doi:10.20944/preprints201806.0455.v1

Peer-reviewed version available at *Int. J. Mol. Sci.* **2018**, *19*, 2390; doi:10.3390/ijms19082390

Omics approaches for engineering wheat production under abiotic stresses

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Peer-reviewed version available at Int. J. Mol. Sci. 2018, 19, 2390; doi:10.3390/ijms19082390

Abstract

Abiotic stresses greatly influenced wheat productivity executed by environmental factors such as drought, salt, water submergence, and heavy metals. The effective management at molecular level is mandatory for thorough understanding of plant response to abiotic stress. The molecular mechanism of stress tolerance is complex and requires information at the omic level to understand it effectively. In this regard, enormous progress has been made in the omics field in the areas of genomics, transcriptomics, and proteomics. The emerging field of ionomics is also being employed for investigating abiotic stress tolerance in wheat. Omic approaches generate a huge amount of data, and adequate advancements in computational tools have been achieved for effective analysis. However, the integration of omic-scale information to address complex genetics and physiological questions is still a challenge. In this review, we have described advances in omic tools in the view of conventional and modern approaches being used to dissect abiotic stress tolerance in wheat. Emphasis was given to approaches such as quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), and genomic selection (GS). Comparative genomics and candidate gene approaches are also discussed considering identification of potential genomic loci, genes, and biochemical pathways involved in stress tolerance mechanism in wheat. This review also provides a comprehensive catalog of available online omic resources for wheat and its effective utilization. We have also addressed the significance of phenomics in the integrated approaches and recognized high-throughput multi-dimensional phenotyping as a major limiting factor for the improvement of abiotic stress tolerance in wheat.

Keywords: Abiotic stresses, GWAS, Ionomics, Omics, Phenomics, QTL

Introduction

Wheat is one of the 3rd most cultivated cereal crop throughout the globe (Acevedo et al. 2002) which covers 22% of the cultivating land. It belongs to the family of Gramineae (Poacea). It mainly grows in the temperate zones with cool weather (12-25 ^{0}C temperature) and having 250-1750 mm annual precipitation [1]. It is widely planted at the end of autumn season as it needs the cold treatment for flower initiation, which is called vernalization process [2]. A recessive allele of Vrn genes on 5A, 5B and 5D genomes is responsible to control this growth habit of winter wheat, which requires 40 ^{0}C temperature prior to tillers and elongation stage [2, 3]. Both Genotypes and

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photoperiod are major factors to control the flowering pattern in wheat which lack photoperiod insensitivity genes (Ppd) need exposure to long growing days [4].

Abiotic stress is one of the key factors limiting the crop production. Environmental stresses like drought stress, salt stress, heavy metals stress as well as water submergence stress influenced the crop yield in different manner. To overcome such problems, local cultivars should be modified by making molecular changes in the gene [5]. Although the multi-selection field trials method has been widely used for direct selection of the tolerant varieties to any harsh environment however, this selection method doesn't provide significant results for the abiotic stress related traits due to highly influenced by environmental condition and low heritability [6]. In addition, this direct selection approach is quite laborious as well as time consuming. The genetic variation in different yielding crops could lead to the development of the tolerant cultivars but there is a knowledge gap which needs strong effort to find the specific molecular marker [7]. The development of molecular markers will provide the new and latest sequenced genomes and organelles in crops [8].

Recently, the development of molecular markers to characterize the complete genome sequence plays a crucial role in marker-assisted breeding [9]. The availability of high density markers helps to identify different alleles involved in agronomics traits and also helps in haplotype analysis [10]. In addition, marker-assisted breeding has been accomplished for the simple traits, which is controlled by a single or fewer loci [11; 12] however, such breeding also suffers due to unsought genetic strains [11]. The phenotypic expression of the newly developed gene (s) is controlled by the genetic makeup of the repeated parents, which is mainly due to epistatic interaction [13], and this epistatic interaction in mostly unpredictable in case of multiple complex traits, unless some proper evidence is available about the molecular processes involved during the developments of new traits. Current improvement in the genomics can easily predict the factors involved in their genetic variation, traits developments, distribution as well as interaction with the host environment [14]. Genetic Engineering is an advanced approach mainly used for the genetic enhancement of the plants. Interestingly, genetically modified (GM) plants has been proven to be successful for herbicide and insect tolerance, and widely used throughout the world [15]. A combination of multi-disciplinary knowledge is required for the development of an ideal plants, which could provide better yield even at adverse climatic conditions. This review has been written to explain the recent achievements in various omics approaches and to elaborate the future outcomes for the development of abiotic stress tolerant varieties.

