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Review

The Importance of Multi-Omics Studies for Stress Tolerance and Plant Growth in Sustainable Agriculture

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Abstract

One of the most important transformative strategies for better understanding of plant resilient against abiotic and biotic stresses are the integration of omics approaches, encompassing genomics, metabolomics, proteomics, transcriptomics, and phenomics. Genomics explores genome structure, evolution, and function, and advances in next-generation genome annotation and sequencing have enabled the accurate and complete decoding of different plant genomes. Epigenetics involves heritable gene expression alterations without DNA sequence changes, mainly through histone modification, and DNA methylation. Among the main epigenetic mechanisms, DNA methylation is particularly important in plants and is maintained throughout mitosis. Transcriptomics is a study of all RNA molecules transcribed in a cell or organism, providing useful information about dynamic patterns of gene expression. Recent advances in sequencing technology have enabled more evolutionary and accurate transcriptomic analysis. Metabolomics is a powerful approach because metabolites and their concentrations Metabolomics is known to provide a direct functional readout of the physiological state of an organism. It can deal with qualitative and quantitative assessment of metabolites, which are necessary intermediates and end products of metabolism. Metabolomics uses targeted approaches such as quantitative and hypothesis-driven as well as non-targeted approaches to characterize plant metabolites. This article aims to study the importance of multi-omics studies for crop abiotic and biotic stress tolerance while considering plant growth in sustainable agriculture. To provide a comprehensive understanding of the metabolic, epigenetic, and genetic bases of main agronomic traits in crops, considering the integration of multi-omics data is necessary. The integration of different technologies can induce better optimized farming activities, sustainable agriculture, and crop improvement.

Keywords: genomics; epigenomics; transcriptomics; proteomics; metabolomics; phenomics; single-cell

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1. Introduction

Plants are subject to different types of abiotic and biotic stress, which can influence physiology, metabolism, growth, and morphology [1–3]. Drought is among the most common severe threats to crop quality and productivity all over the world [4], and recently three main types of researches such as RNA-mediated gene silencing, histone modification, and DNA methylation have found effective to increase resistance exist at both epigenetic and genetic levels [3,4]. Another important abiotic stress parameter is salinity, especially

in arid and semi-arid regions [5]. Another major factor that can determine the cultivation area of crops is temperature [4,5]. Functions of drought-inducible genes in stress responses and tolerance are categorized into two groups: functional proteins such as water channels and transporters, detoxification enzymes to reduce reactive oxygen species (ROS), protection factors of macromolecules (chaperons, late embryogenesis abundant (LEA) proteins), proteases, key enzymes for osmolyte biosynthesis like sugars and proline, and regulatory proteins, protein kinases and phosphatase, transcription factors such as bZIP, MYB, MYC, AREB, DREB2, NAC HB, phospholipid metabolism, and abscisic acid (ABA) regulation [6]. Heat stress (HS)-driven challenges and responses of plants, under heat stress may cause decrease in plant productivity, pollen viability, fruit quality, inflorescence, leaf structure integrity, stomatal conductance, relative water content, shoot and root growth, photorespiration, photosynthetic rate, respiration rate and seed germination as well as increase in cell membrane fluidity, cell membrane permeability, specialized metabolites production and harmful ROS production [5,6]. Plant responses to cope with elevated temperatures are thermomorphogenesis, HS sensing and perception, cell wall remodeling, heat-responsive chemical and phytohormone signaling, heat-responsive genetic elements, activation of antioxidant defense, elevated production of secondary metabolites, leaf rolling, osmolyte production, and improved root architectures [5,6]. Plants have different mechanisms to increase tolerance to freezing during exposure to periods of low temperatures, and the most important phenomenon is known as cold acclimation, and cold response is highly complicated process which consists of an array of biochemical and physiological changes, and alterations of the expression patterns of many metabolites, proteins, and genes in reaction to cold stress have been recognized such as post-translational and post-transcriptional regulations [7]. Salinity stress can inhibit plant growth by decreasing the water potential of the leaf, causing morphological and physiological alterations, ion toxicity, generating reactive oxygen species, increasing osmotic stress, and changing biochemical processes, and it can negatively affect photosynthesis, seed germination, percentage of survival, respiration rate of the plant and morphological characteristics [8]. One of the most important limitations for crop production is soil salinity, which can significantly influence crop yield, fruit yield, vegetative growth as well as marketable quality, and application of integrated programs which can combine physiological knowledge together with biological interventions is important for sustaining production in salt-affected areas [7,8].

Plant microbiome is important in increasing resilience under combined heat stress, and biotic challenges vis priming impacts on plant immunity as well as competition for antimicrobial chemicals such as toxins and antibiotics, and nutrients produced by beneficial microbes restricts the spread and growth of pathogenic strains [9]. The mechanism of abiotic and biotic stress resistance in plants consists of molecular, physiological, phytochemical, and morphological aspects [10], such as changes in anatomical features like significant changes in root system architecture and root morphology [11], as well as maintaining a balance in transpiration and water uptake by alterations in stomatal density, leaf size, waxy cuticle, cell wall thickness, and cell density trichomes [12]. Pests such as spider mites, whiteflies, and aphids need integrated and constant vigilance integrated pest management (IPM) protocols [13], and advanced control strategies such as biological controls to RNA interference (RNAi) and clustered regularly interspaced short palindromic repeats (CRISPR)-Cas9 (CRISPR-associated proteins) gene editing can be used to control invasive species such as the oriental fruit fly (*Bactrocera dorsalis*) [14]. Potential of RNAi technology and genetic engineering can be developed nematode-resistance crops, proving a promising frontier in durable resistance breeding [15]. CRISPR/Cas9 is an important tool for genome editing of Cas9 to guide RNA which directs the complex to a place on the DNA double helix and includes the code for the addition of a new DNA sequence at the double-stranded break.

CRISPR/Cas9 technology-mediated improvements to plants tolerance to abiotic stress such as *TaDREB2* and *TaERF3* in wheat for abiotic stress response [16], *MaAPS1* and *MaAPL3* in banana against cold and salt stress [17], *GhRDL1* in cotton for drought resistance [18], *CpDreb2* in papaya for heat, drought and cold resistance [19], *OsDST* in Indica mega rice cultivar against drought and salt stress, *SlNPR1* in tomato against drought stress, and *Leaf1,2* in rice against drought stress [20]. Khare et al. [21] found that *Trichoderma cerinum* Gur1 enhances pathogen and salt stress tolerance in *Arabidopsis thaliana*, decreases oxidative damage, increases proline-mediated osmoprotection under salinity, and modulates key stress-responsive genes via ethylene (ET), salicylic acid (SA), jasmonic acid (JA), and ABA signaling pathways. Li and Wu [22] concluded that by adopting sustainable agronomic activities, leveraging advanced biotechnological tools, and improving interdisciplinary collaboration, it is possible to enhance agricultural and horticultural systems against some biotic stresses, while the integration of multi-omics data such as metabolomics, proteomics, transcriptomics, and genomics can revolutionize the understanding of sustainable practices and integrated future strategies. Osmolytes production and secondary metabolites for plants under salt stress is proline, glycine betaine (GB), flavonoids, jasmonates (JA), ABA [23], proline, glycine betaine (GB) and polyamines for drought stress, ABA, GB, proline and polyols for heat stress, GB and polyamines for osmotic stress [24]. The omics data focus on the various techniques of genetic engineering that can develop various crops to resist biotic and abiotic stresses. The identification of favorable alleles and candidate genes has enabled the application of genomic selection (GS), marker-assisted selection (MAS), and speed breeding, thereby increasing the effectiveness of breeding programs; also, emerging techniques such as transcriptomics, pangenomics, and CRISPR/Cas-mediated genome editing present new opportunities for the precise improvement and progress of complex traits [25]. The goal of this manuscript is to survey and study the importance of various multi-omics insights for abiotic and biotic stress tolerance, plant growth, and crop production in sustainable agriculture.

In this review article, authors have considered the importance of omics technology which may allow significant parallel studies of molecules including proteins, genes, and transcripts; moreover, considering the detection of both quantitative and qualitative levels of multiple genes and proteins simultaneously. The article also provides a critical and structured review of established omics disciplines and techniques, as well as focusing on the integration of recent advances in multi-omics analysis and both biotic and abiotic stress in plants, with an emphasis on improving crop yield.

Multi-omics study is a transformative research approach that integrates data from transcriptomics, genomics, metabolomics, proteomics, and other omics approaches to provide a comprehensive understanding of modern techniques. The multi-omics approach relies on advanced equipment and techniques to analyze, acquire, and interpret complicated batches of biological data with higher data throughput, faster speed than traditional methods, and better batch consistency. Multi-omics techniques have been used in plant systems for developing effective diagnostic tools for different biotic and abiotic stresses and better understanding of plant responses to them. Omics approaches are also enhancing our knowledge about stress-responsive changes in the proteome, transcriptome, and metabolome of plants, while the sequencing of whole plant genomes is providing resources to guide crop improvement strategies.

In conducting the literature survey for this review article, different articles have been checked in different scientific resources such as ScienceDirect, PubMed, and Google Scholar, with a focus on Scopus and ScienceDirect. The keywords used for collecting literature were “Biotic stress”, “Abiotic stress”, “Omics”, “Genomics”, “Transcriptomics”, “Proteomics”, “Epigenomics”, and “Metabolomics.” Genomics, transcriptomics, metabolomics,

epigenomics, and proteomics play important roles in crop improvement by enhancing knowledge of genetic makeup and gene expression patterns of various gene families in crops. In this survey, we considered all the scientific papers available in the form of full text, in English. All relevant information was examined in the selected articles. This research examines the scientific literature from 1990 to October 2026 by conducting an analysis of the published sources in the literature.

2. Biotic Stress and Crop Improvement, and Plant Growth

Biotic stress in crops is caused by living organisms, including viruses, phytoplasma, bacteria, fungi, insects, nematodes, and weeds, causing damage or diseases [26]. Specific ion channels, phytohormones, ROS, and kinase cascades are activated in crops following exposure to stress [27]. The induction of some of these changes was found to be regulated by an effective and complex signal transduction network involving ethylene, jasmonic acid, and salicylic acid. Both salicylic acid and jasmonic acid are the main nonexpressors of pathogenesis-related protein1 transcription factor, which is responsible for the induction of pathogenesis-related gene expression. Some of the main biotic stress factors influencing common bean are Anthracnose (*Colletotrichum lindemuthianum*) which can infect seeds, pods, stems, and leaves, producing sunken necrotic lesions which can cause tremendous loss in final yield [28], angular leaf spot (*Pseudocercospora griseola*) which can cause depressed and angular lesions on pods, stems, and leaves leading to reduced grain quality, and yield as well as defoliation [29], rust (*Uromyces appendiculatus*) which can produce reddish pustules with a yellow halo on stems, leaves, seeds, and pods, decreasing photosynthesis, grain quality, and pod filling [30], white mold (*Sclerotinia sclerotiorum*) which can lead to tissue necrosis, irreversible wilting and yield loss [31], root rot (*Rhizoctonia solani*) that may cause reddish-brown necrotic lesions, affects roots and decrease final yield [31], vascular wilt (*Fusarium oxysporum* f. sp. *phaseoli*) which can infect the vascular system, cause leaf drop, internal vascular discoloration and yield losses up to 100% [32], powdery mildew (*Erysiphe polygoni*) which can produce white powdery patches with chlorosis and curling, and reduce the assimilation of carbon dioxide and photosynthesis [33], common bacterial blight (*Xanthomonas axonopodis* pv. *phaseoli*) which cause necrotic spots with yellow haloes on seeds, pods, stems, and leaves [34], bacterial halo blight (*Pseudomonas syringae* pv. *phaseolicola*) which can significantly reduce the final yield [35], bean common mosaic virus (BCMV), and bean common mosaic necrosis virus (BCMNV) which can infect seeds, pods, stems, and leaves causing chlorosis, mosaic patterns, necrosis, deformation, and decreased seed quality [36], bean weevil (*Acanthoscelides obtectus*) [37], bean fly (*Ophiomyia phaseoli*) [38], and thrips (*Frankliniella occidentalis*) [39] which can decrease photosynthetic activity, and reduce the final yield. Different secondary metabolites reveal various metabolisms which can help to inhibit the growth and development of herbivores, and the main plant secondary metabolites are nitrogen compounds such as dhurrin and sinigrin, phenolics such as lignin, flavones, flavonoids, tannin, and glyceollin, and terpenoids such as saponin [40]. Pyrethrins which is in the category of monoterpenes is neurotoxic to parasitic, insect, moths and wasps in *Chrysanthemum indicum* [41], hemigossypol that is in the category of sesquiterpenes has shown antifungal activity against *Gossypium hirsutum* [41], gossypol which is in the category of diterpene is antibacterial and antifungal in *Gossypium hirsutum* [42], and cucurbitacin-C which is in the category of triterpene is toxic to spider mites in *Cucurbita* spp. [42]. Examples of phytoalexins discovered in various plants with target pathogens are glycosides in Cruciferae [43] and allicin in garlic [44]. It is also reported *Allium sativum* leaf lectin in *Cicer arietinum* and *Nicotiana* spp. can be used against *Aphis craccivora* and aphids [45], snowdrop lectin in *Oryza sativa*, *Arabidopsis* spp., and *Triticum aestivum* against aphids,

Pieris rapae, *Spodoptera littoralis*, and *Nilaparvata lugens* [46], Nictaba-related lectins NICTABA, PP2 in *Nicotiana* spp. against *Acyrthosiphon pisum*, *Spodoptera littoralis*, and *Manduca sexta* [47] (Vandenborre et al., 2009), and *Bauhinia monandra* leaf lectin, and Jacalin-like lectins in *Nicotiana* spp., and *Triticum aestivum* against *Zabrotes subfasciatus*, *Callosobruchus maculatus*, *Anagasta kuehniella*, and *Mayetiola destructor* [48].

Different plant growth-promoting bacteria and fungi have different roles in plant stress responses, such as *Pseudomonas fluorescens,* which can enhance root length and leaf area, increase accumulation of betaine, glycine, soluble sugars, total chlorophyll, and proline in *Lycopersicon esculentum* Mill. under fluoride stress [49], *Bacillus atrophaeus* and *Bacillus ginsengihumi* which can increase biomass, indole 3 acetic acid (IAA) production and nitrogen uptake of *Lactuca sativa* L. under drought stress [50], *B. subtilis*, *Brevibacillus parabrevis*, and *Mesobacillus subterraneus* which can reduce malondialdehyde (MDA), increase leaf number and plant height of *Oryza sativa* L. under arsenic, saline and drought stress [51], *Bacillus safensis* that may increase leaf area, Enterobacter cloacae with positive effects on phytohormone secretion, enhance 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity and reduce ethylene levels of *Oryza sativa* L. under saline stress [52], *Herbaspirillum seropedicae* which can increase shoot and root length, fresh biomass, and decrease disease incidence with a lower number of leaflets with symptoms in *L. esculentum* Mill. under stress caused *Xanthomonas euvesicatoria* [53], *B. subtilis* which can decrease crown rot incidence in both resistant and susceptible papaya genotypes in *Carica papaya* L. under the stress caused by *Erwinia mallotivora* [54], *P. fluorescens* that may reduce disease symptoms caused by fungus with antagonistic activity in *Olea europaea* L. under stress caused by *Verticillium dahliae* [55].

Funneliformis mosseae increased leaf water content, antioxidant components, phenolic contents, as well as root and shoot size in *Capsiucum annuum* L. under saline stress [56], *Acremonium alternatum* could reduce oxoglutarate, superoxide, and hydrogen peroxide, and enhanced defense components including phenolics, brassinin, and nervonic acid of *B. napus* L. under saline stress [57], *Periconia macrospinosa*, *Neocamarosporium goegapense*, and *Neocamarosporium chichastianum* increased biomass, greater root and shoot length, higher proline and chlorophyll content and enzyme activities of *Hordeum vulgare* L. under drought and saline stress [58], and *Purpureocillium lilacinum* could enhance chlorophyll content, root length and germination rate with reduced disease incidence of *Solanum melongena* L. under stress caused by *Mucor piriformis*, *Trichothecium roseum*, and *Rhizoctonia solani* [59].

