018)
	QTL identified	Flooding, drought	–	Shukla et al. (2015), Barakat et al. (2015) and Merchuk-Ovnat et al. (2016)

(continued)

Table 5.1 (continued)

Crops	Genomic/proteomic tools	Stress conditions	Genes/proteins identified	References
	Nano-LC (LC)-MS/MS, Shotgun tandem MS approach	Waterlogging, drought	TaBWPR-1.2 genes	Haque et al. (2014) and Bernardo et al. (2017)
	2 DE, LC-MS/MS	Salinity	Metabolic enzymes, enzymes involved in ETC and ATP synthesis	Singh et al. (2017)
	QTL identified	Salinity	–	Xu et al. (2012a, 2013)
	2-DE, 2D-DIGE, MALDI-TOF	–	Unique protein spots, DEP identified	Rinalducci et al. (2011) and Kosová et al. (2013)
	MS, 2 DE, iTRAQ, and LC-MS analysis	Heavy metal (Cd, Cu, Zn, Hg)	Proteins and DEP identified	Li et al. (2013), Wang et al. (2016d) and Kang et al. (2015)
	GWAS, QTL	Heavy metal (Cr, Al, Cu, P)	71 loci for plant development, ALMT1 mapped on Chr 4DL (Al tolerance) as transporter for malate efflux against stress	Almas et al. (2018) and Raman et al. (2005)
	GWAS	Cold	63 loci and 76 SNP identified	Zhao et al. (2020)
	LC-MS/MS, 2 DE	High temperature	–	Lu et al. (2017)
	Label-free, MS	Nutrient deficiency (N)	Protein spot detected and QTL identified	Karim et al. (2020), Ren et al. (2017) and Chandna and Ahmad (2015)
	Gel-based and LC-MS/MS	Flooding	Protein identified between susceptible and tolerance	Kong et al. (2010) and Pan et al. (2019)
Sorghum	NILs and gene labelling studies	Drought	BADH1, BADH15	Chen and Murata (2008)
	GWAS	Cold	QTLs, SNP 44,515, marker traits on chr SBI-1, 2, 3,6, 9, and 10	Shakoor et al. (2019) and Parra-Londono et al. (2018)
	2-DE, MS, chromosome loci mapping, WGAS, QTL identified	Heavy metals (Cd, Cu, Al)	DEP identified and Alt_{SB} on Chr 3 identified as aluminum-activated citrate transporter	Roy et al. (2016, 2017)
	iTRAQ, LC–ESI-MS/MS	Cold stress	Stress-responsive proteins identified	Wang et al. (2016c)

	QTL identified	Cold stress tolerance	QTLs on Chr 2,4,8	Rodríguez et al. (2014)
	2DE, iTRAQ, and LC-MS/MS	Heavy metal (Cr, Cd, Pb)	Proteins and DEP found after stress treatment	Terzi and Yıldız (2021), Wen et al. (2019) and Li et al. (2016)
	QTL, GWAS, linkage mapping	Heavy metal (Hg, Cd, Pb, Zn, and As)	SNPs identified with seeds and shoots (Hg) QTL (*qKHC9a*, *qKHC9b*, and *qBHC9*) identified (As, Cd, Pb), QTL gene GRMZM2G137161 and GRMZM2G132995 identified (Cd-Zn transporting)	Zhao et al. (2017, 2018) and Hou et al. (2021)
	2DE, MS	Nutrient deficiency (P)	DEP identified	Li et al. (2007) and Zhang et al. (2014)
	MAS, single-molecule real-time sequencing and optical mapping, GWAS, 2D-DIGE, iTRAQ LC-MS/MS	Flooding	DEP on Chr 4, 8 related to ARF, 184 AP2/ERF stress-responsive genes present on Chr 1–10	Mano et al. (2005), Jiao et al. (2017), Du et al. (2014), Chen et al. (2014) and Yu et al. (2015)
	2DE, LC- MS/MS, MALDI-TOF	Cold	Several up- and downregulated protein spots with DEP and unique proteins identified	Mohammadi (2021) and Longo et al. (2017)
	QTL, GWAS	Frost	Chr 5HL	Visioni et al. (2013)
	2D, MS TMT/LC-MS/MS	Nutrient deficiency (N, K)	DEP spot related to root 67, shoot 49, and 288 tolerance found	Møller et al. (2011) and Zeng et al. (2015)
	QTL and GWAS Tandem mass spectrometry analysis	Flooding	QTL on Chr. 2H and 4H, DEP detected and three potential genes (*PDC*, *ACO* and *GST*) upregulated	Gill et al. (2019), Broughton et al. (2015) and Luan et al. (2018)
Rye and oat	Shotgun proteomics and DRM	Cold	DRM and HSP70 proteins identified with P-type ATPase, aquaporins	Takahashi et al. (2013)