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Technological advances have also provided a high-throughput, reliable, and quick array-based genotyping platforms. The SNP array development require initial information about SNPs, fortunately, information about millions of SNPs is already available in the public domain (Table 1). The Illumina Infinium array (SoySNP50K iSelect BeadChip) for ~50,000 SNPs has been successfully developed and used for the genotyping of several soybean plant introduction (PI) lines [16]. Technological advances beyond this make it possible to resequence hundreds of lines in a cost effective manner and has started a new era of genotyping by re-sequencing [17]. Now, the challenge for plant biologists is how to effectively use these resources for marker-assisted applications.

Omics approaches in technological era

When genetics, nutritional or environmental conditions is changed, diverse omics technologies fulfil the understanding of all the changes that occur. Omics are useful in the understanding of species and thus providing insight into modification of the plant metabolism which results through contact with environment. The era of genomics had been started with the development of automated sequencing methods and led to first whole genome sequencing of *Arabidopsis thaliana* [122]. The genome sequencing has been stretched out to major crop plants such as rice [18; 19], soybean [20], maize [21]. The emergence of highly throughput “Omics” approaches has begun a successful period of plant molecular techniques for adjusting to changes in the environment. Recent development in ‘omics’ after post genomic era such as next generation sequencing, genome scale molecular analysis, modeling of different physiological and molecular understanding and correlation of these observations with physiology of the plant provides an accomplished move to adaptability and productivity under stress. Latest advent of next generation sequencing methods made possible sequencing the plant species quite useful [22]. Allohexaploid bread wheat (2n=6x=42, AABBDD genomes) is one of the complicated genomes in which homologous chromosomes having similar genes could complicates the reconstructing process of biological networks. A draft of wheat genome is completed which shows more than 124,000 gene loci which covers all the sub-genomes (A, B, and D) and proves useful in identifying genes which control biological process. Further, modern utilization of transcriptomics (RNA-seq) and proteomics (targeted vs non-targeted proteins) will help in defining their functions at gene and protein level respectively. As all genes are not always turned on at the same time therefore the metabolism becomes quite dynamic in phenotype which cannot be derived from the genotype. Thus, the

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successful integration of the transcriptomics (gene), proteomics (proteins), metabolomics (metabolite), ionomics (analysis of elemental compositions), epigenomics (inheritance), interactomics (protein-protein or protein-DNA interactions) will facilitate the breeder to select the potential candidates and best traits to generate and improve the crop productivity under abiotic stress (Fig. 1).

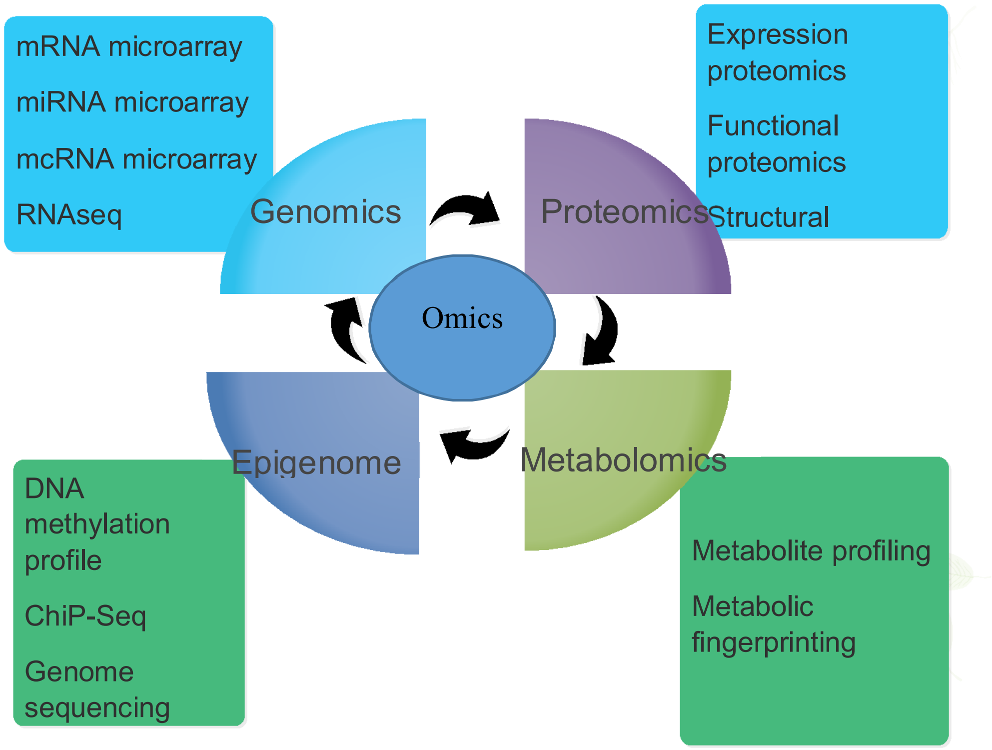

Figure 1. Key branches of omics and their major components being used in different integrated approaches in wheat.