3. Abiotic Stress and Crop Improvement, and Plant Growth

Abiotic stresses can negatively affect crop quality and productivity, and reduce plant growth and development. While heat stress can negatively influence crop yield, product quality, and plant growth, salt stress is responsible for more than 50% of crop losses, especially in semi-arid and arid regions [60]. When plants are exposed to abiotic stress, such as salinity, extreme temperatures, drought, and nutrient deficiencies, they use various signaling pathways to adapt, and JA, ethylene, ABA, and calcium ions are involved in these pathways [61]. These signaling molecules coordinate cellular responses such as osmotic correction, stomatal closure, and the activation of stress-responsive genes [61]. The combination of stress parameters can diminish crop quality and reduce crop yield, posing a significant threat to human health because of the consumption of low-quality products [62]. Salt stress causes different symptoms such as inhibition of plant growth, stunting, shortening of shoots, delayed opening of fruits and buds, necrosis, shrinking of leaves, wilting, and cell death [61,62]. Different mechanisms of plants against salt stress are modulation of gene expression at the transcriptional level, accumulation of osmo-protectants, and closure of the stomata to maintain water homeostasis [63]. Moreover, non-enzymatic antioxidant substances such as arginine, glycine betaine, proline, vitamins,

glucose, and different metabolites act as stabilizing macromolecules, osmoprotectants, and are involved in maintaining proper cellular function under saline conditions [64]. Proteins are directly involved in stress tolerance, and they are important for the stress response [65]. Heavy metal stress responses consist of root avoidance responses and rhizospheric processes, cell wall fixation, intracellular chelation, and vacuolar sequestration, oxidative stress, activation of antioxidant defense, directed allocation and stress memory, and hormonal signaling and epigenetic regulation [61,62]. The exogenous applications such as microbial applications, signaling molecules and remediation of saline soil could increase the conditions of plants alone, however, other strategies such as OMICS applications namely proteomics, transcriptomics, metabolomics, and miRNAomics, gene modification, and priming researches could enhance the regeneration of tolerant and resistant cereal plants. Malik et al. [66] reported the importance of arbuscular mycorrhizal fungi (AMF) such as *Funneliformis mosseae*, *Claroideoglomus etunicatum*, *Rhizophagus intraradices*, and *R. fasciculatum* species in reducing the adverse impacts of salt stress on root length, shoot dry weight, root surface area, root dry weight, root diameter, root volume, the number of leaves, and nodes of buffelgrass (*Cenchrus ciliaris* L.).

Cold stress happens when temperatures fall below the physiologically optimal range for crops, causing irreversible and permanent damage to plant growth, production, and development [67]. He et al. [68] reported that Brassinosteroids are steroid hormones that play a significant role in different stress responses and plant growth, and their signaling is involved in the regulation of plant tolerance to low temperatures. The significant reduction in yield and disruption of growth of wheat plants because of late-spring cold weather is reported [69]. Wen et al. [70] also reported the negative effects of cold stress on broccoli seedlings. The main impacts of high temperature on plants are oxidative stress, reduction of plant growth, inhibition of seed germination, reduction of crop quality, improper development, yield reduction, alteration in photosynthesis, water loss, alteration in dry matter partitioning, and alteration in phenology [71]. Different adaptation mechanisms of crops to high temperature are transpirational cooling, changing leaf orientation, signaling cascades and transcriptional control, leaf rolling, expression of stress proteins, early maturation, antioxidant defense, osmo-protectants, and alteration of membrane lipid compositions [72].

As a meteorological condition, drought stress can induce alterations in plants on biochemical, physiological, morphological, and molecular levels [73], and negatively affect plant growth and development [74]. It can also generate free radicals such as hydroxyl, superoxide, and hydrogen peroxide, which can influence plant defense systems [72–74]. Krishna et al. [75] found that application of plant growth-promoting microorganisms (PGPM) such as *Trichoderma harzianum*, *Paenibacillus polymyxa* BHUPSB17, *Pseudomonas putida* BHUPSB0, *Bacillus megaterium* BHUPSB14, and *Pseudomonas fluorescens* BHUPSB 17 can increase proline accumulation and decrease the formation of lipid peroxidation and hydrogen peroxide under drought stress. In *Arabidopsis*, the coordinated action of a family of twenty-six protein kinases (CIPKs), phosphatases (PP2Cs), and ten calcium sensors (CBLs) produces transient phosphorylation and the activation of various signaling pathways in reaction to environmental stresses [76]. Different samples from the model species *Arabidopsis* show the importance of some of the transcription factors (TFs) which can enhance stress tolerance without negative impacts on growth and development [77]. Lindemose et al. [77] found that TF interaction partners, such as TF regions with intrinsic disorder (ID) that represent E3 ubiquitin ligases, reveal future targets for engineering improved abiotic stress tolerance in crops. As an important non-energy-conserving terminal oxidase in the plant mitochondrial electron transport chain, alternative oxidase (AOX) can provide a degree of metabolic homeostasis to energy and carbon metabolism [78], and AOX's role in metabolic and signaling homeostasis is vital during both biotic and abiotic

stress [78]. Emerging mechanisms underlying plant responses to major abiotic stresses are shown in Figure 1.

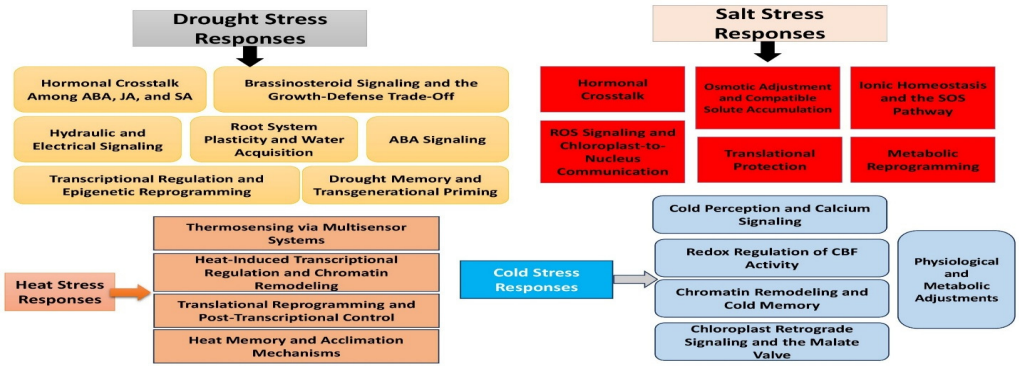


Figure 1. Emerging mechanisms underlying plant responses to major abiotic stresses. ABA: Abscisic acid; JA: Jasmonates; SA: Salicylic acid; SOS: Salt overly sensitive; ROS: Reactive oxygen species; CBF: C-repeat binding factor.

4. Functional Roles of Activated Genes in Response to Different Stresses

One the most important tolerance pathway for salinity stress is the salt overly sensitive (*SOS*) signaling pathway which can keep ion equilibrium, and the pathway was first recognized in *Arabidopsis thaliana* and includes three core ingredients: a *SOS1* Na^+/H^+ transporter, a *SOS2* kinase, and a *SOS3* Ca^{2+} sensor [79]. The *SOS* pathway has an important function in ion homeostasis in cotton [80] and maintains low intracellular Na^+ levels associated with the extracellular environment, which can mitigate salt stress [79,80]. Iqra et al. [81] reported that the *SOS1* gene family encodes plasma membrane Na^+/H^+ antiporters essential for ionic homeostasis and salt tolerance in crops, and that *GhSOS1-5* and *GhSOS1-11* are strongly induced by drought and salt stress in cotton. It is also reported that genome editing can be used in crop improvement against abiotic stresses such as drought, salinity, cold, heat, herbicide, and heavy metal stresses, and these stages consist of identification of targeted stress-responsive genes; after that, targeted genes are edited through zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and CRISPR-Cas9, then incorporation of the edited gene into the plant cell mediated through Agrobacterium, PEG, and biolistic methods, and final confirmation of genome editing in stress-tolerant plants [82]. The fundamental mechanisms involved in genetic modification by programmable nucleases (NHEJ) are binding of the effector DNA-binding domain (DBD) to target genomic loci, double-stranded breaks (DSBs) in target DNA caused by restriction endonucleases (FokI and Cas), and repair of DSBs via homology-directed repair (HDR) or non-homologous end joining [83]. On the basis of transcriptome data, 12 *AnAP2/ERF* genes were significantly upregulated under either flooding or drought stress, with 8 genes responding to both conditions, and these genes also revealed significant induction by GA, IAA, and ABA, proving their potential involvement in stress responses through hormone crosstalk [84]. Many quantitative trait loci or quantitative trait loci (QTLs) linked to yield and stress tolerance in crop [84,85], for example, identification of QTLs which may helpful in marker-assisted breeding of cultivars of maize and rice have been found successful in improvement of yield under stressful conditions [85]. Adaptation to low temperature stress has also been a topic notably studied from the perspective of developing a special metabolic signature which could be linked to gene expression [86]. QTL is a gene or a region of DNA that is linked to the variation of a quantitative/phenotypic trait and may be polymorphic and influence the biological population. Marker-assisted breeding results for improving crop quality under drought and salinity stresses are *RM223* in rice that may develop high-yielding rice cultivars suitable for water-limited environments through marker-assisted

breeding against drought stress [87], *NAL1* in rice which can increase yield through optimizing transportation efficiency of photosynthetic products in rice by marker-assisted selection in salinity stress [88]. *TaCRT-D* in wheat may increase plant tolerance, and the functional markers of *TaCRT-D* for marker-assisted selection in wheat breeding under salt and drought stress [89], *TaCRT-D* in rice against salinity stress [90], and drought stress [91]. Several examples of QTLs for improving crop plant production under drought and salinity stresses are detected QTL relevant to salt-tolerance and sensitive varieties in cowpea in drought stress [92], detected genetic loci to major morpho-physiological traits and grain yield of wheat in drought stress [93], detected QTLs related to stomatal and photosynthetic traits of barley linked to salinity tolerance [94], identified QTLs associated with flowering of sorghum under drought stress [95], detected salinity and drought tolerance varieties of rice based on physiological and developmental traits under flood and drought stress [96], detected two QTLs for drought and one QTL for salt stress of rice under salinity stress [96], and identified QTLs relevant to leaf rolling, leaf relative water content, leaf drying, and relative growth rate of upland rice under water stress [97].

MYB4 gene in *Arabidopsis thaliana* under ultraviolet (UV)-B stress can repair UV-B-induced DNA breaks and negative regulator of sinapate ester and flavonoids [98], *AtMYB111* in *Arabidopsis thaliana* under salt stress can cause salt resistance, regulates CHS, flavonoid 3-hydroxylase (F3H), and flavonol synthase (FLS) 1 genes as well as increase quercetin production [99], *GbMYB1* in *Ginkgo biloba* under UV-B radiation can regulates FLS module, activates flavonoid biosynthesis and cause photoprotection by anthocyanins [100], *VaMyb14* in *Vitis amurensis* under cold and drought stress may increase peroxidase (POD) activity and reduce MDA, activate lipid transfer protein and controls stilbene synthase expression [101], *VviMYB24* in Cabernet Sauvignon grape under drought stress can activate *VviFLS5* expression, forms *MYB24-iMYC2b-FLS5* module, and positively regulates flavonol biosynthesis [102], *MYB-Arahy.J3K16K* in *Arachis hypogaea* under abiotic stress can increase anthocyanins, regulates *PAL*, *CHS*, *CHI*, *F3H*, dihydroflavonol reductase (DFR), and *ANR* [103], *LIMYB3* in *Lilium lancifolium* L. under chilling, drought and salt stress can upregulate ascorbate peroxidase 2 (APX2) and late embryogenesis abundant 14 (LEA) 14, directly binds with *LICHS2*, and cause anthocyanin accumulation [104], *LhMYBC2* in Lilium cb. Sunny Martinique under heat stress can increase isoflavonoids, regulates isoflavonoids biosynthesis genes, and modulates flavonoids biosynthesis [105], *CsYBL2* in *Camellia sinensis* under light and temperature can upregulate anthocyanin and catechin, enhances cold and UV-B tolerance and activates phenylpropanoid biosynthesis genes [106], *RsMYB1* in *Raphanus sativus* under heavy metal stress can increase activity of glutathione S-transferase (GST), PCD, SOD, POD, and catalase (CAT), enhances anthocyanin production, and activates anthocyanin biosynthesis genes [107], *SlMYB14* in *Solanum lycopersicum* under pesticide stress can maintain ROS homeostasis, promotes flavonoid biosynthesis, and binds with *Solanum lycopersicum* phenylalnine ammonia-lyase (SlPAL) gene [108], *SsMYB113* in *Schima superba* under drought stress can modulate ROS generation, bind directly to *SsCHS* genes and accumulates flavonoids [109], FtMYB11 in *Fagopyrum tataricum* under salt and drought stress can regulate MDA and proline, and regulates *Arabidopsis thaliana* cinnamate 4-hydroxylase (AtC4H), AtF3H, AtANS, AtFLS, and At4CL [110], *VvmybA1* from *Vitis vinifera* under cold stress can regulate anthocyanin biosynthesis genes, increase ROS scavenging capacity in citrus trees [111], *AtMYB2* in *Arabidopsis thaliana* under salt stress can regulate phenolic acid genes, decrease ROS accumulation, and triggers phenolic acid synthesis [112], and *AtMYB3* in *Arabidopsis thaliana* under salt stress can reduce ROS, stimulate lignin and anthocyanins, and promote expression of PAL2, C4H, caffeic acid O-methyltransferase (COMT), and DFR [113]. *OsPT8*, a phosphate transporter, has a significant role in abiotic stress signaling via the auxin pathway, and its overexpression may increase tobacco tolerance to high-temperature stress

by influencing auxin content and antioxidant capacity; it can be considered an important candidate gene for breeding plant species that can withstand high temperatures in crops [114]. Ding et al. [115] found significant links between genetic variation in *ZmGRXCC14* and drought tolerance; moreover, previous studies have shown that CC-type *GRXs* are candidate genes that can regulate maize growth and response to environmental stresses [116].

Changes in the expression of ABA-induced transcription repressors (AITR) genes may result in abiotic stress tolerance, including both salinity and drought in *Arabidopsis* [117], and a *CRISPR/Cas9*-induced mutation in the *Arabidopsis* Open Stomata 2 (*OST2*) structural gene showed drought resistance [118]. In another trial, it was found that knockout of *Arabidopsis* plants, *genemiR169*, through *CRISPR/Cas9* led to significantly increased drought tolerance [119]. Also, drought tolerance in Arabidopsis was enhanced after the vacuolar H+-pyrophosphate regulating gene was expressed using *CRISPR/Cas9* [120], as *CRISPR* confers drought resistance in different plants. It has been shown that increasing rice's ability to withstand drought can be attained by decreasing the expression of the regulatory genes *SPP*, *MYB5*, *MSH1*, *PMS3*, and *DERF1* [121]. In rice plants, *CRISPR/Cas9* has been used to enhance drought resistance by knocking out the *ERA1*, *SRL1*, and *SRL2* genes [122]. In chickpeas, two genes, *4CL* and *RVE7,* have been recognized to be linked with drought tolerance [123]. *ARGOS8* can also provide drought tolerance because of its role as a negative regulator of ethylene signaling pathways [124]. Gene mutation of the *SlLBD40* gene caused by *CRISPR/Cas9* noticeably enhanced drought tolerance in tomatoes [125]. It is also reported that CRISPR/Cas genome editing of the *HB12* gene can enhance cotton's resistance to drought [126], and it can also modify the *BnaA6.RGA* gene in oilseed crops to increase tolerance to drought stress [127]. A cultivable heat stress-inducible rice mutant was created using CRISPR/Cas9 technology [128], and CRISPR-edited mutant plants have enhanced agronomic characteristics and were resilient to abiotic stresses [129]. It is also reported that CRISPR-Cas9-based bzr1 mutants can decrease temperature tolerance and reduce hydrogen peroxide generation in the apoplast [130]. CRISPR/Cas-mediated heat-stress-sensitive albino 1 (HSA1) mutants could decrease sensitivity to temperature stress in tomato plants [131]. CRISPR in maize [132] and knockouts of NCED4 in lettuce [133] could promote thermos-susceptible male-sterile plants and allow the seeds to germinate at a higher temperature, respectively. Some of the notable targeted genes via CRISPR/Cas9 technology for development of tolerant genotypes against cold stresses are *OsMYB30* in rice [134], *OsaAnn3* in rice [135], *OsAnn6* in rice [135], *OsPRP1* in rice [136], *SiCBF1* in tomato [137], and *AtCBF1* and *AtCBF2* in *Arabidopsis thaliana* [138]. Genome editing has the capacity to improve crops under salinity stress [139].

It is also reported that enhanced plant tolerance to heavy metals is affected by different genes [140], by using different transporter genes in rice, including *OsNramp5* and *OsLCT1,* which are implicated in Cd absorption by roots [141]. Various reported targeted genes via CRISPR/Cas9 technology for metal stress tolerance and herbicide resistance are *C287T* in rice for herbicide resistance [142], *ALS1* and *ALS2* in maize for herbicide resistance [143], *MS26* in maize for herbicide resistance [143], *ALS* in tomato for resistance to chlorsulfuron [144], and *OsPRX2* in rice for potassium deficiency tolerance [145]. It is also confirmed that genome-wide association studies (GWAS) identify associations between phenotypes of genotypes of interest, enabling the detection of genomic regions with significant impacts on specific characteristics [146]. GWAS studies have proven to be a uniquely effective tool for investigating the genetic architecture of complex traits, providing insights into the polygenic contributions of common variants, and yielding replicable genetic signals in contrast to many candidate gene studies [147]. It is also important to adopt high-throughput technologies and advanced genomics to find candidate alleles and genes for crop traits, genomic selection models, develop molecular markers, design appropriate

ideotypes, and create new genetic variation that suits the changing climate [148]. Table 1 shows key information on the effects of various genes under different stresses to reduce negative effects of stressors.