5.3.5 Flooding Stress

The decade of scientific advancement has artificially separated nature from mankind. The revolutions of industrial progress and urbanization in the twenty-first century have enhanced the rate of global warming, deforestation, cyclone, and climatic discrepancy. The emission of greenhouse gases has not just depleted the ozone layer but also exerted a profound impact on the precipitation patterns. These varying conditions have affected the whole ecosystem (Eigenbrod et al. 2015).

Flooding is one of the major abiotic stress factors that have a significant impact on crop growth, eventually resulting in a lower yield of cereal crops (Normile 2008). Unpredictable heavy or sometimes irregular rainfall and cyclones induce waterlogging stress in the soil due to poor drainage. It causes a detrimental impact by reducing the gaseous exchange between the soil and the water (Bailey-Serres and Voesenek 2010). Flooding ruins about 13% of the world's total area and nearly 10% of agricultural land (ten million hectares in India alone). The overall yield loss in different cereal crops affected by the aftermaths of flooding ranges from 15% to 80%, depending on the kind of plant, soil, and severity of the stress. It has a profound impact on rice and wheat farming, causing a global yield loss of 18% and 39–40%, respectively.

The incompetency of the crops to tolerate stress is generated due to prevailing anoxic conditions by reducing the level of oxygen diffusion to 104-fold as compared to air (Armstrong and Drew 2002). It alters the respiration and nutrient uptake pathways due to submergence or accumulation of water around, affecting root-shoot development, overall plant yield, and sustainability. The hypoxic conditions (reduced level of oxygen) further transmute to anoxia (absence of oxygen), which facilitates the anaerobes to participate conveniently for the partial respiration and other anticipated activities.

Floods affect several crops, including maize, wheat, rice, and soybeans. Intolerant plants are barred from growing in flood-prone areas, whereas tolerant plants grow, based on escape and quiescence strategy (Colmer and Voesenek 2009). The escape strategy allows reaeration of flood-damaged tissues by inducing anatomical and morphological alterations. At the same time, the quiescence strategy follows the conservation of carbohydrates for a prolonged supply of energy underwater (Bailey-Serres and Voesenek 2008). Flooding alters several morphological, physiological, and anatomical changes in plants that include reduction of dry mass, growth, pH, nutrient deficiency, and microelement toxicity (Voesenek and Bailey-Serres 2015). Developmental adaptation involves changes in organ anatomy and cellular composition to improve oxygen accessibility. It includes the growth of adventitious roots (Zhang et al. 2017a, b), aerenchyma tissue formation (for the ease of oxygen passage from root-shoot), and hypertrophied lenticels. Flooding leads to the transport of 1-aminocyclopropane-1-carboxylate (ACC, precursor of ethylene) from roots to shoots. It triggers the activation of ethylene for regulating systemic responses such as tissue chlorosis, leaf petiole elongation to reach water surface, nastic movements, etc. (Sasidharan and Voesenek 2015). The activation of auxin, abscisic acid, gibberellic acid, and polyamines also directs the stress signal transduction cascade. Ethylene response factors (ERFs), specifically ERF VII, are a low-oxygen detecting group (Licausi et al. 2011). ERFs govern the adaptation mechanism of plants in flooding stress by changing the course of biochemical pathways to preserve the viability of the cell. It deviates from OXPHOS (oxidative phosphorylation) to less energy-efficient glycolysis, fermentation, and anaerobic respiration. The primary limitation of the pathways is the rate of NADH oxidation. Ethanolic fermentation uses alcohol dehydrogenase (ADH), and lactic acid fermentation requires LDH (lactic dehydrogenase) (Bailey-Serres and Voesenek 2008). There is also an upregulation in the production and accumulation of antioxidants, osmoprotectants, and HSF (heat shock proteins). It occurs in response to oxidative damage by ROS via the NADPH-oxidase pathway during anoxia. Antioxidants include catalase, glutathione reductase, ascorbic acid, glutathione, etc. (Lekshmy et al. 2015). HSF act as sensors of the hydrogen peroxide generated during stress. Activation of genes and TFs encoding HSF for proteolysis promotes flood amelioration.