Genomics progresses for abiotic stress tolerance in wheat

Genomics emphasis on the genome physical structure, aiming to recognize, detect, and order genomic structures along chromosomes. Here we discuss some of genomic progresses to understand an abiotic stress tolerance in wheat.

Molecular marker resources

The emergence of genomic technology has opened a new window in genetic enhancement of more complicated traits such as salt and drought tolerance. The amalgam of genomic approaches along with marker assisted selection (MAS) can be helpful in the identification of specific genes at a much fast rate in breeding population as compared to classical breeding [23, 24, 25, 26].

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Developments in MAS for wheat was lagged behind due to limited genomic data but recent progress in DNA sequencing and genotyping techniques have developed genome datasets which are much useful in designing sequence based simple sequence repeats (SSRs) and SNP markers [27, 28, 29]. SNPs are frequently used for genome mapping and germplasm characterization as compared to other molecular markers. As SNPs are highly-throughput, rapid, cost-effective, co-dominant, sequence tagged and highly abundant, they are appropriate for division of complex traits using highly multiplexed marker microarrays such as the Affymetrix GeneChip [30, 29]. For instance Axiom Wheat Breeders' genotyping array, robust system for screening large wheat population, is developed recently. It is a cost effective and efficient genotyping method having 35,143 pre-validated SNPs which covered all wheat chromosomes and have ability to genotype 384 samples at once. In duram wheat, it has been applied recently in the development linkage map of high density and also in identifying the genomic areas of complex traits such as drought [31].

QTL Mapping for abiotic stress

For agronomically important traits, linkage maps are necessary for mapping the QTLs as they are constructed from genotypic data from multiplexed marker assays [32-35]. High-density linkage maps also offers a genomic resource for positional cloning of significant genes. They can also be applied in comparative genomics to assess chromosomal organization and evolution as they are constructed from sequence tagged markers. In the linkage map, markers are helpful in identifying regions having QTLs of selected traits and several QTLs have mapped previously for salt tolerance [36, 17, 35] and drought tolerance [37-39] in wheat cultivars (Table 1).

Advances in genomics and phenomics provide us more precise and broad characterization of the QTLs that control a targeted trait known as QTLome. The vast knowledge on QTLome put a responsibility on breeders to utilize this knowledge in effective way. Enhanced QTL meta-analysis, valuation of QTL effects and upgraded crop modeling will allow an actual utilization of the QTLome [40].

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Table 1: Major and stable QTL with PVE ranging from 19% to 59% for agronomic and physiological traits

S.No.	QTL	Linked markers	Position	Env. [a]	PVE (R2) [b]	References
Agronomic traits						
1. Grain yield						
a	qGYWD.3B.2	Xgpw7774	97.6	7/4	19.6	[41]
b	4A	Xwmc420	90.4	Mean/2	20	[42]
c	4A-a	Xgwm397	6	7/5	23.9	[43]
d	Qyld.csdh.7AL	Xgwm322	155.9	21/11	20.0*	[44]
2. 1000-grain weight						
a	3B	Xbarc101	86.1	Mean/2	45.2	[45]
b	QTgw-7D-b	XC29-P13	12.5	11/10	21.9	[46]
3. Days to heading						
a	QDh-7D.b	XC29-P13	12.5	11/11	22.7	[47]
b	QHd.idw-2A.2	Xwmc177	46.1	13/16	32.2	[46]
4. Days to maturity						
a	QDm-7D.b	X7D-acc/cat-10	2.7	11/10	22.7	[48]
Physiological traits						
1. Stem reserve mobilization						
a	QSrm.ipk-2D	Xgwm249a	142	2/2	42.2	[48]
b	QSrm.ipk-5D	Xfbb238b	19	2/2	37.5	[48]
c	QSrm.ipk-7D	Xfbb189b	338	2/2	21	[48]
2. Water Soluble Carbohydrate						
a	QWsc-c.aww-3A	Xwmc0388A	64.9	2/2	19	[49]
3. SPAD/Chlorophyll Content						
a	Qchl.ksu-3B	Xbarc68	67.2	3/2	59.1	[50]

[a]Number of environments in which QTL was detected/number of total environments; [b]highest PVE (R2) values under drought/water stress, * with >20% higher yield per ear.