Table 1. Key information on the roles of activated genes on different crops in response to different stresses.

Plant	Genes	Stress Condition	Key Information	References
Alfalfa (*Medicago sativa* L.)	*MsCIPK2*	Salt Stress	* It increased salt tolerance via osmotic, antioxidant and root growth regulation.	[149]
	MsCML genes	Salt Stress; Cold Stress; Drought Stress	* *MsCML* gene respond to cold, salt and drought stress.	[150]
Apple (*Malus domestica*)	*MdRH28*	Cold Stress	* It could significantly increase by alleviating low-temperature-induced osmotic and oxidative damage, regulate the balance of endogenous hormones, and activate genes in low-temperature response pathways.	[151]
	MdCBL5	Salt Stress	* It could increase apple salt resistance by promoting *MdSOS* gene expression, and increase fruit quality traits.	[152]
Arabidopsis (*Zygophyllum xanthoxylum*)	*ZxNAC48*	Heat Stress	* It showed the most significant upregulation of leaves of samples under heat stress. * *ZxNAC48* could increase the plant thermotolerance.	[153]
	AtMAPK6	Heat Stress	* It directly interacts with *AtPIF4* and promotes its degradation in mediating plant reactions to high-temperatures.	[154]
	VviAHA10	Drought Stress; Salinity Stress	* It restores anthocyanin and PAs accumulation in the *Arabidopsis tt13-6* mutant, and improves *Arabidopsis* root growth under salinity stress, as well as significant contribution to vacuolar flavonoid accumulation.	[155]
Barbados nut (*Jatropha curcas* L.)	*JcDREB*	Salt Stress; Cold Stress	* Its overexpression could increase resistance.	[156]
Benthi (*Nicotiana benthamiana*)	*BrbZIP-S*	Heat Stress; Dark Stress	* Its overexpression resulted in delayed Chlorophyll degradation during the response to dark conditions, and regulated plant stress responses via a complicated network mediated by proline, sugar, and abscisic acid.	[157]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
Buckwheat (*Fagopyrum tataricum*)	*FtRALF6*	Heat Stress; Cold Stress	* It alleviated the inhibition of stresses on the development of plants, and weakened the inhibitory impact of stresses on photosynthetic capacity.	[158]
Cabbage (*Brassica oleracea* var. *capitata*)	*BoPYL8*	Cold Stress	* It increased the freezing tolerance in plants.	[159]
	BrADF11	Heat Stress	* Silencing *BrADF11* increased the heat tolerance of Chinese cabbage.	[160]
Chicory (*Cichorium intybus*)	*CiXTH29*; *CiLEA4*	Drought Stress	* High *CiLEA4* and *CiXTH29* basal expression, linked with a high level of vegetative growth. * They are potential markers for drought stress tolerance.	[161]
Chinese foxglove (*Rehmannia glutinosa*)	*RgRLK19-RgRLK27-RgRLK30*	Stress	* *RgRLP* genes significantly decreased continuous cropping-induced stress damage.	[162]
Chinese Wild Grape (*Vitis amurensis*)	*VaMAPK9*	Cold Stress	* It may increase cold tolerance by coordinating C-repeat binding factors (*CBF*) and inducer of CBF expression (*ICE*) signaling pathways with the antioxidant defense system.	[163]
Chinese Skullcap (*Scutellaria baicalensis*)	*SbDREB10*	Salt Stress	* It could reduce ROS levels and enhance antioxidant enzyme activities. * Positively regulated the transcriptional levels of stress-related genes like *DREB2A* and *APX2*.	[164]
Chrysanthemum (*Chrysanthemum morifolium*)	*CmBBX22*	Drought Stress	* It could negatively regulated drought tolerance by mediating stomatal conductance, ABA, and antioxidant responses.	[165]
Cotton (*Gossypium hirsutum*)	*GhCOX11*	Drought stress	* It could mediate the mechanism of reactive oxygen species clearance.	[166]
	MAH1-L	Drought Stress	* *MAH1-L* genes increased drought tolerance and wax biosynthesis in cotton.	[167]
Cucumber (*Cucumis sativus*)	*CsF3H2*	Salt	* Its overexpression could significantly increase flavonoid/anthocyanin content, and increase antioxidant enzyme activity. * Upregulated expression of ion homeostasis genes such as *CsHKT*, *CsNHX*, and *CsSOS1* and improved salt tolerance.	[168]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
	CsFAR3-like	Drought Stress	* It shows the highest expression and is induced by salt, drought, JA, and *Podosphaera xanthii*.	[169]
	OSCA genes	Salt Stress; Drought Stress	* They have important functions in response to osmotic-related abiotic stresses and pathogen invasion.	[170]
Dahurian bush clover (*Lespedeza davurica*)	*LdALDH2-19*	Drought Stress	* It could significantly reduce oxidative damage, and increased antioxidant enzyme activity. * It had considerable contributing ROS homeostasis.	[171]
Dendrobium (*Dendrobium officinale*)	*DoTIP1-1*	Salt Stress	* Its overexpression could increase salt tolerance through accumulation of proline and water-soluble polysaccharides, and a key genetic determinant for increasing salt tolerance.	[172]
Grapevine (*Vitis vinifera* L.)	*VvRAX82*	Salt Stress	* Its overexpression positively regulates salt tolerance in grapevine calli.	[173]
	VvBiP3	Drought Stress	* It could be involved in regulating sugar transporter expression under drought stress.	[174]
Honey Clover (*Melilotus albus*)	*MaPIP2; 1-MaTIP2; 2-MaPIP1;1*	Salinity	* The overexpression of genes coincided with less severe salt-induced growth inhibition. * Reduced salt-induced damage with root length increasing by 14.8–25.0%, and fresh weight by 26.2–53.2%, and increased soluble sugar and soluble protein associated with osmotic adjustment.	[175]
	ZmBAF14	Drought stress	* *ZmBAG14* expression could decrease ROS accumulation in stomatal guard cells and water loss rate. *ZmBAG14* expression could elevate superoxide dismutase (SOD) and peroxidase (POD).	[176]
Ioquat (*Eriobotrya japonica*)	*EjCBF3*	Cold Stress	* It could increase the cold resistance.	[177]
Kiwifruit (*Actinidia deliciosa*)	*AcSnRK2.4*	Heat Stress	* Its overexpression showed higher SPAD, but lower relative electrolyte leakage (EL), ROS content and malondialdehyde (MDA). Moreover, It can positively regulate kiwifruit's response to heat stress.	[178]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
	CsFAR3-like	Drought Stress	* It shows the highest expression and is induced by salt, drought, JA, and *Podosphaera xanthii*.	[169]
Lavender (*Lavandula angustifolia* Mill.)	*Lavender metallothionein* (*LaMT*) gene	Metal Stress	* Under heavy metal stress *LaMT2B* and *LaMT3C* were consistently upregulated across leaves, stems, and roots. *LaMT3C* and *LaMT3B* could increase heavy metal resistance by elevated proline content, reduced malondialdehyde levels, and increased antioxidant enzyme activities.	[179]
Maize (*Zea mays* L.)	*nhaA-nhaB-maeN*	Salinity Stress	* *Enterobacter asburiae* LL-1 could enhance maize salt tolerance via coordinated impacts on stress-responsive gene expression, and ion homeostasis.	[180]
	ZmGATA17	Salt Stress	* It showed involvement in salt stress tolerance.	[181]
	ZmLACS9	Heat Stress	* It could influence photosynthesis by affecting chloroplast content and structures.	[182]
	ZmHIPP genes	Cadmium Stress	* The expression of *ZmHIPP30*, *ZmHIPP11* and *ZmHIPP48* was higher in shoots than roots. The expression of *ZmHIPP57* and *ZmHIPP02* was higher in roots than shoots. * *ZmHIPP* genes can be used for future studies for breeding Cd-tolerant maize.	[183]
Oat (*Avena sativa* L.)	*AsHD-Zip49*	Salt Stress; Drought Stress	* It positively regulates drought tolerance in oat.	[184]
Passion fruit (*Passiflora edulis* Sims)	*High-affinity* K^+ (*HAK*) genes	Salinity stress	* The HAK family of potassium transporters plays an important function in plant adaptation.	[185]
Patchouli (*Pogostemon cablin*)	*PcCDPK5*	p-hydroxybenzoic acid (p-HBA) stress	* It can reduce the damage caused by p-HBA stress.	[186]
Pea (*Pisum sativum*)	*PDH45*; *PDH47*	Cold Stress	* The genes could increase stress tolerance by activating the antioxidant system, and regulating photosynthesis effectiveness.	[187,188]
Peach (*Prunus persica*)	*PpTALE19*-*PpTALE21*	Cold Stress	* The genes show tissue-specific expression patterns during fruit development, and they are promising candidate genes for increasing cold tolerance and decreasing chilling injury.	[189]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
	CsFAR3-like	Drought Stress	* It shows the highest expression and is induced by salt, drought, JA, and *Podosphaera xanthii*.	[169]
	PpAPX1	Salt Stress	* Most *PpAPXs* were upregulated under salt stress. * Overexpression of *PpAPX1* increased the salt tolerance of peach callus.	[190]
Peanut (*Arachis hypogaea*)	*AhDi19-3B*	Drought Stress	* It is a key regulator of drought tolerance via reduced oxidative damage and improved water retention.	[191]
	AhLAC63	Drought Stress; Heat Stress; Cold Stress	* AhLAC63 significantly changed phenylpropanoid metabolism flux and enhanced lignin content in peanut hairy roots.	[192]
	Nonexpressor of Pathogenesis-Related (*NPR*) genes	Cold Stress	* They are key integrator of cold and pathogen signaling.	[193]
Pecan (*Carya illinoinensis*)	*CiPawSnRK2.1*	Salt Stress	* It shows central role in response to salt stress.	[194]
Pepper (*Capsicum annuum* L.)	*CaAIMK1*	Drought Stress	* ABA-dependent pathways.	[195]
	CaDHN3	Drought and Salt Stress	* Increased resistance by enhancement in SA and ABA signaling pathways.	[196]
	CabHLH18	Flooding stress	* Significant increase in SOD activity, root activity, proline, amino acids, and soluble sugar.	[197]
	CaDIM1	Drought stress	* It regulated ABA-mediated gene expression.	[198]
Potato (*Solanum tuberosum* L.)	*StMATE1/4/98*	Aluminum stress	* It mediated Al-induced citrate exudation and increase Al tolerance.	[199]
	StTIFY3- StTIFY12	Drought stress	* They were strongly induced in roots under drought.	[200]
	StICE1-OE	Cold Stress	* *StICE1-OE* increased cold tolerance.	[201]
	StMAPKKK44	Salinity Stress; Drought Stress	* It may upregulate antioxidant genes, and increase biomass under drought and salt. It can also modulate redox and osmotic balance for drought and salt stress resilience.	[202]
Rapeseed (*Brassica napus* L.)	*BnATGs*	Salinity Stress; Cold Stress	* *BnATGs* were significantly down-regulated and up-regulated responding to dehydration, cold, abscisic acid, and salinity.	[203]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
	CsFAR3-like	Drought Stress	* It shows the highest expression and is induced by salt, drought, JA, and *Podosphaera xanthii*.	[169]
	BnaA6.TINY	Drought Stress	* It could increase proline accumulation and reduced levels of ROS.	[204]
Rice (*Oryza sativa* L.)	*OsWRKY45-OsWRKY72*	Drought and salinity stress	* They could increase resistance of plants to both salinity and drought stress.	[205]
	OsDi19-4	Drought Stress	* It can increase tolerance to drought by modulating ABA sensitivity.	[206]
	OsDEAD58	Salt Stress; Cold Stress	* It could enhance cold and salt tolerance by affecting chlorophyll synthesis.	[207]
Ryegrass (*Lolium perenne* L.)	*LpBBC* family	Drought and Salt	* *LpBBX* genes are extensively involved in regulating development and growth and stress responses. * It may increase tolerance to both salt and drought tolerance.	[208]
Silver poplar (*Populus alba*)	*PoalbERF73/80/86124*	Cold stress	* The four ERF genes responding to cold stress were found in *Populus alba*. * Knockouts of the gene increased cold sensitivity in plants.	[209]
Soybean (*Glycine max*)	*GmTGD2.1*	Cold stress	* It is highly expressed in leaves, and upregulated under cold stress. * It can inhibit membrane lipid peroxidation and decrease ROS.	[210]
	GmHKT1-GmTPK5-GmSKOR-GmVIT2.1-GmNramp5-GmIRT1-GmKUPs-GmAMTs	Acidity stress	* These genes were significantly down-regulated by acidity stress.	[211]
	GmMATE	Low Phosphorus Stress	* It could increase phosphorus efficiency, and root length under low-phosphorus stress.	[212]
	GmPP2C113	Salt Stress	* A positive modulator of salt tolerance, and a novel function as a molecular node which sustains symbiotic nodulation under stress.	[213]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
	GSK2-8	Salinity stress	* It can directly phosphorylate the transcription factor *GMNSP1a*. * Inhibit transcriptional activity, thereby mediating the negative regulation of soybean nodulation under stress.	[214]
	CsFAR3-like	Drought Stress	* It shows the highest expression and is induced by salt, drought, JA, and *Podosphaera xanthii*.	[169]
Summer pumpkin (*Cucurbita pepo*)	*CpJAZ5*	Drought stress	* It increased plant drought tolerance by mitigating the over-activating of jasmonic acid signaling.	[215]
Sunflower (*Helianthus annuus* L.)	*HaOFP10-HaOFP14*	Drought stress	* They are important genes for sunflower tolerance breeding. Overexpression of the genes could increase drought tolerance in sunflowers.	[216]
Sweet potato (*Ipomoea batatas*)	*IbBBX24*	Salt and drought	* It could regulate PRX17-mediated ROS scavenging in plants.	[217]
Tobacco (*Nicotiana tabacum* L.)	*NtHDT605*	Cold stress	* Its overexpression could increase cold tolerance, decrease ROS, and enhance activities of antioxidant enzymes.	[218]
	PsnPAL1	Drought Stress; UV-B Radiation Stress	* *PsnPAL1*-overexpressing transgenic tobacco plants showed increased tolerance to UV-B radiation and drought stress.	[219]
	NtCaM13	Drought Stress	* It could increase drought tolerance in tobacco through ABA-mediated stomatal closure. * It could strengthen cuticle/cell walls.	[220]
	NtGSTF6	Cold Stress	* It is involved in oxidative stress responses and metabolic pathways, and it reduced malondialdehyde and enhanced proline content under stress.	[221]
	NtGPX8a	Cadmium Stress	* It could significantly augment activities of glutathione peroxidase (GPX), superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) under cadmium stress. It emerges as a promising candidate gene for cadmium-contaminated phytoremediation.	[222]

Table 1. *Cont.*

Plant	Genes	Stress Condition	Key Information	References
Tomato (*Solanum lycopersicum*)	*SlBBX17*	Cold Stress	* Its overexpression significantly increased C-repeat binding factor-dependent cold tolerance.	[223]
	CsFAR3-like	Drought Stress	* It shows the highest expression and is induced by salt, drought, JA, and *Podosphaera xanthii*.	[169]
	MFS gene	Salt Stress	* Over-expression of SlZIF1/SlMFS4 reduced the ROS content and influenced the K^+ and Na^+ ion balance in shoots to increase tolerance.	[224]
	SlTPP3	Salt Stress	* Its overexpression increased antioxidant activity, decreased ROS accumulation.	[225]
	SlTRX2	Salt Stress	* It may aid regulation of tomatoes in response to abiotic stress. It could also decrease the damage of photosynthesis under salt stress.	[226]
	BEL1-like genes	Drought Stress; Cold Stress; Heat Stress	* Displayed different tissue-specific expression patterns.	[227]
	SlAIM1	Salt Stress; Oxidative Stress	* Overexpression of *SlAIM1* may increase oxidative and salt stress tolerance. * These two abiotic stimuli are made more sensitive by SlAIM1 silencing.	[228]
	SlMBP8; *SlHB2*; *SlAGO4A*	Salt Stress; Drought Stress	* The overexpression increase tolerance to both drought and salt stress.	[229]
Trifoliate Orange (*Poncirus trifoliata*)	*PtASMT23*; *PtSNAT18*	Drought Stress; Cold Stress	* They participate in melatonin synthesis under stress conditions.	[230]
Watermelon (*Citrullus lanatus*)	*ClGPAT8*	Cold Stress	* Its expression was strongly induced under cold stress conditions.	[231]
Wheat (*Triticum aestivum* L.)	*TaSnRK2.8-5A*	Drought Stress	* Increase proline biosynthesis, ROS scavenging and root activity.	[232]
	TaCSNCED18; *TaCSNCED27*; *TaCSNCED26*	Drought Stress; Heat Stress	* The genes significantly upregulated under heat and drought stress.	[233]
White poplar (*Populus alba* L.)	*PoalbERF73/80/86/124*	Cold Stress	* These genes are involved in the cold stress response.	[234]
Yellowhorn (*Xanthoceras sorbifolium* Bunge)	*XsWRKY30*	Salt Stress	* It could significantly decrease malondialdehyde (MDA) accumulation. It could decrease oxidative damage and Na^+ toxicity under osmotic stress.	[235]

It is also reported that the Mediator complex shows an important role in orchestrating the transcriptional responses by linking stress-responsive transcription factors (TFs) to the core transcriptional machinery [236], for example *AtMED5a* and *AtMED5b* take part in active transcriptional processes which inhibit lignin biosynthesis and growth in plants [237], *PFT1* can encourage *Arabidopsis* flowering [238], *OsMED14-1* can decrease vasculature, reduced seed set and panicle branching, and smaller seeds in rice [239], *SlMED18* can limit the growth of tomato leaves and internodes [240], *AtMED18* and *AtSUF4* can influence flowering [241]. Different genes have various roles in crops; it is reported that *BADH* in rice is for heavy metal stress [242], *CodA* in rice is useful for drought, cold, and salt stress [243], *bet A* in maize is for drought and cold stress [244], *P5CS* in wheat is useful under drought stress [245], *bZIP4* in maize is useful against salinity stress [246], and *bZIP16* in rice is important under salt stress [247]. *ZmHKT1* in maize against salt stress [248], *HKT1* in wheat against salt stress [249], and *HKT1* in rice against salt stress [250]. Various gene editing tools used against biotic and abiotic stressors such as CRISPR/Cas9 which can improve tomato traits, as targeted gene editing may increase resistance to drought, cold, heat and salinity by modifying stress-related genes [251], CRISPR/Cas9 which may disturb negative regulators at the genetic level for multi-stress tolerance, and changes proline-rich proteins, disrupting stress-regulating protein pathways for enhanced tolerance [252], TALENs and CRISPR/Cas9 which can regulate sugar transporter protein to improve stress response at the proteomic level, and engineering sweet genes can regulate abiotic stress responses such as salinity and drought in sweet sugar transporters [253], CRISPR/Cas that may regulate stress-associated proteins like ion transporters and heat shock protein and modified genes regulating tolerance to temperature extreme and salinity, and other abiotic factors in abiotic stress tolerance in Arabidopsis and rice, genetic modification in climate-smart banana development which can changes genes to increase resistance to biotic and abiotic stress, and increase protein networks associated to resistance against environmental and pathogen-induced stress [254].