The unpredictable onset of floods due to climatic variations has drawn a significant concern for researchers. The transformation of the traditional knowledge into contemporary has only been possible with the approach of omics. The notable flood-tolerant genes and proteins that have been identified and characterized with genomics and proteomics have been described in Table 5.1. Appreciable conclusions have been embarked with the identification, screening, and characterization of the genes and proteins. It has given an impetus for further advancement of genomics and proteomics (like validation of the biomarkers, marker-assisted breeding, GWAS, LC-MS, etc.). The identified stress-tolerant genes and proteins have been used for genetic engineering to increase agricultural production and subdue the impact of the flood. Metabolomics is yet in a nascent stage of advancement. An amalgamation of metabolomics with genomics and proteomics through a consolidative phytochemical pathway would give a complete picture of flood-tolerant cereal crops (Tewari and Mishra 2018).

5.3.6 Heavy Metal Stress

Among the various abiotic stresses, heavy metal toxicity has a detrimental effect on plants. The bioavailability and leaching of heavy metals (HMs) contaminate the soil. Along with that, the anthropogenic invasions for urbanization and food production result in several contemporary man-made activities. It includes mining, sewage sludge flow, and wide-scale usage of artificial fertilizers and chemicals (Gupta et al. 2010). Natural causes include weathering of soil and climatic change that leaches the minerals, altering the eco-physiological properties of the elements into toxic HMs (Rajkumar et al. 2013). The toxic heavy metals, which are potential carcinogens (transition elements at mild concentration), mix with the environment on a higher scale, negatively impacting soil, water, and air quality, worldwide. Based on the physicochemical properties, atomic number (greater than 20), and specific gravity (greater than 5), the elements have been recognized under non-essential and essential HMs. Zinc, copper, molybdenum, nickel, cadmium, arsenic, beryllium, chromium, aluminum, lead, etc. are very critical for biological growth and developmental process (Tiwari and Lata 2018). The detailed role of every element is mentioned in Table 5.1. Exceeded concentrations above supra-optimal levels cause a detrimental impact on the ecosystem by entering the plant metabolism through ion carriers and channels (Pierart et al. 2015). Due to soil contamination, a low concentration of the HMs accumulated by the plants results in high toxicity levels as it passes on to the subsequent trophic levels of the inverted pyramid in the ecosystem. HMs alter and deteriorate the quantitative and qualitative crop yield. To safeguard from the toxic effects of HMs, plants have evolved intricate defense and escape mechanisms. Escape mechanisms include compartmentalization and sequestration of the HM inside the cellular organelles (mostly vacuoles) or reduction in the passive absorption of HM into the plant cell. Defense mechanisms include activation of the antioxidant armory (SOD, APX, betaine, proline), binding to phytochelatins, deactivation of organic compounds, and elimination of the HM via transporters, ion channels, TFs, signaling molecules, etc. (AbdElgawad et al. 2020; Jamla et al. 2021). The impacts of copper (Cu), zinc (Zn), lead (Pb), magnesium (Mg), and sodium (Na) were investigated on cereal crops grown on contaminated soil. It was concluded that these metals have detrimental effects on the cellular mechanism, gene expression levels, seed germination, and plant physiology. Phytotoxicity results from the accumulation and interaction of toxic heavy metals with ROS. It interrupts the lipid peroxidation (Branco-Neves et al. 2017) cellular homeostasis and causes oxidative damage (Huihui et al. 2020) whose impacts are chlorosis, reduced nutrient uptake, protein biosynthesis, photosynthesis, biomass production, and loss in plant growth and development at all stages (germination, vegetative, reproductive) (Chandra and Kang 2016).