Genome wide association studies

Alternative strategy to resist the shortcomings is association mapping based on traditional meiosis in the divergence analysis and gives accurate results [51]. It is quite feasible and cost effective to establish association mapping in comparison to RIL development. In association mapping, experimental structures and statistical evaluation is constantly fluctuating to diminish the results of confounding factors, decrease false positives and also control minor allele effects (Fig. 2). Genetic interaction and population designs confuse marker-trait relations results in the disequilibrium without true linkages [52]. To decrease false positives and minor allele QTL effects, several diagnostic and precise statistical analyses have been developed. Studies have been carried out on the correct genomic locations of developing genes such as reduced height (Rht), vernalization (Vrn), and photoperiod responsiveness (Ppd) and used as standard measure in order to incorporate phenotypic diversity and markers present in the study [3]. As genetic reference, these genes possess the stress adaptive capability by changes heading date, plant height, maturity and other physiological processes [53].

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Figure 2. Combined approach of QTL mapping/Genome-wide association study (GWAS) and Genomic selection (GS).

Genomic selection

The emergence of model based association and easy availability of molecular markers, a correlated concept known as genomic selection has emerged to assess genotypic breeding value [54]. This technique is utilized to minimize the shortcomings of map based genetic analysis that identify very few QTL to explicate the divergence in targeted traits [54, 123]. The concrete significance of evaluated QTL effect and linkage disequilibrium based on the genetic relatedness and divergence of the population under study. Populations that shows more allelic variants of targeted traits display more precise evaluation of QTL effect compared to populations which are more closely related. Linkage disequilibrium is often overvalued in closely related inter-mating individuals and diminish

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in further meiotic events [55]. Genomic breeding value can be predicted by genomic selection by transforming marker assisted selection with the help of markers. A model that is established and evaluated using genotypic and phenotypic data of study population will be utilized to assess phenotypic variation of sample population based on their genetic composition only. This will enhance genetic gain in comparison to both QTL and phenotype-based selection [56].

Statistical methods are used to develop genomic selection models that explains the properties of various markers and traits [57, 123]. The distribution of marker effects and random sampling of germplasm from selected population is being considered by the multiple regression models [58]. Genomic best linear unbiased prediction evaluates genetic relatedness among individuals on the basis of molecular marker composition similarity and also assess their phenotypic performance. Such a model is similar to estimation of breeding value (BV) from heritability and phenotypic performance of related genotypes in a pedigree [54, 123]. Statistical analyses shows that forward and mixed type regression models have ability to remove markers on the basis of their relative significance effect. Ridge regression have an additional feature of incorporating penalty parameter in the design for the markers in excess of statistically accepted number (> number of genotypes) [59].

Transcriptome profiling for abiotic stress tolerance

In wheat, expressed sequence tag databases showed that homologous genes can show expression in one but remain silent in one or both of the remaining genomes in the analysis of gene expression [60]. For the cereals, various microarray and macroarray platforms have been developed. There are various significant arrays like 10000 cDNA array reported by Leader [61] and Affymatrix arrays have been developed for wheat and barley recently [62]. In abiotic stress conditions in variety of plants, microarray is one of the successful method for the genome wide transcript expression profiling and is being widely used to generate transcriptional profiles (Fig. 3). Studies have been carried out in barely in response to salt stress [63, 64] and the model cereal *Brachypodium* [65] but there are limited research on wheat due to polyploidy genome [66]. The high-throughput analyses of gene expression is being enabled by deep genome sequencing technology (RNA-Seq) which proves to be successful technique to identify precise changes in the genome. Next-generation sequencing technology is in the emerging phase in plant studies but it is predicted to replace microarray technique due to its accurate results. Due to lack of fully sequenced and complex genome (hexaploid) in wheat present many difficulties to “OMICS” studies. Meng

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et al. [67] assessed alkalinity stress by digital expression tag profiling method in wheat. Poersch-Bortolon et al. [68] assessed the extreme drought stress in roots and leaves by examining their expression profiles which prove to be helpful in marker development and selecting the significant important genes. These expression profiles are also prove useful in wheat drought stress by examining their metabolic processes. Ma et al. [69] conducted an RNA-seq analysis to analyze the effect of drought on wheat genome during reproductive stages. Salt stress responsive gene networks and functional annotation was identified by differential root transcriptome analysis which prove to be helpful in understanding the process and genes role in salt tolerance as analyzed by Goyal et al. [70].