CRISPR/Cas9 is one of the powerful tools increasing precision in genetic modification and an advanced genome-editing tool, and it may target and modify specific genes, and genome editing enables breeders to fine-tune plant traits and increase adaptation to changing environmental conditions [255]. Some examples to improve tolerance by application of CRISPR/Cas9 are OsRR22 in rice, which may cause mutants with improved salt tolerance without compromising performance against salinity [256]; *OsDST* in rice, which may lead to greater tolerance to salinity and drought stress [257]; *OsDERF1* and *OsERA1* in rice, which can enhance drought resistance [258], and mutants with longer roots and better response to drought [122], respectively. *TaERF3* in wheat which can increase water efficiency and photosynthesis under drought stress [259], *TaHKT1;5* that may improve ionic regulation and salt tolerance under salt stress [259], *TaDREB2/3* and *TaHAG1* that may promote tolerance and improve multi-source resistance against drought and salt stress in wheat plants [260]. *MdNHX1* in apple which may induce to salt tolerance high K^+/Na^+ in leaves under salinity stress [261], *GhHB12* in cotton which can increase the tolerance to abiotic stress under drought and salt stress [262], *AVP1* in peanut that may cause improve in photosynthetic rate and higher yield under salt and drought stress [263], *eIF4E*, *CsLOB1* and *SlDmr6-1* in cassava, cucumber and tomato that may broad resistance through gene knockouts under virus and bacteria stress [264].

5. Multi-Omics and Plants

Omics-driven elucidation of mechanisms underlying crop tolerance to different environmental stresses via identification of key candidate proteins, genes, metabolic pathways, and metabolites related to specific traits that have been successfully analyzed, validated,

manipulated, and incorporated into crops [265]. Multi-omics approaches provide a significant framework to investigate complexity, enabling resolution of stress-induced trade-offs between defense, growth, and metabolic homeostasis [266]. Multi-omics data can inform breeding programs by recognizing resilient genotypes that exhibit desirable characteristics under stress conditions [267]. Multi-omics studies permit scholars to study the composite interactions between different biological molecules and their functions in stress response, leading to more effective crop improvement strategies [268], and in the field of biotic and abiotic stress, genomics helps identify quantitative trait loci (QTLs) [267,268]. Multi-omics frameworks combine epigenomics, metabolomics, proteomics, and transcriptomics to map dynamic and context-specific regulatory networks that mediate cross-tolerance mechanisms [269]. Beyond these core omics, emerging layers such as immunomics, lipidomics, glycomics, and RNomics capture lipid diversity, complex carbohydrates, immune signaling, and regulatory RNAs, broadening applications in plant biology [270]. The advent of omics technologies, viz transcriptomics, genomics, metabolomics, proteomics, and epigenomics, has fundamentally transformed plant stress biology through high-throughput analyses of molecular, biochemical, and regulatory responses to biotic and abiotic stresses [271]. The integration of these omics layers, supported by computational platforms, systems biology tools, and advanced bioinformatics, has facilitated the identification of main regulatory nodes, such as miRNAs, and has improved the development of stress-resilient crop varieties via genetic engineering, precision breeding, and genome editing [271]. Transcriptomics and genomic analyses assess induction of genes encoding surface recognition parameters as well as cell wall-degrading enzymes (CWDEs), priming the fungus for host entry [272]. Single-cell multi-omics (scMulti-omics) technologies have increased understanding of cellular functions and interactions by enabling the simultaneous measurement of various cellular modalities. Moreover, integrating these heterogeneous data types offers noticeable challenges because of differences in resolution, scale, and biological variability across the omics layers. A single-cell multi-omics deep learning model based on contrastive learning, called scMDCF, is designed to extract joint representations from single-cell multi-omics data, and it adopts multi-omics-informed encoders to independently learn the processed feature representations of each omics type. This contrastive learning-based framework for single-cell multi-omics integration harmonizes cross-modality representations while preserving biological heterogeneity, and applications across diverse scMulti-omics datasets demonstrate improved clustering performance, effective batch-effect mitigation, and mechanistic insights into underlying biological processes [273].

The integration of multi-omics technologies, especially proteomics, transcriptomics, and metabolomics, has revolutionized the study of medicinal herbs and plants, and these approaches allow for the comprehensive profiling of secondary metabolites, as well as the discovery of novel biomarkers related to therapeutic application, and the study of biosynthetic pathways [265–270]. By combining proteomics and transcriptomics with metabolomics in research on herbs and plants, scholars can link cause and effect in the plant's responses, especially under elicitation or other treatments; multi-omics shows shifts in gene/protein expression correspond to changes in metabolite profiles. Multi-omics can lead to finding both new components and assigning biosynthetic roles to genes/proteins, essentially piecing together new metabolic pathways.

In the last few years, a number of techniques have been designed to cover the entire three aspects of an organism's biology, namely metabolomics, proteomics, and transcriptomics, with many new software and algorithms published every year [274]. The main platforms to better analysis of gene transcripts are the gene microarray technique allowing the analysis of various genes at a time [275], the extremely accurate qRT-PCR which permits only a limited number of genes to be analyzed [276], and RNA Seq oriented to the performance of unbiased analysis of RNA transcripts [277], which significantly generates

gigabyte size readouts with all the RNA transcripts of a given cell, tissue or organisms. Also, with RNA-seq, it is also possible to study various variants of mRNA and other RNA molecules such as small RNAs and noncoding RNA in different organisms [278].

The developments of some modern omics tools, such as proteomics, genomics, metabolomics, and transcriptomics has rationalized the research of crop plants and complete researches related to plant breeding and biological components. Omics tools allow comparative studies of cultivated and wild species of plants, which can lead to the identification of proteins and genes, the elucidation of their roles, and assist in the development of multiple stress-tolerant crop designs. Choudhary et al. [279] reported that the integration of techniques or transcriptomics, proteomics, and genomics such as LC-MS, MALDI-MS, IT-MS, ESTs, DIGE, WGS, SAGR, GBS, GWAS, CRISPR-Cas, 2D-PAGE, HLS, cDNA-AFLP, MPSS, HRPF, MAS, CAGE, MudPIT, IEF, sequential window acquisition of all theoretical fragment ion spectra-mass spectrometry (SWATH-MS), SRM/MRM, ESI have significantly increased the ability to comprehend the regulatory networks and molecular pathways, involved in balancing the ecology/ecosystem stress adaptation.

Genomics techniques include the study of structure, evolution, and function, and, on the basis of epigenomic studies, the precise selection of genes responsible for traits like crop productivity and stress tolerance. Transcriptomics, utilizing digital gene expression profiling, microarrays, RNA sequencing, next-generation sequencing, and quantitative PCR, provides insights into gene expression patterns in different environmental conditions. Metabolomics means the quantification and identification of low molecular weight metabolites in a given organism, in a given organ, and at a given developmental stage, cell or tissue type [280]. The most important metabolomics technique focuses on metabolites with specific and similar chemical properties and is globally recognized as metabolite profiling, covering a fraction of the metabolome. It is reported that data and results from Omics findings, including molecular markers, putative QTLs, metabolites, candidate genes, proteins, etc., should be cross-tested with wet lab research before they can be accurately applied in commercial breeding and scientific research [281]. Omics data are important in genome editing to design effective CRISPR targets, with reduced off-target mutations in crop breeding [281]. Gupta et al. [282] found that genetic engineering can help to boost cotton fiber, yield, and cottonseed oil quality by modifying and identifying gene sequences and expression levels. Platforms like OmicsNet, COLOMBOS, PlantMetabolomics, and OMICTools offer researchers tools to visualize and compare multi-omics data, analyze and construct gene co-expression networks, access curated lists of software databases and tools for omics data analysis, and better understand plant metabolomics data analysis resources. Various approaches have already made considerable headway in integrating gene expression and metabolism, and the most developed studies are based on combining new models of metabolic networks and gene expression data, which means that gene expression levels are used to parameterize the flux capacity of metabolic reactions to create context-specific models. It is also important to know the fact that metabolism is driven by specific enzymatic products of gene expression, and in turn, gene expression may need the continual synthesis of certain metabolites and ATP. Therefore, the two processes are coupled and should coordinate with one another as cells navigate changing conditions of existence. Furthermore, the coordination should be considered in particular cellular strategies such as growth, division, and differentiation on the basis of the prevailing conditions. The coupling of these two fundamental processes should be considered together with their individual dynamics; moreover, the timescale of metabolic supply-demand is much smaller than the timescale of gene expression [280–285].

The integration of different databases and omics tools has significantly enhanced our understanding of intricate biological processes in crops, which can improve knowledge of gene regulation, metabolic pathways, protein functions, and other molecular interactions in plant biology. It is reported that in the interaction of transcriptomics + proteomics + phosphor-proteomics in rice-*M. oryzae*, defense protein abundance was not correlated with transcript levels in susceptible cultivars [284], and in the interaction of proteomics + metabolomics in rice-*M. oryzae*, metabolite shifts did not align with predicted pathway activity from proteomics [285], while in proteomics, protein accumulation was lower in susceptible lines despite high transcript levels [286]. Rice has been studied as an important model species to reveal the application of multi-omics in trait discovery and practical breeding [287]. Recent soybean and maize multi-omics maps showed networks linking genetic variation with metabolomic, transcriptomic, and transcription-factor regulation [288]. A multi-omics transcriptional regulatory network in soybean revealed key transcription factors regulating agronomic traits such as quality and yield [289]. Spatial metabolomics integrated with proteomics and transcriptomics enables tissue-level mapping of regulatory networks [290]. The development of spatial multi-omics technologies, including spatial proteome, spatial transcriptome, and spatial epigenome, has provided new opportunities to decode cellular ecosystems through complementary molecular layers; nevertheless, the inherent heterogeneity among various modalities in both technical noise and biological variation offers challenges for integration and requires advanced computational approaches for data harmonization [291]. Spatial transcriptomics aims to count the number of transcripts of a gene at distinct spatial locations in a tissue, and there are two ways to profile transcriptomes while preserving spatial information: firstly, by imaging mRNAs in situ via microscopy, and secondly, the other broad method of spatial transcriptomics is to extract mRNAs from the tissue while preserving spatial information and subsequently profiling mRNA species via next-generation sequencing (NGS) techniques [292]. Spatial metabolomics is a field of omics study concentrated on the interpretation and detection of lipids, metabolites, and other small molecules in the spatial context of organisms, tissues, cells, and organs [293]. It is also reported that genome editing and AI-driven breeding accelerate the precise development of stress-tolerant crop cultivars [294].

Some strategies for integrating proteomics, transcriptomic, and metabolomics data using the correlation-based approaches are gene co-expression analysis which is about transcriptomics and metabolomics that may identify co-expressed gene modules with metabolite, gene-metabolite network which is about transcriptomics and metabolomics that may perform a correlation network of genes and metabolites, similarity network fusion which is about proteomics, metabolomics, and transcriptomics that may build a similarity network for each omics data separately, and subsequently, all networks are merged, and the edges with high associations in each omics network are highlighted, enzyme and metabolite-based network which is about metabolomics and proteomics that may identify a network of protein-metabolite or enzyme-metabolite interactions using genome-scale models or pathways databases [295]. It is also important to say that sometimes multi-omics integration fails because of unmatched samples across omics layers, misaligned resolution and missing cell type anchors, improper normalization across modalities, blind feature selection without biological guidance, overinterpreting weak correlations across omics, ignoring batch effects that compound across layers, using the wrong dimensionality reduction for integration, mixing static and dynamic signals without temporal context, and tools that promise integration but mask biological conflicts. Multi-omics integration is fragile, as each layer comes with its own biases, temporal dynamics, and resolution, and successful integration is about an appropriate understanding that the data represent.

During integration, some different scenarios depending on the types of omics involved may occur which are horizontal integration, which involves merging the same type of omics data across different experiments, datasets and studies; vertical integration which combines multiple types of omics data collected from the same biological samples, and diagonal integration which combines different omics types across samples or cohorts.

It is reported that multi-omics techniques are highly innovative, leading to a higher resolution and a deeper understanding of complex traits in plants, and plant breeding using omics technologies is significantly promoted by the rapid development of high-throughput platforms and successful omics-based breeding in crops [296]. Genomic selection has revolutionized the field of plant breeding by enabling the selection of superior genotypes based on genomic estimated breeding values obtained from dense molecular marker information [297].

Multi-omics can be broadly categorized into unmatched multi-omics, where data is created from various, unpaired samples, and matched multi-omics, where multi-omics profiles are acquired concurrently from the same set of samples. Unmatched data may need more complex computational analyses involving diagonal integration to combine omics from various technologies, studies, and cells, and matched multi-omics is arguably more desirable as it may keep the biological context consistent, enabling more refined associations between often non-linear molecular modalities. The main challenges in multi-omics data integration are the lack of pre-processing standards, the special bioinformatics expertise required, the difficult choice of the appropriate integration method, and the challenging interpretation of biologically meaningful profiles [298–300]. Appropriate integration of the multiple-omics profiles must be performed to fully take advantage of the interactions between omics and their interdependencies, and the challenge of multi-omics integration is to present interpretation regulations adapted to the multiplicity and heterogeneity of designs such as number of conditions, data types, timepoints and samples [301].

Machine learning-driven interrogation of omics data significantly reduces the time taken for biomarker discovery and candidate validation [302]. It is a subfield of artificial intelligence (AI) that focuses on developing algorithms that can learn from data, identify hidden patterns, and make decisions; moreover, machine-learning algorithms can be applied to build predictive models, recognize objects in images, and control robotic systems [303]. AI facilitates the optimization of the entire production chain, from cultivation conditions to extraction parameters [304]. In plant breeding, data collection is an important step involving the collection of data for target traits from a wide range of environments, plant populations, and trials, and plant breeders usually work in different environmental settings in order to obtain an accurate understanding of the genotype-by-environment interaction in various trials within each environment [303]. It is reported that integrating predictive machine learning with spatial engineering presents promising strategies to design complex biosynthetic pathways; hybrid approaches, combining constraint-based metabolic models with generative algorithms, decrease trial-and-error in crop engineering [304]. Some of the most important AI and machine learning techniques used in horticulture science are supervised learning, unsupervised learning, reinforcement learning, deep learning, and convolutional neural networks (CNNs) [305].