Omics methods have advanced considerably because of the evidence of biochemical and molecular alterations in the plant due to HM stress. The resources and updates on plant genome, transcriptome, and proteome plasticity against the HM resilience have been developed with the accession of the HM stress response on the cereal crops. Apart from the elemental assessments via omics, significant upregulation of the epigenetic regulators (like metal detoxification transporters) was identified (Shafiq et al. 2019). The massive sequencing and omics data are further developed through several in silico tools for proper annotation and ultimately generates improved resilience in the plant systems for HM stress research. Comprehensive and detailed investigations can lead to unraveling novel candidate genes for phytoremediation, hyperaccumulation of HMs, transporter or carrier system of the retrograde signaling, and metal co-uptake in HM resilient plant species.

5.3.7 Nutrient Deficiency

Plants cannot complete their life cycle unless they receive the necessary nutrients. Plants require approximately 14 elements, which are classified as micro- and macronutrients, based on the levels of such elements in plant dry matter. The occurrence of both micro- and macroelements throughout plant growth and development is fundamental to the overall physiological condition. Micronutrients required in small concentrations include boron, chloride, copper, iron, manganese, molybdenum, nickel, and zinc. These elements are essential for enzyme function and protein stability (Hänsch and Mendel 2009). Macronutrients needed in relatively significant quantities with more than 0.1% of dry mass include calcium, magnesium, nitrogen, phosphorous, potassium, and sulfur (Maathuis 2009).

The mineral elements like carbon, nitrogen, hydrogen, and sulfur are absorbed from the soil or environment in ionic form from carbon dioxide, oxygen, bicarbonate, water, nitrate, ammonium, nitrogen, sulfate, and sulfur dioxide. These are components in the basic cellular structure like amino acids, proteins, enzymes, and nucleic acids and play crucial roles in enzymatic or oxidation-reduction reactions. Potassium, sodium, calcium, magnesium, manganese, and chlorine are nutrients that contribute to maintaining osmotic potential, enzyme conformation (enzymatic activity), regulating anions, membrane permeability, and electrical and chemical potentials. Inorganic compounds containing lead, boron, and silicon are frequently generated from the soil and contribute to the maintenance of electrochemical potential, electrostatic interactions, and power transmission reactions (Mengel et al. 2001).

The poor and unpredictable presence of many of these essential nutrients, particularly macronutrients, significantly inhibits crop development and yield in most soil samples (Gojon et al. 2009). Plants exhibit extensive morpho-physiological responses to mineral nutrient deprivation, including lower productivity and seed yield, significant changes in leaf color through alteration in pigmentation, as well as modification in the root system. During the early emergency response phase, the plant strives to compensate for mineral deficits by employing bidirectional adaptation mechanisms such as increased root zone absorption, mobilizing existing resources, and avoiding biosynthetic activities. Lateral root growth is decelerated in support of main root exploration expansion (Gruber et al. 2013). Furthermore, any kind of macronutrient shortage has an instantaneous deleterious effect on photosynthesis, reducing carbon availability (Wulff-Zottele et al. 2010). The continuous depletion of one or more mineral elements causes an instantaneous reaction phase. The developmental program of the plant is irrevocably turned to maturation and senescence (Watanabe et al. 2010). Plants alter their root development in response to nutritional requirements, and these variations can serve as a nutrient status indicator. Transporters in the root plasma membrane are the entrance point for nutrients into the plant, and their selectivity is significant in determining the toxicity of specific elements (Miller 2014).

Nutrient scarcity has a severe negative impact on crop productivity worldwide, resulting in decreased yield and poor-quality food and feed. At the same time, improper fertilizer use can contaminate both terrestrial and aquatic habitats and a significant amount of energy required in fertilizer production, which leads to climate change. Mineral nutrient efficiency in crops is usually characterized as the ability of the crop to absorb mineral nutrients and produce biomass or yield using the mineral nutrients obtained. As a result, due to inadequate nutrient efficiency, more than half of the chemical fertilizers applied are lost. So, creating crops with high mineral nutrient efficiency is crucial for agricultural sustainability, which needs a better understanding of crop responses to mineral nutrient insufficiency (Xu et al. 2012a, b).