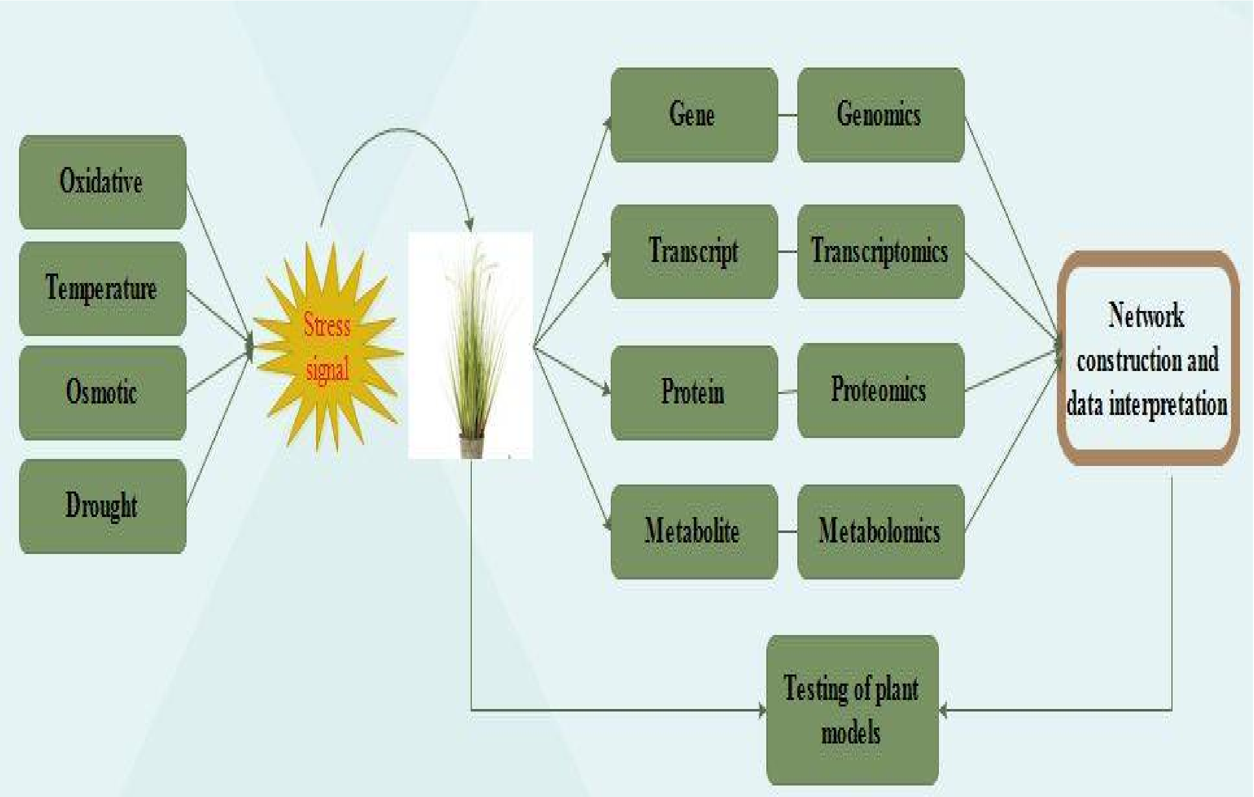

Figure 3: General outline of ‘omics’ approach for network construction, data interpretation and model testing.

Proteomics in wheat

It is imperative to study proteome alterations at various stress conditions as proteins play a role in plant stress response. The initial plant response to stress conditions is the cellular processes of

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stress sensing and signaling processes. In order to understand the stress coping mechanisms in plant, effective characterization and isolation of stress responsive proteins is required step. Understanding of post-translational modification of proteins is necessary in plant stress conditions. Study of proteomics provides vast information on the fine-tuning of cellular pathways that once took part in stress mitigation. The significant data related to changes in response to abiotic stress and their major role in differential stress response is elaborated in Table 2.

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Table 2. A list of wheat proteomic studies focused on response to abiotic stresses and others

Stress/ Conditions	Treatment time and dose	Cultivar	Organ/ Organelle	Proteomic technologies	Stress induced modulation of metabolic pathways	Differentially expressed protein classification		References
						Functions	Localizations	
Flooding	7 d	Bobwhite line SH 9826	Seminal root	2-DE, nano LC-MS/MS	Antioxidant defense	StrRes	-	[71]
Flooding	2 d	Shiroganekomugi	Root	2-DE, nano LC-MS/MS	Carbohydrate (Glycolysis)	EnMet, ProtMet, SigTran, Tranp	Cell wall	[72]
Drought	100 d	Opata, Nesser	Root	iTRAQ	Energy metabolism, Replication, Repair	EnStr, Oxired, Trans	Mem, Cyto, Cell wall, Mito, Nucl, Plast, Vacu	[73]
Drought	7 d	Ofanto	Leaf	2-DE, MALDI-TOF	Carbohydrate (Glycolysis, gluconeogenesis)	PTR, StrRes, TCA, ROSsca, AAB, GG	-	[74]
Drought	7 d	Katya, Sadovo, Zlatitza, Miziya	Leaf	SDS-PAGE, 2-DE	Energy (photosynthesis)	EnMet, EnvDevS	Chlo	[75]
Drought	9 d	Keumkang	Leaf	2-DE, MALDI-TOF/TOF	Energy (photosynthesis)	Photo	Chlo	[76]
Drought	10, 15, 20 and 25 d	Janz, Kauz	Seed	2-DE, MALDI-TOF	Carbohydrate metabolism	ROSsca, CarMet,SigTran	-	[77]
Drought	14, 24 d	Kukri, Excalibur	Leaf	iTRAQ	Energy (photosynthesis)	Photo, GG, ProtF, Tranp, EnStr	-	[78]
Drought	20% PEG	Hanxuan 10 and Ningchun 47	Leaf	nano LC-MS/MS	Antioxidant defense	DRM, SigTran,	-	[79]