In science related to multi-omics, the systems paradigm was limited by technology to bulk analysis of tissues, and typically, omics levels were analyzed individually, even though it was recognized that cells within tissues displayed significant heterogeneity. Recent improvements in single-cell and spatial biology, together with advances in artificial intelligence and cloud computing, have now made it possible to conduct multi-omics analyses on individual cells of complex organisms and to place that information in a spatial context, resulting in spatially oriented whole system analyses. Systems biology is an at-

tempt to correlate multiple omics levels together for the purpose of building mathematical models of organisms as well as metabolic pathways which could be applied to test predictions and to engineer metabolic networks. The most important challenges of multi-omics data integration are choosing the omics layers most relevant to the analysis to simplify integration, integrating horizontal and vertical datasets as necessary, under the particular statistical properties of each omics layer, including normalization and accounting for missing data, better understanding of biological anchors between layers for either paired or unpaired data, accounting for temporal differences between omics layers, dimensionality reduction, and identifying layer-specific effects vs. latent impacts common to all omics layers [265–273].

6. Genomics

One of the most important methods for creating agricultural and horticultural crops that can withstand abiotic and biotic stress is genomic-assisted breeding. By considering the science of genomic technology, breeders may enhance pest and disease resistance while keeping productivity and quality. Genomics considers studying and exploring the genomes, the complete set of DNA or genetic material within an organism, with the help of a range of approaches and techniques [306], and it consists of interpreting and analyzing the structure, function, and evolution of genomes [307]. Genomics is divided into three parts: functional genomics, structural genomics, and comparative genomics. Functional genomics' goals are to study gene functions and interactions within regulatory networks, analyze gene expression, and emphasize the importance of overexpressing genes; the goals of structural genomics are DNA sequencing, providing data on genome features, coding and non-coding genes, and repetitive elements; the aims of comparative genomics are to compare characteristics between species, analyze differences and similarities between two or more genomes, identify and analyze gene families in crop genomes, and discover stress-inducible promoter regions [308].

Integrative genomics shows regulatory networks in fragrance and stress adaptation [309]. While genome sequencing has provided important insights into the physiological and ecological functions of PGPR, genome annotation, comparative genomic analysis, and in silico construction of metabolic pathways have noticeably enhanced our understanding of microbial physiology and morphology [310]. Integrating genomics, speed breeding, and digital methods can provide a transformative framework to enhance genetic gain and deliver smarter, faster, and more resilient crop improvement for nutritional and global food security [311]. The important points of functional genomics in trait gene discovery are crop phenotyping, diverse genetic resources, genomics tools integrated with bioinformatics, and proof of gene function in planta. Two important points in functional genomics are understanding the desired phenotypic trait of crops in the field, and increasing the knowledge through genomics, as well as the mechanisms which have been used for genomic information to achieve improved crop phenotypes [312].

RNAi technology can be applied for gene inactivation and functional research, which consists of the introduction of small interfering RNA (siRNA) or short hairpin RNA (shRNA) molecules into the cell, and these molecules bind to the target mRNA, inducing inhibition and degradation of its protein translation [313]. Virus-induced gene silencing (VIGS) is a transient induction of RNAi by utilizing modified viral vectors for plant functional genomics [314], and both VIGS and RNAi have been used for improvement of different traits in crops [315]. To functionally characterize plant genes, genome editing techniques like targeted mutation, INDEL creation, and genomic sequence modifications can be used, and common genome editing tools include CRISPR-Cas9, transcriptional activator-like effector nucleases (TALENs), and Zinc finger nucleases (ZFNs) [316]. One

of the examples of adaptation of tolerant halophytic plants to salinity in level of study of genomics is gene duplication (increased gene copy number) and promoter adaptation of different salinity-responsive genes (transcription factors: adenosine triphosphatase ATPase AVP1, Myb24, ion transporters: Na^+/H^+ (NHX), superoxide dismutase (SOD1); ABD) [317]. Jeon et al. [318], after studying the genomic insights into the adaptive evolution of the memorial rose in saline environments, concluded that salt tolerance in rose is associated with detoxification, homeostasis, and stress response, and multiple gene duplication modes can shape salt tolerance-related gene diversification. Yu et al. [319] reported that for sorghum functional genomics and molecular breeding, noticeable achievements include the establishment of effective transformation systems, CRISPR/Cas9-mediated genome editing increased by morphogenic regulators, and the development of mutagenized populations for gene function validation. GWAS and QTL mapping pinpoint causal genes for marker-assisted breeding, and CRISPR-Cas allows targeted editing of defense regulator and susceptibility genes in sweet potato [320]. Sharma et al. [321] found that genome-wide analysis identified 22 *StTIFY* genes in potato, and the genes were classified using conserved phylogeny and domains; moreover, *StTIFY12* and *StTIFY3* were strongly induced in roots under drought. Jha et al. [322] revealed that main quantitative loci and genomic regions linked with salinity and drought stress, and emerging CRISPR/Cas-based genome editing, provide precise opportunities to increase stress resilience and are vital for developing climate-resilient chickpea cultivars.

Genomic studies in *Amaranthus* species are Random amplified polymorphic DNA (RAPD) which is used to classify the amaranth family into two subfamilies: Gomphrenoideae and Amaranthoideae based on DNA polymorphism [323], Inter simple sequence repeat (ISSR) which can detect 87.15% polymorphism among *Amaranthus* genotypes, aiding genotype differentiation [324], Simple sequence repeats (SSR) which can assess genetic diversity and population structure across 94 *A. hypochondriacus* accessions using 36 in-house developed genomic-SSR markers [325], Amplified fragment length polymorphism (AFLP) in which phylogenetic relationships among 98 accessions were studied based on UPGMA clustering method [326], Single nucleotide polymorphism (SNP) which used a 15K SNP set for taxonomic annotation and interspecific GWAS, enabling QTL discovery and trait introgression across different species [327], Restriction fragment length polymorphism (PCR-RFLP) in which a PCR-RFLP marker targeting the starch branching enzyme (SBE) locus was developed to differentiate *A. cruentus* from other cultivated grain amaranth species [328], Diversity arrays technology (DArT) [329], chloroplast DNA (CpDNA markers) [330], Quantitative real-time PCR assay [331], Agrobacterium mediated transformation, and Transcriptome-wide association studies (TWAS) [332]. The integration of omics technologies and genomics, together with advanced computational tools, holds promise for unraveling the complexities of stress responses in organisms and developing new methods for enhanced stress tolerance in crops [333].

It is also important to establish a link between the genomic and metabolomic fragments to understand genetic elements involved in regulatory pathways that can enhance crop quality. Comparative genomics compares genomes of various crop species, including stress-tolerant variants, to identify genetic changes associated with stress resilience by scrutinizing genetic diversity between and within species, which helps researchers identify key genomic regions or genes accountable for stress tolerance traits [334]. Functional genomics uses methods like CRISPR/Cas9 gene editing, which can target modifications in specific genes to discern their function in stress responses [335]. Functional genomics is an important aspect of genomics that consists of the comprehensive study of gene functions and their interactions within regulatory networks [336], and different approaches, including hybridization- or sequence-based methodologies, gene overexpression, gene inactivation, or editing, have

been used to characterize and identify gene functions [336]; this knowledge contributes to a better understanding of gene regulation, expression, complex stress-responsive characteristics at a genome-wide level, and is important in the development of climate-resilient crops [334]. CRISPR/Cas system has many advantages over previous genome engineering technologies, as it is simple, easily programmed to target specific DNA sequences, and has a wide range of applications, including gene editing, gene knockout, gene regulation, and even epigenome modifications [336]. Both structural and functional genomics studies play an important function in deciphering the intricate connections between structure and sequence, presenting a comprehensive understanding of the entire genome and addressing diverse biological inquiries [334,336]. Comparative genomics involves analyzing two or more genomes to uncover their differences and similarities [336]. Comparative genomics offers to be especially beneficial for the assessment of less-examined botanical species under varying stressful conditions [336]. Comparative genomic studies significantly depend on different databases and tools that cater to various areas such as gene function analysis, phylogenetic investigation, sequence examination, orthologous research, intron scrutiny, and cis-regulatory element detection [334]. The integration of genomics and omics technologies, together with computational tools, may lead to unraveling the complexities of stress responses in organisms and developing strategies for enhanced stress tolerance in plants [337]. Microarrays can be applied for both anchoring markers to genome maps and analyzing gene expression, and functional markers show both phenotypes and genetic locations. QTL-seq uses a reference genome sequence to isolate QTLs based on phenotypic variation. Higher knowledge about structural genomics information may cause better usage of genomics tools such as genome zippers to elucidate the structure of unsequenced genomes and as a shortcut to design targeted functional research. Schematic utilization of genomics findings for crops against abiotic stresses by considering functional, structural, and comparative genomics approaches is shown in Figure 2. An overview of genomics methodology in the study of abiotic stress tolerance is shown in Figure 3.

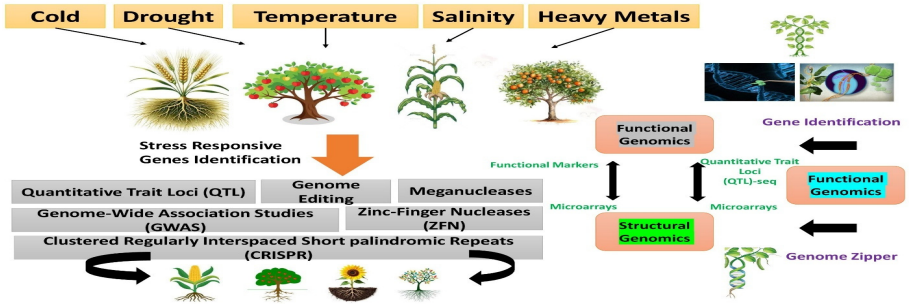


Figure 2. Schematic the application of genomics approaches for crops against abiotic stresses by considering comparative, structural and functional genomics approaches.

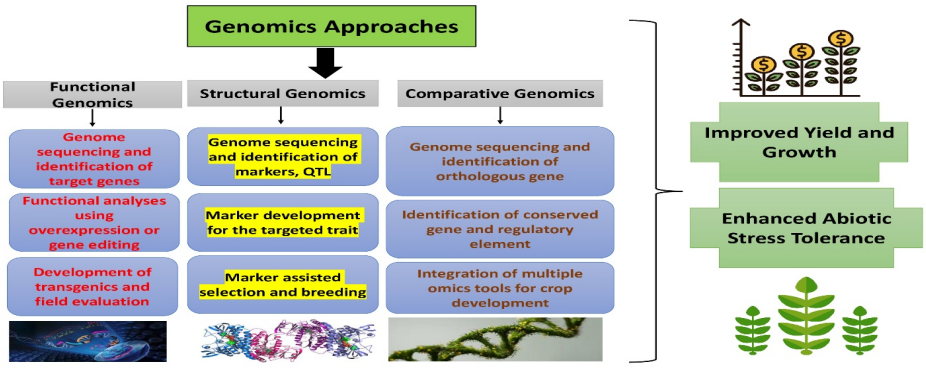


Figure 3. Genomics approaches for increasing abiotic stress.

7. Epigenomics

Epigenomics studies heritable alterations in gene expression mediated by DNA methylation, histone modifications, and non-coding RNAs such as miRNAs, which affect transcriptional regulation and chromatin dynamics [338]. Stress memory is plant memory is an important trait which involves DNA methylation, that may enhance stress tolerance response in plants, and these memories are because of epigenetic changes [339]. It is reported that epigenetics plays an important role in transcriptional regulation in *Brassica* vegetables [340]. They have also found that in both *Brassica* vegetables and *A. thaliana*, histone modification or DNA methylation may regulate gene expression under biotic stresses and can mediate reversible and rapid responses to pathogen attack, and in both crops, the importance of epigenetic regulation in controlling plant immune responses has been emphasized [340]. As different DNA methylation enzymes are involved in various plant processes, priming drives a wide range of epigenetic mechanisms, and an epigenetic code is available in response to environmental stresses in crops [341]. The main sequencing technologies for plant abiotic stress epigenetics are Micrococcal nuclease-based 3D genome mapping technology (Micro-C), chromosome conformation capture (Hi-C), chromatin immunoprecipitation sequencing (ChIP-seq) maps activating and repressive histone landscapes and factor occupancy, Cleavage under targets and tagmentation (CUT&Tag), Transposase-accessible chromatin sequencing (ATAC-seq) profiles promoter- and enhancer-proximal accessibility and TF footprinting [342].

DNA methylation has an important role in the chromatin remodeling process, and it may contribute to the regulation of gene expression without changing the primary DNA sequence. LncRNAs are generally known as RNA transcripts in eukaryotes, and plant lncRNAs play important roles in response to light, flowering regulation, root organ formation, gene silencing, response to stress, seedling photomorphogenesis, and reproductive growth [343]. LncRNAs are also involved in tolerance to abiotic and biotic stress, such as heat stress, disease resistance, drought resistance, cadmium stress, nitrogen starvation, expression regulation of adjacent genes in rice [344,345], as well as resistance to the rice blast pathogen *Magnaporthe oryzae* [346]. Dinkar et al. [347] also reported that abiotic stresses in crops are significantly regulated by their genetic makeup and stress-responsive genes and are controlled epigenetically [348]. The dynamics of DNA methylation are controlled by specific DNA methyltransferases, which mediate cytosine methylation in various sequence contexts [349]. Histone modification, DNA methylation, and chromatin remodeling are the most important epigenetic mechanisms [350]. DNA methylation involves the addition of a methyl group (CH_3) to cytosine bases in DNA, forming 5-methylcytosine (5mC). Parkin et al. [351] reported that there is no correlation between gene expression and DNA methylation, but DNA methylation plays an important role in the functional diversification of duplicated genes. In *Arabidopsis*, drought-induced hypermethylation of stress-responsive genes increases tolerance to subsequent stress events, establishing stress memory and priming mechanisms [352], and in rice, miR820 and the methyltransferase gene OsDRM2 modulate salinity tolerance by changing DNA methylation patterns [353] (Nosaka et al., 2013). Epigenomic regulation is also important in biotic stress responses [353]; epigenetic studies are necessary for better identification of long-term stress adaptation and developing epigenetically primed crop varieties [354]. Different responses of plants to stress such as environmental and developmental factors are changes in nucleosome positioning, the redistribution of heterochromatin and euchromatin in the nucleus, and the differential binding of chromatin-modifying proteins and methyl-CpG binding domain (MBD) proteins to DNA [355].

It is reported that the enzymes accountable for epigenetic changes are not directly involved, but transcriptional and protein factors and others play a mediatory role in the function of the enzymes in gene regulation for better and higher yield [356]. Several differential histone modifications and chromatin marks, such as *H3K27me3* and *H3K27ac*, enhance DNA accessibility, promoting the transcription of cold-responsive genes in indica rice [357]. Wang et al. [358]

analyzed metabolome and transcriptome changes in cotton seedlings YM11 which was subjected to cold stress, in their experiment consistently and significant changing histone modifications and the gene expressions were screened, of which transcription factors were emphasized, and the results showed a positive correlation between the changes in H3K9ac and H3K4me3 modifications and cold stress-responsive gene activation. Li et al. [359] concluded that DNA demethylation induced higher expression levels of some Ca^{2+} sensor genes in *Pyrus betulaefolia* roots, and the higher K^+/Na^+ ratio in the roots of the salt-tolerance ecotype is related to Ca^{2+} sensor gene transcription caused by hypomethylation. Mutations in genes that encode DNA methyltransferases or histone-modifying enzymes can lead to alterations in epigenetic patterns, and epigenetic variation has special potency to contribute to genetic diversity and the process of evolution [360]. Liu et al. [361] reported that, on the basis of integrative epigenomic and transcriptomic analyses, GhERF14 in Arabidopsis impairs abiotic stress resilience by suppressing ROS scavenging capacity and plays an important role in hormonal and metabolic signaling pathways. It is reported that the DNA methylome is stable in response to drought and excess light stress, in which a few 5mC DNA methylation alterations were found upon the stress treatment [362]. Drought stress-induced gene expression is associated with changes in histone modification dynamics [363]. The expression of *TaHKT2;3* and *TaHKT2;1* was downregulated under NaCl stress in wheat root and shoot tissues, and their downregulation was correlated with the increase in cytosine methylation on the coding regions of *TaHKT2;3* and *TaHKT2;1* [364]. It is also reported that heat stress may reduce DNA methylation and enhance chromatin accessibility at some transposons and DNA repeats [365]. DNA methylation and histone modification dynamics have been monitored upon plant exposure to pathogens and changes in plant-pathogen interactions of some DNA methylation and histone modification factor mutants [366].