5.4 Integrated Omics for the Development of Abiotic Stress Resilience in Cereals

According to recent research, among all the abiotic stresses, drought has been the most severe one affecting cereal crop productivity. Traditional breeding programs including screening were more laborious, yield-oriented, and focused on disease resistance rather than ameliorating the underlying mechanism of abiotic stress. The decline in the rate of major cereal crops prompted scientists to build a molecular breeding approach related to the constitutive (stress avoidance) and intrinsic traits (stress tolerance) of plants. The cumulative effect of several stresses at the same time just exacerbated the situation (Dolferus et al. 2011). Hence, to reduce the gap between studies and challenges, multidimensional modern omics approaches reduced the technical difficulties to a large extent and substantially expanded the depth of research in physiology and systems biology (Shelden and Roessner 2013). The advancement in MAS (marker-assisted selection) (Akpinar et al. 2013), WGS, RNA sequencing, etc. removed several limitations of QTL studies, EST, and microarray for generating genomic data. It was validated by both organellar and tissue-specific proteomic studies which provided insight into stress-acclimatized proteins. Proteomic research resulted in the identification of several abiotic stress-sensitive proteins. The most common technique for separating proteins is through two-dimensional electrophoresis (2-DE). The emerging proteomic advancement has enhanced the accuracy for screening the developmental phase of the stress, analyzing the resistivity of cereal crops, and monitoring their high-throughput stress-responsive proteins by MS.

The discovery of abiotic stress-resilient mechanisms with omics has provided enormous opportunities in cereal research including (1) genome similarity and conserved genome order on the chromosome (synteny) between several cereal species for positional cloning, (2) development of the mutant line of populations with single base pair mismatches in cereals and transposon-tagged lines with Ac/Ds, (3) extensive mapping of the stress-resilient traits and map-based cloning by merging of the QTL identified on different chromosome maps of cereals for analysis, and (4) exploiting alternative efficient screening methods and designing a plant model system (*Arabidopsis*) to compare, identify, and transform stress-resilient germplasm by the omics approach. Interactome studies with traditional approaches proved complex due to the massive genome sequences, products, and related defense responses. Therefore, a shift toward transgenic methods through omics approaches offered a lot of potential for transferring stress-tolerant genes across species (Jha et al. 2014). Omics approaches are being seen as a prominent and promising tool for venturing into the profiles of stressed tissues.

5.5 Future Perspectives

A targeted research point of view is desirable to combat environmental stress and reuse natural resources. The impact of stress during the reproductive stages in the field are critical for rain-fed, drought-prone environments. The current omics studies dominate more with the comparative analysis of the differential expression of the stressed plant with respect to wild-type crops. However, focused strategies on proper integration and interpolation of the genomic and proteomic accessible data are emerging exponentially. Specific omics tools will play an important role to widen the window of molecular breeding, genetic-phenotypic mapping, QTLs, hybridization, single-cell genome sequencing, positional cloning, alternatives to gene silencing, transgenic approaches, etc. Future studies would be more specific on tissue, cell line, or growth stages, rather than the whole plant organ with improved dissection and isolation techniques. PTM, protein-protein interactions, protein isoforms, GWAS, and stress markers are the emerging fields of studies, revealing novel candidate genes in response to abiotic stress (Fig. 5.1). This advancement not only would open up new avenues for co-expression and network analysis but are highly recommended to produce high-yielding and stress-resilient crops.

Omics is an essential step toward accelerating such breeding initiatives throughout the world, which may provide massive insight into stress physiology and metabolism. Identification of novel genes controlling stress tolerance can increase crop yield. It has been reported that drought and salinity hit crop productivity more severely. Hence, in-depth attention is required for the characterization of the traits, compatibility evaluation, and development of stress-resilient crops under various environmental conditions. Both environmental stress and population growth has put alarming pressure on plant breeders. It is becoming increasingly evident that crop development must rely on omics tools for gene identification and high-yielding germplasms to ensure future food security across the world.

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