						StrRes, ROSsca		
Heat and Drought	10 d	Vinjett	Kernel	2-DE, MALDI-TOF	Carbohydrate (Glycolysis)	CarboMet, STP	-	[80]
High Temperature	37°C d, 28°C N/10 d, 20 d	Butte 86	Endosperm	2-DE, QSTAR PULSAR-TOF	Carbohydrate metabolism	CarboMet, NitMet, ProtMet, StrRes, STP, SigTran, Tranp, Trans	-	[81]
Salt	150 mM NaCl/1 d, 2 d, 3 d	Keumkang	Leaf	2-DE, LTQ-FTICR-MS	Energy (photosynthesis)	Photo, StrRes	Chlo	[82]
Salt	1.0, 1.5, 2.0 and 2.5% NaCl in HS/2 d	Zhenhmai 9023	Leaf	2D-DIGE/Q-TOF-MS	Carbohydrate metabolism	CarMet, ProtF, Tranp, ROS, ATP	-	[83]
Salt	200 mM	Wyalkatchem, Janz	Shoot	2-DE, LC-MS/MS	-	-	Mito	[84]
Aluminum	250 µM/2 d, 3 d	Atlas-66, Fredrick	Root	SDS-PGE, Immunoblot	Signaling pathway	Oxi	-	[85]
Aluminum	100, 150 µM/5 d	Keumkang	Root	2-DE, LTQ-FTICR-MS	Energy (Glycolysis)	Gly, Tranp, SigTran, StrRes, EnMet	-	[86]
Copper	100 µM/3 d	Yumai 34	Root, Leaf	2-DE, HPLC-Chip/ESI-Q-TOF/MS/MS	Energy (photosynthesis), antioxidant defense	StrRes, SigTran, ProtMet, CarMet, Photo, EnMet	-	[87]

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Protein Profiling	20 d	Keumkang	Leaf	SDS-PAGE, LTQ-FTICR	Energy (photosynthesis)	COB, DevPro, DRM, ProtF, ProtMet, StrRes, Tranp, Trans	Chlo	[88]
Protein Profiling	Mature seed	Wild type (AA, BB, DD genome)	Seed	SDS-PAGE, nano LC-MS/MS	Carbohydrate metabolism	StrRes, EnMet, ProtS, CGD, COD, ProtF, SigTran, STP, Tranp	-	[89]
Cadmium	10, 100, and 200 µM	Yangmai 15	Leaf	IPG, MALDI-TOF	Energy (photosynthesis)	Oxi, ProtMet, Photo	-	[90]
Cadmium	0.5mM/L	Yangmai 13	Leaf	IPG, MALDI-TOF	Antioxidant defense	ROSsca	-	[91]

AAB- Amino acid biosynthesis; ATP-ATP synthase; CarMet-Carbohydrate metabolism; CGD-Cell growth and division; COB- Cell organization; COD-Cellular organization and development; DevPro-Developmental process; DRM-DNA and RNA metabolism; EnMet-Energy metabolism; EnStr-Environmental stress; EnvDevs-Environmental and developmental signals; GG-Glycolysis and gluconeogenesis; Gly-Glycolysis; NitMet-Nitrogen metabolism; Oxi- Oxidative stress; OxiRed-Oxidation-reduction process; Photo-Photosynthesis; ProtF-Protein folding; ProtMet-Protein metabolism; ProtS-Protein synthesis; PTR-Post-transcriptional regulations; ROSsca-ROS scavenging; SigTran-Signal transduction; STP- Storage proteins; StrRes-Stress response; TCA- Calvin cycle; Tranp-Transport, Trans-Translation; Chlo-Chloroplast; Mem-Membrane; Cyto-Cytoplasm; Nucl-Nucleus; Mito-Mitochondria; Plast-Plastid; Vacu-Vacuole; HS-Hoagland solutin

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Metabolomics advances for abiotic stress

Metabolites provides the energy which is necessary for metabolism and growth of protoplasm as they are basic elements of various structural and enzymatic molecules. Metabolites not only serve as a link between phenotype and genetic information but also play a role in determining the physiological condition of organism. Metabolomics along with other disciplines played a significant role in understanding the inter-related biological processes linked to phenotypes. In functional genomics, metabolic profiling is an emergent tool [92]. The co-existence of gene transcript and metabolites provides a foundation for generating data-driven theoretical models of the biological phenomenon [93-95]. In the study of mutants and transgenic lines, metabolomics not only help in understanding metabolic systems but also give information about candidate gene [96-98]. The metabolic study also explains that how some particular gene effects metabolic pathway and its intervention with other pathways which is not possible with other techniques such as microarray [99, 100].