It is also reported that DNA methylation is important for the adaptive response of rice to salinity stress, permitting the plants to maintain ionic homeostasis and survive in a saline environment [367], and the differences in methylation were related to osmotic tolerance in rice seedlings [368]. DNA methylation also has an important role in the resilience of rice to extreme temperature stress and increasing tolerance [369], and it may improve the tolerance of rice to heavy metal pollution [370]. Rice produces large amounts of ABA under drought stress, which may decrease transpiration water loss and stomatal conductance, and different *MYC* and *MYB* transcription factors are involved in ABA synthesis [371]. The overexpression of both *OsMYB48-1* and *OsMYBR1* [372] influences ABA synthesis in rice and increases drought stress tolerance. In rice seedlings, the molecular mechanisms that play a role in response to heat stress include changes in cell membrane fluidity, cell wall structure remodeling, changes in cell membrane-localized respiratory burst oxidase homolog-mediated ROS concentrations, and alterations in cell membrane-localized Ca^{2+} channel-mediated Ca^{2+} contents [373]. It is reported that DNA methylation in rice influenced the up-regulation and down-regulation of gene expression by acting on the promoter of the gene in rice seedlings [374]. DNA methylation is associated with short-term drought memory in rice along with long non-coding RNA (lncRNA) and endogenous phytohormones such as ABA [375]. DNA methylation in response to drought stress in rice is related to genome-, species-, tissue-, and period-specific effects [376]. Epigenetic mechanisms in plant interaction with potentially toxic elements (PTEs) include PTE-induced modulation of modifying enzymes [377], PTE-induced chromatin modifications [378], transgenerational memory of the PTE stress response [379], and epigenetic modifications in the evolution of PTE-tolerant species [380].

Transcriptome, miRNA, and DNA methylation analysis in maize showed that plants improved water retention under drought stress [381]; DNA methylation analysis showed the resistance of soybean plants to salt stress through demethylation and hypomethylation [382];

DNA methylation analysis in clover seedlings showed high resistance to heavy metal stress via hypomethylation [383]. Some examples of intergenerational stress memory resistance development in crops through modifications are stress resistance to drought in chickpea seedlings [384], resistance to salt and drought stress in canola [385], resistance to low temperature in okra [386], resistance to salinity and drought in sugarcane [387], resistance to salinity and abiotic stresses in tomato [388], resistance to salt and drought stress in soybean [389], resistance to drought and heavy metal in mung bean [390], and resistance to salinity and non-ionic osmotic/thermotolerance in strawberry [391]. In citrus, DNA methylation patterns with an increase in ABA levels under drought stress are reported [392], while in water shortage conditions, increased expression of drought response genes or dehydration memory genes encoding transcription factors, protein phosphatase 2Cs, and late embryogenesis abundant proteins in *Glycine max* is found [393]. In other experiments, histone modifications of *Gossypium hirsutum* L. [394], and higher photosynthetic efficiency, higher proline and sugar contents, as well as more active antioxidant machinery in *Olea europaea* L. [395] under drought stress have been found.

Activation of antioxidant defense redox homeostasis mechanisms, miRNA-induced osmoregulation [396], and phytohormone JA- and ABA-induced activity of detoxifying enzymes in wheat plants [397] under drought stress have been identified in many studies. Under heat stress, increased metabolites and antioxidant defense mechanisms [398], HSPs, redox homeostasis genes, and downregulation of lipid metabolism genes involved in membrane rigidity [399] in wheat plants, and increased expression of 22 genes associated with biological processes active in the heat stress response in *Phaseolus vulgaris* L. are reported [400]. Under salinity stress, reduced ammonium accumulation and glutamate dehydrogenase activity, seed-halopriming elevated activities of nitrate assimilatory enzymes resulting in improved nitrate uptake in Leguminous species [401], and improved catalase activity, higher water contents, lower accumulation of proline, MDA, and ROS, reduced DNA damage, and enhanced growth in Leguminous species [402] have been found. Under waterlogging stress, alteration in expression and chromatin level of flooding-responsive genes in *Oryza sativa* [403], increased activities of antioxidant enzymes and photosynthetic capacity, higher chlorophyll content, and light use efficiency in wheat plants [404], and enzymatic and non-enzymatic processes involved in ascorbic acid-glutathione (ASA-GSH) cycle, enhanced plant biomass, maintenance of root growth, induction of ethylene biosynthesis and formation of aerenchyma in roots of wheat [405]. Plants have been found.

Histone modification has been involved in different stress memories, such as *HSFA2*, which can maintain high levels of *H3K4me3/2*, thereby sustaining heat stress memory in Arabidopsis thaliana under elevated temperature [406]; *FGT1* induces and maintains the expression of memory genes and mediates stress memory by regulating nucleosome occupancy in *Arabidopsis thaliana* under heat stress [407]; *REF6* can maintain heat stress memory regulated by *H3K27me3* demethylation in *Arabidopsis thaliana* under elevated temperature [408]. High levels of *H3K4me3* modification can increase the transcription of *RD29B* and *RAB18* genes in *Arabidopsis thaliana* under drought stress [407,408]. A decrease in the level of *H3K27me3* modification accelerates the transcription of the *HKT1* gene in Arabidopsis thaliana [409], and high levels of *H3K4me3* modification accelerate the transcription of the *P5CS1* gene under salt stress [410]. Under low temperature, decreased *H3K27me3* modification promotes the transcription of *COR15A* and *ATGOLS3* genes in *Arabidopsis thaliana* [411]. DNA methylation in barley caused *HvDME* expression which may induced by drought stress, which is correlated with the differential DNA methylation patterns within the gene [412], histone methylation in wheat may cause the expression of the wheat *TaGCN5* gene in Arabidopsis gcn5 mutant plant complemented the heat and salt tolerance [412], and *TaHDA6* represses histone acetylation at promoters of defense-related

genes and negatively regulates their expression in plant defense [413], chromatin remodeling may cause *TacCHR279* promotes *H3K4me3* at the *TaKCS6* promoters and positively regulates the *TaKCS6* expression and cuticular wax biosynthesis in wheat plants [414].

8. Transcriptomics

Transcriptomic profiling has shown the transcriptional reprogramming that occurs upon identification of pathogen-associated molecular patterns (PAMPs) or effectors, shedding light on both effector-triggered immunity (ETI) and pattern-triggered immunity (PTI). It is reported that integrating metabolomics with transcriptomics has created a link between transcriptional regulation and metabolic adaptation during multi-stress responses [415]. Because of the importance of transcriptomic data for regulatory mechanisms of cell functions and for revealing gene expression patterns, RNA sequencing analyses such as RNA-seq and expressed sequence tags (ESTs), and microarrays are important in studies associated with plant responses to abiotic stresses [416]. Some of the examples of transcriptomic applications in plant-pathogen interactions are dual RNA-seq in *Arabidopsis-P. syringae*, which coordinated regulation of JA and SA signaling genes [417], RNA-seq in rice-*M. oryzae*, which can activate WRKY and NAC transcription factors in resistance [418], and time-series RNA-seq in wheat-*Fusarium graminearum*, which has a role in early upregulation of secondary metabolite biosynthetic genes [419]. Transcriptomics elucidates tissue responses that drive plant developmental pathways [420]. While genomics considers whole-genome sequencing and analysis to identify genetic variations that can facilitate the better discovery and annotation of miRNA genes, transcriptomics, primarily through RNA-Seq, complements genomics through profiling global gene expression and identifying differentially expressed genes (DEGs) under stress conditions [420]. Transcriptomic research can reveal candidate targets of miRNA-mediated regulation, and these transcriptomic datasets also provide important resources for better understanding miRNA-target modules that can regulate osmotic stress responses and ABA signaling [420].

One of the examples of adaptation of tolerant halophytic plants to salinity in level of study of transcriptomic is enhanced constitutive expression of different salinity-responsive transcripts superoxide dismutase (SOD), salt overly sensitive (SOS1), glutamine synthetase (GS), pyrroline-5-carboxylate (P5CS), L-*myo*-inositol-1-phosphate synthase (INPS), cytochrome P450, heat shock protein, Hsc70-3, antifungal protein PDF1.2) [421]. Dasanya and Hewadikaram [422] found that the outcomes of the *de novo* transcriptome research performed in Solanaceae medicinal plants have been widely elucidated, with a primary focus on the identification of candidate genes, the discovery of molecular markers, pathway analysis, differential gene expression analysis, and the identification of transcription factors. Important transcriptomics technologies in plant science are RNA-seq, which has roles in improving gene annotation and building transcriptome databases, analyzing differentially expressed genes and regulatory networks, revealing the complexity of the plant transcriptome, and studying the origin and evolution of plants [423–426]; and spatial transcriptome technology, which has roles in establishing spatial transcriptome databases and spatial expression atlases, revealing cellular spatial heterogeneity and spatial developmental trajectories, and understanding gene expression and metabolic mechanisms [427,428].

RNA sequencing has many advantages such as high accuracy, wide detection range, low cost, and high throughput, with some limitations such as the sample preparation is cumbersome, it can not reveal the heterogeneity of expression among single cells, and the bioinformatics analysis tools are limited [429]. RNA-sequencing analysis revealed that the expression patterns of genes related to translation, membrane, and oxidoreductase activity pathways were changed under drought stress [430]. scRNA-seq has many advantages such as high accuracy and specificity, clarify cell function and locations, but some disadvan-

tages such as high requirements for sample quality, high cost, difficulties in data analysis and interpretation [431], moreover, single-cell analysis of Arabidopsis root tips shows specific transcriptional responses of epidermal and cortical cells under salt stress [432]. Transcriptome and RT-qPCR analyses identified *ZmNUDX-15*, *ZmNUDX-9*, *ZmNUDX-2*, and *ZmNUDX-25* as strongly induced genes, while *ZmNUDX-28* revealed dynamic expression under maize smut (*Sphacelotheca reiliana*), and stem rot (*Fusarium graminearum*) [433]. It is reported that in maize, RNA-Seq identified nearly 3000 drought-responsive genes that have roles in NCED-mediated ABA biosynthesis, ABA signaling, and proline metabolism, contributing to osmotic adjustment [434]. In another study, transcriptome analysis under drought in maize and rewatering identified ZmbZIP33 as a strongly up-regulated ABA-responsive transcription factor [435]. In rice, transcriptomics showed OsNAC6 and OsDREB1A as central regulators of salinity and drought stress [436]. In rice, RNA-Seq showed upregulation of pattern recognition receptor (PRR) genes such as Xa21 during bacterial blight caused by *Xanthomonas oryzae* [437]. Together, transcriptomics and genomics enable the construction of co-expression networks, mapping of stress-related QTLs, and identification of hub genes, which may support marker-assisted breeding techniques [438]. It is reported that proteomic and transcriptomic markers linked with drought-induced regulatory modules have enhanced selection effectiveness in crops such as maize and rice [439].

Transcriptomics can be used for both abiotic and biotic stresses, for instance, drought/salt tolerant varieties of wheat such as JM22 and salt sensitive YM20 under drought and salinity stress in transcriptomics studies annotated to cellular process, osmotic regulation, metabolic process, and MAPK signaling pathway, were co-identified as salinity and drought tolerance-associated DEGs contributing to better stress tolerance in JM22 [440], drought-tolerant CML69 and susceptible LX9801 inbred lines of maize under drought stress showed significantly higher leaf RWC, and lower electrolyte leakage and MDA levels than the susceptible lines, which probably contributed to its better drought tolerance [441], tropical line Suwan-2 and temperature line Cim-3 of maize under waterlogging stress revealed crucial waterlogging-responsive DEGs in Suwan-2 which were related to TF modulation, cellular redox homeostasis maintenance, and plant hormone biosynthesis regulation [442], salt-tolerant HH11 and salt-sensitive IR29 cultivars of rice under salinity stress, showed more favorable antioxidant and osmotic adjustments than IR29 upon salt stress exposure, with better salt tolerance [443], heat-tolerant genotype WH-730 of wheat under heat stress revealed HSPs, antioxidant defense as well as metabolic adjustments [444], cold-tolerant cultivar Huaidao5 and cold-sensitive cultivar of rice under cold stress showed better panicle tolerance to cold stress because higher expression levels of cold-responsive genes associated to pathways, MAPK signaling pathway, plant hormone signal transduction, and glutathione metabolisms [445], ZZ143 (low grain Cd) and YX409 (high grain Cd) of rice showed higher root Cd tolerance than the susceptible genotype under cadmium stress [446], and N-efficient (398B), and the N-inefficient (CS3541) inbred lines of sorghum showed superior low nitrogen tolerance under low nitrogen stress [447].

Through proteomics and transcriptomics approaches, it has been found that *OsDREB1 TFs*, *OsDREB1A*, and *OsDREB1C* showed resistance to cold, drought and salt stresses via proline accumulation and control of the expression of genes that respond to stress [448], under heat stress, transcriptomics and RNA-seq showed that *OsDREB2B* had role in control of gene expression through alternative splicing brought on by stress [449], transcriptomics and functional genomics showed that *SNAC1* showed an increase in the expression of genes associated to stress tolerance and stomatal closure under salt, cold and drought stress [450], transcriptomics and functional genomics showed that *OsNAC10* caused increased grain production under drought [451], transcriptomics, gene expression analysis revealed that

AP37 increased grain yield under drought stress [450], metabolomics and transcriptomics showed that *ZFP252* had role in buildup of proline and sugars under salt and drought stress [452], transcriptomics and metabolomics revealed that *ZFP245* increased activity of the ROS enzyme under cold and drought stress [453], and functional genomics and transcriptomics proved exhibited that *DST* caused H_2O_2-induced regulation of stomatal closure under salt stress [454].

The potential uses of RNA methylation in stress response, fruit development, genetic improvement, and breeding of cucurbit plants include RNA methylation regulation and shape, fruit size, sugar content and flavor component synthesis, the synergistic impact of hormones/transcription factors and DNA methylation, integration of dynamic changes in methylation under different stresses, synergistic impacts of DNA methylation with hormone and transcription factor networks, high-throughput sequencing technologies, and RNA methylation maps in multiple species and different developmental stages [455]. Yao et al. [456] used an omics study in potato plants infected with *Phytophthora infestans*, and they found the importance of transcription factors involved in stress adaptation, defense, and hormone signaling. Usman et al. [457] found that the combination of spatial transcriptomics and scRNA-seq advances precise gene discovery and trait improvement in plants. Xie et al. [458], after integrating transcriptomic and metabolomic profiling studies, revealed that the CsMYC2-CSWRKY23-CsLOXs regulatory cascade orchestrates JA-dependent defense in tea leaves against *Basilepta melanopus*. Integrated metabolomic and transcriptomic analysis shows that key structural genes for isoflavonoid synthesis, namely *IF7MAT*, *IFR*, *12′H*, *HI4′OMT*, *HID*, *IFS*, *CHR*, and *CHS*, along with five MYB transcription factors, acted as main regulators to alleviate drought stress in *Sophora tonkinensis* Gagnep [459]. Emerging directions and future applications of spatial transcriptomics in plant research include applications to different plant species, multi-omics data integration, sample processing, population-level studies, and enhancing spatial resolution [460]. Transcriptomics and metabolomics analyses revealed that the overexpression of *TaMGD* in wheat may influence multiple metabolic pathways such as amino acid metabolism, photosynthesis, and carbon metabolism in response to high-temperature stress via changes in cell fatty acid unsaturation, cell membrane lipid content, and other parameters [461]. Transcriptomics approaches for increasing abiotic stress tolerance in crops are presented in Figure 4.

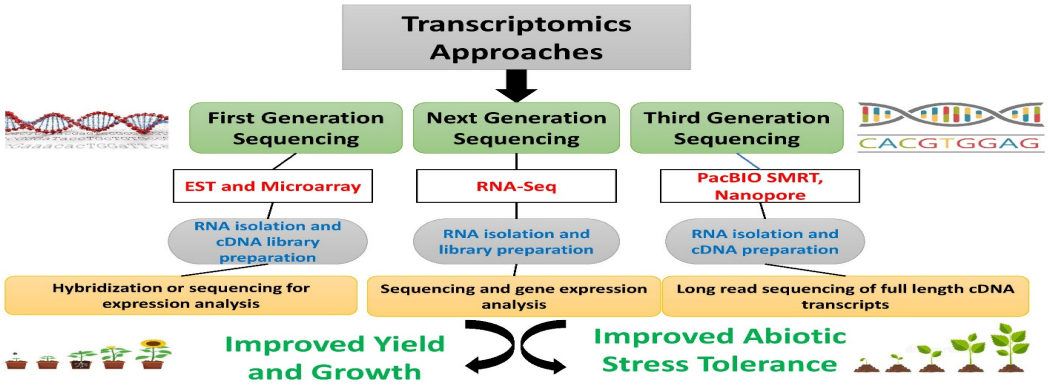


Figure 4. Transcriptomics approaches for increasing abiotic stress.

9. Proteomics

Proteomics studies have been divided into structural and functional traits, encompassing all proteins within an organism. Proteomics complements transcriptomics by providing insight into post-transcriptional regulation, protein modifications, and dynamic signaling events, and comparative proteomic studies have recognized stress-responsive proteins involved in heat-shock responses, ROS scavenging, and pathogenesis-related (PR) protein

accumulation [462]. Plant proteomes are profoundly influenced by abiotic and biotic stress, including cellular localization, protein abundances, protein interactions with other protein partners, and protein biological functions. Proteomics can be categorized into sequence, structural, and phosphoproteomics [463], and structural proteomics aims to analyze the functions of proteins by studying their structures using methods like X-ray diffraction, electron microscopy, crystallization, nuclear magnetic resonance (NMR), and computer-based modeling [464]. Methods such as tandem mass tag (TMT) and isobaric tags for relative and absolute quantification (iTRAQ) may lead to better identification and precise measurement of heat-responsive proteins [463,464]. A proteomics approach, such as identification of abiotic stress-specific biomarkers, study of the selected protein accumulation pattern in response to various stresses, and elucidation of functional protein pathways, is most important [465]. As it is an important method for studying plant stress tolerance, it may enable the profiling of the entire proteome and help in better understanding of structural, functional, and developmental dynamics under different environmental conditions [466]. Comparative proteomics allows protein profiling across individuals exposed to stress treatments, revealing proteins and pathways for adaptation [467]. Proteomics also considers the importance of protein-protein interaction (PPI) networks in coordinating multi-stress reactions [468]. Integrating proteomic and transcriptomic data identifies main discrepancies between protein levels and mRNA because of translational control and protein degradation, presenting important views into the mechanisms underlying plant adaptive plasticity [467,468]. Different proteomic methods have different advantages and limitations, for example, 2DE-mass spectrometry (MS) (2-dimensional polyacrylamide gel electrophoresis (2DE-PAGE); 2-dimensional difference gel electrophoresis (2D-DIGE) is simple and easy to use, and it needs high resolution proteome coverage together with advanced techniques, and its limitations are low reproducibility, less effective to identify low abundant and low molecular weight proteins; Data dependent acquisition (DDA: Label-free) which has precise quantification of all peptides of a sample with high reproducibility, however it is inefficient to identify extensive low abundance peptides and proteins; Data independent acquisition (DIA: SWATH-MS) which has ability to identify protein and proteoforms precisely, higher data consistency than other methods with high data reproducibility, but its identification of unknown proteins is challenging, dependent on DDA-MS for spectral library and sophisticated software is needed for precise peptide identification [469]. The main techniques used in crop proteomics are differential gel electrophoresis (DIGE) (Cy3,Cy5)/matrix-assisted laser desorption and ionization time of flight (MALDI-TOF)/MS, multidimensional protein identification technique (MudPIT), liquid chromatography-mass spectrometry/mass spectrometry (LC-MS/MS) (11), MALDI-TOF/MS, gel-enhanced liquid chromatography (GeLC)-MS/MS, iTRAQ-LC-MS/MS, and SWATH-MS) [470].

It may provide knowledge of functional outcomes of gene expression through post-transcriptional modifications (PTMs), profiling protein abundance, and protein-protein interactions under stress. Different defense mechanisms may arise from alterations in the proteome during stress responses. One of the examples of adaptation of tolerant halophytic plants to salinity in level of study of proteomic is enhanced abundance of different stress-and defense-related proteins (Late embryogenesis abundant (LEA), redox, pathogenesis-related (PR), ion transporters, protective proteins involved in activation of photosynthesis (D2 protein) and protein biosynthesis, activation of biosynthesis of protective components (lignin) [471]. Mass spectrometry-based proteomic studies showed phosphorylation of HSPs under heat stress, which can increase cellular and thermal tolerance [472]. Under salinity stress, proteomic studies in barley could enhance the abundance of ion transporters such as HKT1;5, which may facilitate ion homeostasis and sodium exclusion [473]. Proteomic analyses showed enhanced

defense-related proteins regulated by the *Meloidogyne incognita* resistance gene-1 (mi-1) in tomato during nematode infestation [474].

In proteomics studies, tolerant BW35695 and drought-sensitive BW4074 cultivars of wheat showed greater antioxidant capacity, osmotic adjustment, and high upregulation of protein synthesis-related proteins, contributing to better stress tolerance to drought stress [475], drought-tolerant YE8112 and drought-sensitive MO17 cultivars of maize showed better tolerance to drought because of its activation of photosynthesis proteins associated to balancing light capture and utilization [476], heat-tolerant variety 9311 and sensitive variety Guangluai4 (GLA4) of rice showed a core set of HS-responsive protein kinases, regulatory factors, and splicing factors, especially those involved in starch metabolism [477], tolerant XM 55 and sensitive genotypes YM 158 of wheat through iTRAQ proteomic analysis of wheat responses to waterlogging showed high tolerance [478], tolerant and sensitive accessions of pearl millet through 2DE-based whole proteome analysis of pearl millet response to 150 mm NaCl treatment, and their salinity tolerance of the tolerant accession was attributed to its higher upregulation of stress-responsive proteins [479], Kharchia-65 salt-tolerant via LC-MS/MS based proteomic analysis of wheat responses to 0 and 300 mM NaCl treatment for 48 h showed high tolerance to salinity stress because of higher upregulation of stress-responsive proteins, peroxidase, auxin-responsive in tolerant genotype and comparative downregulation in susceptible genotype [480], LT-tolerant Gurez local and LT-sensitive GM6 of maize through 2D-PAGE based proteomic analysis of maize leaf responses to low temperature stress exposure for 12 h at 3-leaf stage which showed high tolerance because of 19 and 10 proteins that were identified in Gurez local and GM6 [481], Al-sensitive barley cultivar ZU9 through TMT-based quantitative proteomic analysis of barley response to aluminium stress under phosphorus-*Piriformospora indica* interaction, and DEPs were mainly enriched in the phenylpropanoid biosynthesis pathways, among which peroxidases were prominent [482], drought-sensitive S4 and S4-1, and drought-resistant T33 and T14 of sorghum through nano-LC-MS/MS-based leaf proteome analysis of sorghum response to drought, a total of 3927 proteins were quantified, and tolerant genotypes revealed enhanced TCA cycle and influenced aminoacyl-tRNA biosynthesis [483].

Some proteins to combat abiotic stress tolerance in tomato are *COR15* protein which adheres and folds to the chloroplast membranes to support leaf cells during freezing under cold stress [484], *P5CS* protein involved in proline biosynthesis and inducible upon salt shock in drought-resistance which is useful in both salt and drought tolerance [485], *SpPKE1* which interacts with an F-box protein associated with drought tolerance [486], *LEA* proteins that may prevent membrane leakage, membrane and protein stabilization under drought stress [487], *SlbZIP1* which can reduce ABA-mediated stress and reduced drought and salt stress [488], *MdVHA-B* that may cause better tolerance to drought stress [489], and *LeHSP21.5* which improved tolerance to tunicamycin-ER stress inducer and enhanced tolerance [490]. Tosto et al. [491] reported that most of the proteins found belong to the group of proteins that are active in the metabolism of organic components, and changes in the proteomic profile promoted maintenance of root system growth and cellular homeostasis during stress in young cacao plants. In tea plant (*Camellia sinensis*), differentially expressed proteins (DEPs) are mainly involved in catalytic, transport, binding, and antioxidant activity, and DEPs involved in stress/defense/detoxification pathways may have vital roles in the response to glyphosate stress [492]. Kushalappa and Gunnaiah [493] found that metabolo-proteomics is the state of art tool for biotic stress resistance gene discovery, and metabolo-proteomics is used in forward and reverse genetics to decipher gene function. Subramani et al. [494] found that both conserved and genotype-specific DEPs can be applied as targets in selective breeding and developing drought-tolerant common bean genotypes, and the tolerant genotypes uniquely revealed DEPs related to sugar metabolism and plant signaling, while

the sensitive genotypes showed more DEPs involved in plant-pathogen interaction, carbohydrate metabolism, and proteasome function. Proteomic investigation in foxtail millet showed that the appropriate content of auxin could activate downstream SiARFs-SiSAURs expression, and two genes, namely *SiTCH4* and *SiGH3*, were found to be associated with plant height regulation [495]. Tang et al. [496] reported the functional validation of SlTAS14 as an important regulator in coordinating proteomic adaptation to salt stress in tomato plants.

Some of the most important proteomics of drought tolerance in crops are 2D-E with MALDI-TOF-TOF mass spectrometer in barley in which 38 differentially abundant proteins involved in energy, stress response, amino-acid biosynthesis, and photosynthesis [497], iTRAQ (isobaric tags for relative and absolute quantification) in which 721 differentially abundant proteins (DAPs), RNA transport (nine proteins), ribosome, carbon metabolism, biosynthesis of amino acids and carbon fixation in photosynthetic organisms are active [498], 2D-E with MALDI-TOF/TOF mass spectrometer in rice in which 102 identified proteins involved in metabolism and bioenergy, cell defense and rescue, protein biogenesis and storage class, cell signaling, and proteins with miscellaneous function [499], LC-MS/MS analysis in sorghum that genotype-specific drought responsive involved in flowering time control, starch biosynthesis, and Rubisco activation, ROS scavenging, HSPs epicuticular wax production, and phospholipid metabolism and abscisic acid signaling [498,499], 2D-E with LC/MS/MS in chickpea in which 34 differentially expressed proteins related to stress response, photosynthesis, gene transcription, protein synthesis and degradation and signaling [500], 2D-DIGE in cotton that around 8 DEPs were found in the Bt cotton leaves, which showed differential expression and were involved in essential plant growth mechanism, cell defense, photorespiration, and metabolism of amino acids [501], 2D-E with MALDI-TOF/TOF-MS in barley in which 184 proteins in leaves and 231 proteins in root tissue, related to nitrogen metabolism, defense mechanisms, photosynthesis, and secondary metabolism [502], 2D-E with LC-MS/MS analysis in potato in which 18 differentially abundant proteins identified related to energy and carbohydrate metabolism and defense and detoxification processes [503], and 2D-E with MALDI-TOF/TOF mass spectrometer that around 39 differential proteins involved in metabolism, response to heat, redox process, protein refolding, and photosynthesis [504].

10. Metabolomics

Metabolomics consists of the study of the whole set of metabolites synthesized in crops under stressed and normal conditions, showing the plant's metabolome. It is an important component of post-genomic omics studies which deals with the comprehensive chemical analysis of the whole metabolites, in a particular biological system such as a tissue, a cell, or an organism at a specific developmental stage or under an induced circumstance [505]. Metabolomics profiles stress-induced changes in small molecules, including sugars, amino acids, secondary metabolites, and osmo-protectants, providing a functional perspective on stress adaptation [506]. Metabolomic datasets can show physiological results of miRNA-mediated regulatory networks. Metabolomic studies showed drought-induced accumulation of proline, GABA, and trehalose, which stabilize membranes and protect cellular activities [506,507].

The main metabolomic techniques that have been used in studying plant pathogen interactions are Capillary Electrophoresis Mass Spectrometry (CE-MS), Gas Chromatography Mass Spectrometry (GC-MS), High-Performance Liquid Chromatography Mass Spectrometry (HPLC-MS), NMR, High-Performance Liquid Chromatography-UV, Ion Exchange Chromatography, LC-MS, MALDI mass spectrometry, and NMR [507]. Metabolomics is an important approach to understanding how plants respond to different stresses, and it may offer a comprehensive and high-throughput assessment of metabolites in crops [508]. Important techniques such as LC-MS and GC-MS are necessary for assessment of a broad range of metabolites,

namely primary metabolites, such as amino acids and sugars, and secondary metabolites such as alkaloids and flavonoids, which show important functions in plant defense [509]. The integration of metabolomics with different omics disciplines such as proteomics and transcriptomics provides multi-dimensional perspectives on plant stress responses [508,509]. It is important to say that no single metabolomics method can determine all metabolites in a sample, and metabolomes shown by any combined metabolomics methods reflect only the tip of the iceberg of an organism, a tissue, and a cell [507–509]. Because of the importance of salinity stress in agriculture, there is a lot of metabolomics research on crop species such as the legume genus Lotus [510,511], poplar [512], sea lavender [513], tomato [514], and *Arabidopsis* [515], showing the components involved in tolerance and resistance to salt stress, which may improve identification of candidate genes associated with abiotic stress responses. In barley, elevated levels of flavonoids and polyamines under salinity stress may have a role in ROS detoxification and osmotic adjustment [516]. miRNAs such as miR398, miR159, and miR156 regulate these metabolic pathways by targeting transcription factors for antioxidant enzymes, linking regulatory networks to physiological results [517].

Metabolomics presents an accurate and rapid analysis of metabolites, providing an overview of cellular metabolites involved in various processes [518], which may increase understanding of biochemical pathways associated with molecular mechanisms and is important for high-throughput research of resistance traits to herbicides. The phytohormone jasmonic acid imparts resistance to tomato plants against various types of herbivorous attacks, such as *Manduca sexta*, *Tetranychus urticae*, and *Spodoptera littoralis* [519]. Salicylic acid is an important precursor of methyl salicylate to protect tomato plants against *Bemisia tabaci* [520]. It is also reported that importance of fluopimomide which is a succinate dehydrogenase-inhibitor fungicide with nematicidal activity against *Meloidogyne incognita* with important function in enhancement of plant growth [521]. Melatonin can prevent damage to membranes and proteins and increase tolerance against abiotic stress in tomato plants [522]; ABP19a protein is involved in various developmental processes and drought tolerance [521,522]; SpUSP, which is an annexin-interacting universal stress protein, can reduce oxidative stress by preventing the generation of ROS, activating several stress-responsive genes that may cause the accumulation of some osmo-protective solutes and enhance drought tolerance in tomato plants [523]. In tomato plants, SINAC4 can improve oxidative stress response through fruit ripening and carotenoid accumulation [524], SINAM2 inhibits extreme water loss by flower-boundary morphogenesis [525], and SINAC1 enhances tolerance to lower temperature and phytopathogens through increasing viral replication and chill tolerance via interactions with replication accessory proteins [526]. Metabolomics studies have become an important tool to monitor plant responses to various environmental stress conditions [527], and with the help of advanced metabolic tools such as NMR, LC-MS, Fourier transform infrared spectroscopy (FTIR), and GC-MS, it is possible to perform appropriate data analysis, identification, detection, and evaluation of the metabolites [528]. Recently, metabolite profiling of transgenic lines and mutants has provided insights into metabolic networks and identified candidate genes underlying specific traits [529]. It is reported that metabolomics may increase the chance of accelerating the selection of superior breeding stock and the screening of elite crop types [530]. It is noteworthy to say that the identification of various classes of metabolites in plants is largely according to using hyphenated mass spectrometric techniques to chromatographic equipment and electrophoretic findings [531], and selection of suitable ionization technique and analyzer type for metabolite technique is vital in a mass spectrometer [531]. Designing the trial according to the Metabolomics Standards Initiative (MSI) is also important for analytical protocols, appropriate procedures for metabolite extraction, and the right biological material preparation [532]. Various statistical calculations could be considered to determine the metabolites, capabilities that allow the definition of alterations of a specific component

in definite environments [533]. MSI techniques do not need antibody or chemical labeling, and it is possible to visualize the geographic distribution and relative abundance of molecules, which include desorption electrospray ionization (DESI), laser desorption/ionization (LDI), MALDI, secondary ion mass spectrometry (SIMS), and laser ablation electrospray ionization (LAESI) [534]. Machine learning (ML) based methodologies, deep learning (DL), and in-depth multi-omics data analysis approaches are enabling scholars to construct models and metabolic reports for desired plant species under particular settings [535]. Integrated metabolomic and transcriptomic analyses show important mechanisms of melatonin and selenium in increasing tea plant resistance to gray blight disease, as both of them decreased the accumulation of triterpenoids and significantly enhanced the production of the antifungal components such as Cinchonain and Tangeretin [534,535]. GC-MS is an advanced analytical technique for metabolic profiling in plants and is necessary to recognize different components belonging to different classes, such as amino acids, organic acids, sugars, amines, alcohols, and fatty acids [536]. The value of LC-MS is enhanced in metabolomics, particularly after the adoption of ultra-performance liquid chromatography technique, which can boost separation effectiveness and reduce analysis time [537]. NMR spectroscopy suggests an entirely different analytical technique compared to MS-based findings, which has lower sensitivity [537]. NMR has other advantages such as simple preparation, convenience, and non-destructive capability [538]. The metabolomics of plants is very varied and complex in their chemical structure [539], and metabolomics analyses include three key methods, namely, sample preparation, data gaining and identification of components via utilizing the statistical analysis of the data [540].

Plant metabolites are structurally varied with high complications, such as solubility, dissimilar size, separation, explosive nature, stability, and amount [541,542], and the extraction technique of metabolites depends on different parameters such as chemical and physical properties of the targeted metabolites, different types of plant organs, the solvent used, and chemical structure [541]. The main metabolite extraction methods are supercritical fluid extraction, solvent extraction, sonication, and solid-phase extraction [543], followed by vapor-hydrodistillation, hydrodistillation, hydrodiffusion, vapor-distillation, cold pressing, and organic solvent extraction [543]. Key steps in metabolomics are sample collection and organization, metabolite extraction, derivatization and separation, data acquisition, data analysis, metabolite identification, and data submission to public repositories [544].

One of the examples of adaptation of tolerant halophytic plants to salinity at the metabolomic level is alterations in carbohydrate metabolism- activation of catabolism (starch degradation, Krebs cycle, glycolysis), enhanced biosynthesis of organic osmolytes, lignin, and phenolic components) [545]. The data gathered from proteomics, transcriptomics, and metabolomics need to be combined to achieve better findings of the plant as a system, and the main research groups have provided workflows to integrate all this information into a single pipeline with topics of transcriptomic-proteomic, transcriptomic-metabolomic, and metabolomic-proteomic [543,544]. Metabolomics has developed and is considered an important technology in assessing or elucidating phenotypes in assorted living systems under changing climatic conditions, necessary for stress biology studies of plants and different organisms by understanding different molecules [546], as well as its application in different fields such as imitation biology, medicinal biology, and analytical modeling of animals, plants, and microscopic organisms [547].