The advances in metabolomics, the availability of whole genome sequence, genome-wide genetic variants, and cost-effective genotyping assays has opened exciting doors to blend metabolomics with crop breeding programs [101, 102]. Mass spectrometry (MS) and nuclear magnetic resonance (NMR) spectrometry proved to be successful technologies. Metabolomics cover not only familiar metabolites but also unfamiliar metabolites as confirmed by wide scale metabolite assessments. But managing the ample data is still a challenge [103, 104]. Metabolic annotation can be progressed through metabolomics approaches when coupled with advance bioinformatics techniques, for instance, the one for model plant *Arabidopsis* [105, 106]. Genomic data can also be improved through the sequencing of DNA, RNA, and MS quantification of proteins and metabolites which helped in the improving of targeted traits [107]. A number of studies have been conducted on agriculturally useful crops to evaluate the effect of salinity and drought on metabolic activity of crop as metabolic study are helpful in studying stress responses [108, 109]. The enhance tolerance of some particular gene may be due to different phenotypic responses which explains the specific metabolic changes. Improvement of breeding material and selection of higher traits can be facilitated through metabolomics approaches [110]. In bread wheat genome, the polyploidy nature is quite distinctive as it has ability to tolerate considerable chromosomal aberrations and allowing phenotypic assessment as a result of multiple gene loss. Aneuploidy genetic lines of wheat proved to be effective experimental design to assess genetic networks as they are helpful in

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identifying those genes which control phenotypes [111, 112]. Michaletti et al. [113] concluded that the study of metabolomics and proteomics reveal drought stress responses of leaf tissue from spring wheat and provide a better framework for understanding the mechanisms that command plant cell response to drought stress with knowledge of molecules that can be used for crop improvement programs.

Ionomics for wheat

Ionomics is a high-throughput elemental profiling approach to study the molecular mechanistic basis underlying mineral nutrient and trace element composition of living organism. It also represents the inorganic component of cellular and organismal systems [114]. Its wide role in forward and reverse genetics, screening of mutants, uncovering the mechanisms of ion uptake, compartmentalization, transport and exclusion, useful in understanding the processes of abiotic stresses in plants [115]. Ionomics along with relevant genomic data can identify the cellular changes during abiotic stresses and the basic processes involved as well. Ionomics are also helpful in identifying rare genes which code for ions by using phenotypic and genotypic data as obtained from mapping populations. It is prove to be helpful in understanding the gene networks which control ion accumulation at varied growth steps under the conditions of abiotic stress [116]. The literature available on ionomics approaches is limited, however, the highly effective ion profiling will open new doors in understanding the signaling mechanism for abiotic stress tolerance.

Phenomics prospective in wheat

Phenomics is a study of high-throughput phenotypic analysis. It has become possible to predict abiotic stress genotypes through phenotyping approaches [117]. For high throughput plant phenotyping, the automated Greenhouse system is a successful procedure. This system permits the non-destructive screening of plants over a particular period with the help of image acquisition techniques. The different images of each plant are recorded and then evaluated using advanced image analysis algorithms to predict plant with certain phenotypes [118]. The plant with tolerant phenotypes proved to be best sources of genomic resources and also became target for different molecular approaches including the high-throughput sequencing to identify the alleles of interest. However, phenomics also have some disadvantages as it did not provide accurate correlation among the values obtained in the pot culture versus field experiment.

Role of Online Databases for Effective Integration of Omics Platforms

The emerging progress in the omic approaches has established a huge data which prove to be helpful in number of research activities. Computational resources have helped to store, catalog and analyze data and make it easily available through user friendly "databases."

A number of databases have developed for wheat (Table 3). The most reliable database is (http://www.gramene.org) which gives wide information for omics data from number of other sources. These databases provide useful information regarding wheat translational genomics and molecular breeding research. It contains information of genes, proteins, microRNAs, sRNAs, metabolites, molecular markers, and phenomic information of soybean plant introductions (PI). Integration of multi-omics datasets information are also present in these databases. For example, genes in the QTL region can be retrieved very easily along with the functional annotations, associated protein information in respect of structure and functional features, syntenic information with other model plants, sequence variation among different cultivars, gene expression data including tissue specific variations and many other types of information for wheat.

Table 3: Online transcriptomics resources in wheat

Resources	Description/URL
Genome sequence	• Coordinated effort underway by the IWGSC (http://www.wheatgenome.org) • Recognized as a priority by research community (http://www.csrees.usda.gov/nea/plants/pdfs/wheat_conference_summary.pdf)
ESTs1	1 050 791 entries
Oligonucleotide microarray	1 050 791 entries
cDNA microarray	Multiple including ~9 K array
Tiling microarray	Not currently available
Serial Analysis of Gene Expression (SAGE)	Applied for studying developing wheat caryopsis
Massively Parallel Signature Sequencing (MPSS)	Not reported
Sequencing-by-synthesis	Roche 454 cDNA sequencing (Deven See, personal communication, 2008)
Deletion and aneuploid genetic stocks	Roche 454 cDNA sequencing (Deven See, personal communication, 2008)
Transformation	Biolistic- and Agrobacterium-mediated DNA delivery systems
Gene knockdown	• RNA interference • Viral-induced gene silencing
Databases/tools	• Graingenes (http://wheat.pw.usda.gov) • Gramene (http://www.gramene.org)

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- TIGR Genome Database (http://www.tigr.org/tdb/e2k1/tae1)
- Wheat Genome Project (http://wheat.pw.usda.gov/NSF/htmlversion.html)
- Wheat Genome Project (http://wheat.pw.usda.gov/NSF/htmlversion.html)
- wEST (http://wheat.pw.usda.gov/wEST)
- CerealsDB (http://www.cerealsdb.uk.net)
- HarvEST Wheat (http://harvest.ucr.edu)
- PLEXdb (http://plexdb.org)
- Gene Expression Omnibus (http://www.ncbi.nlm.nih.gov/geo)
- ArrayExpress (http://www.ebi.ac.uk/microarray-as/ae)
- GrainSAGE (http://www.scu.edu.au/research/cpcg/igfp/index.php)
- Wheat SNP Project (http://wheat.pw.usda.gov/SNP/new/index.shtml) [121]

Conclusion and future perceptive

Different omics tools have been employed to understand how soybean plants respond to abiotic stress conditions. We realize that the studies to integrate multiple omics approaches are limiting in soybean due to the increased cost and potential challenging integrated omic scale analysis. Recent developments in computational resources, statistical tools, and instrumentation have lowered the cost of omics in many folds but integrated analysis needs novel tools and technical wizards. The comprehensive nature of multiomic studies provides an entirely new avenue and future research programs should plan to adapt accordingly. In soybean, genomics and transcriptomics have progressed as expected but the other major omic branches like proteomics, metabolomics, and phenomics are still lagging behind. These omic branches are equally important to get clear picture of the biological system. Notably, phenomic studies need to be extensively employed along with the other omics approaches. Desired phenotype is ultimate aim of crop sciences; therefore it needs to be understood intensely. Different omic tools and integrated approaches discussed in the present review will provide glimpses of current scenarios and future perspectives for the effective management of abiotic stress tolerance in soybean.

A major focus in the future will be the merging and comparative analysis of transcriptome data between researchers. In particular, there are large resources of wheat microarray data now available, which provide opportunities for gene coexpression network analysis. The merging of data derived from a standardized platform, such as the Affymetrix Wheat GeneChip, will be much easier than cross-platform merging. For example, the authors of this review have participated in

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four studies of the wheat transcriptional response to rust pathogens using the Affymetrix Wheat GeneChip platform. The data from these four studies will be integrated to perform a gene coexpression network analysis that has the potential to identify key gene expression signatures involved in rust resistance. This type of analysis has been successful in associating abiotic stress phenotypes in A. thaliana with underlying common and unique gene expression pathways and marker genes [115]. The linking of gene expression data to genetic information is also of great importance to understand the interplay among genome, transcriptome and phenotype. Simultaneous surveying of the genome and transcriptome on a single platform through, for example, the ELPs and SFPs discussed earlier, is a valuable technique for uncovering genetic elements that influence the transcriptome. Overall, wheat transcriptomics is progressing rapidly and in the future we will see a complete systematical approach that integrates the transcriptome with genome, proteome and metabolome. Additionally, gene expression databases will expand and become more standardized, which will accelerate the discovery and characterization of all genes in the wheat genome.

Acknowledgments

We are very thankful to all staff of Oil Crops Research Institute, Wuhan for their support and motivation. This research was funded by the National Key Research and Development Program of China (2017YFD0101700), the National Natural Science Foundation of China (31301361, 31171589).

Author's contribution

TS wrote the manuscript, JX help in literature XZ helped in making diagrams and XZ read the paper

Conflict of Interest

The authors declare that they have no conflict of interest.

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