Various studies show the importance of metabolomics in different studies under environmental abiotic stresses such as drought and salinity, temperature, and soil flooding. It is reported that GC-MS method can be used for exploring the temperatures stress metabolome in *Arabidopsis thaliana* L. under different temperature stress [548]; GC/MS and LC/MS method can be used to reveal the short-term responses to salt stress in *Arabidopsis thaliana* L.

under water and salinity stress [549]; metabolic profiling is beneficial to identify the responses of plants to abiotic stresses in *Arabidopsis thaliana* L. under flooding and drought stress [550]; multi-parallel and high-throughput analysis can reveal novel findings in *Arabidopsis thaliana* L. under sulfur stress [551]; transcript profiling can investigate global gene expression and metabolic responses in *Phaseolus vulgaris* under phosphorus stress [552], NMR is beneficial in study change metabolic consequences of stress, and metabolomics analysis of the consequences of cadmium exposure under heavy metals stress in *Arabidopsis thaliana* L., and *Silene cucubalus* Wibel [553], GC-MS can be used for metabolomics analysis in the roots of different Soybean varieties under salinity stress [554], while CE-MS can be used for proteomic profile investigation of different Soybean varieties under Cd stresses conditions [555].

Both proteomics and metabolomics techniques offer comprehensive analyses of proteins and metabolites involved in stress responses, providing a holistic knowledge of biochemical alterations in crops under stress [554,555]. It is also believed that identifying key proteins and metabolites linked with stress tolerance aids in developing biomarkers for elucidating stress adaptation pathways and stress screening. Yu et al. [556] revealed the novel metabolomic and transcriptomic insights into the secondary metabolites response mechanisms of tea seedlings under various temperatures, in which the purple-leaf cultivar showed significantly increased anthocyanin accumulation under low temperatures, whereas the green-leaf cultivar accumulated higher levels of catechins under the same environment, and main transcription factors such as WRKY (*CSS0024910*), MYB (*CSS0002706*), MYB (*CSS0000220*), AP2/ERF (*CSS0000647*), NAC (*CSS0035736*), and bHLH (*CSS0002807*) closely associated to these metabolites.

Varieties *02428* (japonica) and *YZX* (indica) of rice through LC-MS/MS-based metabolomics analysis of rice response to LT (15 °C for 4 days) at germination, and 7 key LT-responsive metabolites were recognized, and these metabolites were found to participate in biosynthesis of amino acids and phenylpropanoids, as well as metabolism of glutathione and inositol phosphate under low temperature stress [557], drought-tolerant T13 and drought-susceptible T2 of wheat through integrated transcriptome and metabolomics analyses of wheat responses to drought showed drought tolerance because of phenolic acids and flavonoids metabolism [558], warm-adapted Fahng60 and heat-sensitive Samerng2 cultivars of wheat via physiological and metabolomics analysis of seedlings, response to salt and heat stress treatments and sugars, amino acids and sugar derivatives were the main responsive metabolites in leaves under the stress [559], drought-tolerance line si287 and a drought-sensitive line X178 of maize through transcriptomic and metabolomics analysis of maize responses to a 7-day drought at the 3-leaf stage showed that they were significantly enriched in starch, flavonoid biosynthesis, and sucrose metabolism as well as amino acids biosynthesis-related pathways under drought stress [560], GN2 (salt-tolerant) and GN18 (salt-sensitive) of barley via metabolomics and proteomic analysis of barley response to salt stress at germination stage, and a total of 187 salt-regulated metabolites were identified, which were mainly associated to ABC transporters, CHO metabolism, amino acid metabolism, and lipid metabolism under salinity stress [561].

Recent multi-omics and metabolomic studies showed that heat stress reshapes amino acid, central carbon, lipid, and hormone-associated pathways across diverse crop species, and the nitrogen-rich metabolites showed important roles in stress signaling, redox homeostasis, and regulation of stomatal behavior [562]. The integration of metabolomics with other omics data such as proteomics, transcriptomics, and genomics through systems biology approaches provides researchers a better understanding of metabolic network regulation and cellular functions [563]. Metabolomics has been successfully applied to assess tea quality under stressful and normal conditions, during various processing processes,

and to construct metabolic pathways [564]. Metabolic markers recognized by metabolomics are important parameters for effective evaluation of tea quality in different situations [565]. Metabolomics has been applied for quality control of natural components by monitoring the effectiveness of phytomedicines [566], and it has increasingly been applied to detect potential contamination and adulteration in herbal preparations or medicines for key bioactive components such as rosavin, ginsenosides, artemisia, etc. [567].

Spatial metabolomics is a research method based on the development of mass spectrometry imaging technology, whose birth and further progress are inseparable from that important technology [568]. Advantages of spatial metabolomics are the sampling process of spatial metabolomics is relatively simple so that the test results have high accuracy, spatial metabolomics has a wider range of applications and can detect more abundance substances, and the spatial distribution information of spatial metabolomics is clear, and the analysis dimension is comprehensive. Spatial metabolomics does not require special treatment before sample detection, and after the sample is simply cleaned or wiped clean, it can be embedded with reagents such as carboxymethyl cellulose, frozen section embedding agent, and gelatin, which maintain the original state of the metabolite to a greater extent to enhance the accuracy of the test results [569]. The detection sensitivity of traditional metabolomics is relatively low, and it is difficult to detect metabolites with large differences in high throughput at the same time [570]; however, spatial metabolomics can detect thousands of metabolites at the same time because of its high sensitivity, high coverage, and high resolution, so it is easier to detect differential metabolites in some metabolic pathways [571]. Moreover, spatial metabolomics is embedded in the original state of the sample, which can describe the specific location of changes in the micro-area directly related to the research target [572], and raise the metabolomics information from the two-dimensional level to the three-dimensional level, providing visual data information for plant research. Spatial metabolomics has different applications in different plant types; its application purposes in medicinal plants are visual analysis of natural ingredients, quality control of medicinal materials, assisting specificity identification, and analyzing anabolic pathways of metabolites, and its application purposes for food crops and economic crops are exploring the regulation of growth and development, revealing the interaction mechanism between crop and environment, and verifying gene function [573].

11. Phenomics

It is an important field in crop research that can be used to identify the large-scale responses of crops to different stresses. Phenomics approaches such as high-throughput phenotyping (HTP) have a significant role in assessing resistance traits in crops [574], with special capability to evaluate salinity tolerance by assessment of some traits such as growth inhibition, ion accumulation, and osmotic regulation [575]. Because of complex and non-distinct mechanisms involved in the responses of crops to abiotic stress, including drought, salinity, nutrient deficiencies, and extreme temperatures, the phenotyping of abiotic stress resistance is usually an important challenge, and high-throughput phenotyping methods are needed for better understanding and to enhance the ability to reliably screen various traits under different stress conditions [576]. It is also reported that plant phenomics has studied the development of high-throughput mechanisms rather than a theoretical framework [577]. The incorporation of advanced studies in phenomics has transformed stress analysis with imaging techniques such as hyperspectral, thermal, and fluorescence imaging, enabling precise monitoring of plant responses [578]. It is also reported that nondestructive imaging such as visible and near-infrared reflectance methods has been developed for plant physiology and stress status, and thermal imaging and canopy temperature are sensitive methods of the stomatal response to abiotic stress [579].

The Control-Stress data Integration with Overlapping Clustering (CSI-OC) workflow shows significant progress in stress response research, providing a comprehensive framework for recognizing stress-responsive genes and their associations with phenotypic traits, and it has been found effective as a comprehensive approach for identifying pertinent genes associated with drought stress in sugarcane, and the number of genes selected by CSI-OC showed a contrasting pattern between roots and leaves [580]. Root system analysis, which is an important phenotyping platform, can be used for studying root traits for drought resistance, which has high-precision root scanning, understanding root-soil interactions, studying root growth in different soil conditions [581], and screening root traits for improved nutrient uptake. Leaf and shoot phenotyping can be used for assessing leaf traits for yield improvement [582], measurements of water-deficit related traits and drought tolerance screening in crops, and precision agriculture and stress detection [583]. The five main pillars of plant phenomics are data acquisition, data management, data interpretation, modeling, and applications. Phenotypic analysis of two distinct wheat genotypes, namely SSD397 and SSD69, showed that during heat stress, SSD69 showed changed accumulation of MDA content as well as H_2O_2 under heat stress conditions [584].

12. Metagenomics

Metagenomics is a culture-independent study for identification of microbial communities, and it has the special ability to enable the direct sequencing of environmental DNA [585]. Progress in metagenomics can enhance knowledge of plant microbiome regulation, increasing plant health, and promoting food production and sustainable methods [586], and by application of metagenomics, scholars can design synthetic communities particularly appropriate to increase plant resistance, productivity, and nutrient uptake [587]. Greenman et al. [588] also showed the strengths of long-read metagenomic sequencing for microbiome research, including relative abundance estimates and the accuracy of the classification. The most important metagenomics approaches and next-generation sequencing platforms are amplicon sequencing, shotgun metagenomics, metagenome-assembled genomes (MAGs), single-cell genomics, and metagenome-wide association studies (MWAS) [589]. Fouad et al. [590] found metagenomic studies of the rhizosphere of wheat can highlight the potential benefits and diversity of microbes as well as focusing on the need for innovative findings to benefit from unculturable bacteria to resist salt stress. Moreover, according to the metagenomic studies, the phyla *Actinobacteria*, *Proteobacteria*, *Firmicutes*, *Bacteroidetes*, *Fibrobacteres*, and *Verrucomicrobia* can induce systemic resistance in crops under saline conditions [590]. Alsaedi et al. [591] concluded that metagenomic analysis of medicinal plants may induce a better understanding of novel genes and organisms that may have an important function in abiotic stress resistance in crops. El-Halim et al. [592], after studying metagenomic insight into drought-induced changes in the Egyptian wheat rhizosphere microbiome, found that classes such as *Cytophagia* and *Alphaproteobacteria* were significantly enriched under drought, which could be a promising enhancement of plant stress altruism, and some genes may play an important role in stress adaptation through energy-dependent cellular processes involved in plant survival. One study about metagenomic study of the communities of bacterial endophytes in the rubber *Hevea brasiliensis* leaves showed that *Cyanobacteria* and *Firmicutes* were the dominant phyla, with noticeable differences in community structure between diseased and healthy leaves [593]. In one shotgun metagenomic study on the maize rhizosphere revealed that an abundance of *nifA*, *nifH*, *csp A*, and *groES* genes can be used to reduce environmental stress and increase plant development [594], and metagenomic researches also can make able precise detection of novel viruses belonging to *Tombusviridae*, *Betaflexiviridae*, and *Geminiviridae* families in maize [595].

13. Single-Cell and Plants

Plant single-cell microsystem environments, such as chip-based platforms and microfluidic systems, provide new insights into omics, environmental sensing, and cell biology. The application of single-cell technology in different biological research domains has been transformative, especially in the exploration of plant metabolomics [596,597]. Advancements in single-cell research now enable better analysis and study of gene expression in individual plant cells that interact with pathogens, and this technology may permit better examination of different cell types implicated in resistance, exploration of cellular behaviors at the individual cell level, and the responses of cells targeted by pathogens [597]. SmartSeq2 and CelSeq2 are the two most popular plate-based methods [598], and Smart-seq is one of the most successful plate-based methods for single-cell RNA sequencing in studies of plants [599]. Omics analysis of single cells has become possible with novel advances in techniques for single-cell isolation, which may improve the revealing of the inherent properties of single cells at high resolution. Single-cell omics can improve identification of proteins, metabolites, and expressed genes in individual cells of a given population, which can improve the science of better determining the role of various cell types in plants and biological processes. Single-cell multi-omics research aiming at analysis and simultaneous extraction of various analyte biomolecules in a cell will assist in validating the relative alterations occurring in a cell to a specific elicitor [600]. In genomics, single-cell methods empower researchers to understand the complexity of plant tissues, showing the distinct cell types and their specific contributions to natural product formation. In single-cell epigenomics, recent approaches have enabled accurate and comprehensive profiling of various epigenomic characteristics, and the cell-specific epigenome improves the dissection of molecular mechanisms underlying biological processes in crops [601].

Single-cell genomics has progressed beyond model systems into crops such as rice and maize with new knowledge of tissue-level expression and accessibility [602]. Single-cell transcriptomics has shown the dynamic gene expression patterns within individual plant cells, presenting a precise view of the molecular machinery driving the biosynthesis of secondary metabolites [603]. Metabolomics and proteomics at the single-cell level may increase knowledge of metabolites and proteins involved in natural product pathways [604]. Single-cell technology is important for optimizing the production of valuable components, uncovering novel bioactive molecules, and progressing the sustainable production of nutraceuticals, industrial products, as well as plant-derived pharmaceuticals [605]. Single-cell omics have enabled the differential analysis of gene expression and genomic DNA expression between plant cell types [606]. Single-cell approaches are important to discover genotype-phenotype relationships and reveal hidden cellular heterogeneity in mitochondrial diseases [607]. With the study of single-cell metabolomics, scholars and scientists can discover the metabolic distinctions among individual cells and better understand how such variability contributes to the plant's overall function and the identification of diverse environmental challenges.

The application of advanced techniques such as capillary electrophoresis, mass spectrometry, and fluorescence assays, in conjunction with micro-sampling and cell isolation techniques, improves our science for the meticulous metabolic characterization of single plant cells. Usman et al. [608] reported that CRISPR/Cas9 validation of scRNA-seq-predicted genes confirms their functions in development and stress responses, and combining scRNA-seq with spatial transcriptomics advances precise trait improvement and gene discovery in crops. Jain [609] reported that an integrated multi-omics finding can improve understand of cell-type-specific gene regulatory networks (GRNs) to prove the main components which coordinate adaptive responses to various stresses, and coupling spatial transcriptomics with scRNA-seq can provide spatially resolved gene expression and

insights into cell-to-cell interactions. It is also reported that overexpression of *SaPEPC1* enhanced the photosynthetic performance of *Arabidopsis*, particularly under intense light, and *SaPEPC1* can promote carbon metabolism by utilization of photosynthates and increasing the synthesis in *Arabidopsis* [610]. Although single-cell transcriptomics has revolutionized the science of cellular diversity and gene expression, it may not fully capture the functional state of the cell, and as the direct effectors of cellular function and signaling, proteins can provide immediate readouts of biological cases, although single-cell proteomics also faces some challenges in terms of dynamic range, sensitivity, and sample loss, as well as limiting detection to only high-abundance proteins [611]. The main limitations of single-cell transcriptomics are concerning the specific cell types, profiling of transcriptome responses in cell types, and technical variability in interpreting the results [612], as well as biological changes and false positives in scRNA-sequenced cell types because of RNA degradation, amplification bias, and sequencing errors influencing data reliability [613]. One of the most important frontiers in plant science is single-cell metabolomics because of dynamic range, extreme chemical diversity, and small volume of intracellular metabolites [614]. Single-cell RNA sequencing has been applied to provide detailed maps of cell types in crops, which has been restricted to cell types, tissues, and organs [615]. It is reported that techniques such as CEL-Seq, Smart-Seq, and 10xGenomics have significantly advanced single-cell research, especially in crop sciences [616]. Other methods such as BD Rhapsody and Nextera XT system, present versatility for analyzing different plant tissues, inducing protein analysis and simultaneous gene studies [617]. The scRNA-seq process creates high-dimensional and complex data which may require meticulous preprocessing, normalization, and quality control [618].

It is reported that scRNA-seq has provided important insights into the distinct ways individual cell types in crops respond to environmental challenges [619]. scRNA-seq research in *Arabidopsis* under heat stress has shown differences in heat shock gene responses among different cell types [620]. Under high-temperature stress conditions, energy redistribution at the single-cell level showed a noticeable dichotomy in multiple cells of *Arabidopsis* roots [621]. scRNA-seq in *Arabidopsis* was used to prove the cell-specific and coordinated defense responses in Arabidopsis leaves under pathogenic *Pseudomonas* attack, showing characteristic transcriptional reprogramming in various cell types during immune and susceptible processes [620]. Application of scRNA-seq in analysis of gene expression patterns in strawberry leaves during early *Botrytis cinerea* infection showed distinct early defense responses in hydathode, mesophyll, and upper epidermal cells [622]. Results of scRNA-seq of rice varieties exposed to brown planthopper have shown considerable cellular differences in sheath and phloem parenchyma cells between resistant and susceptible strains [623]. Recent research has also used scRNA-seq to discover cell-specific mechanisms in plant-microbe interactions, such as root nodule development in soybean and *Medicago truncatula* [624]. Graeff et al. [625] used scRNA-seq analysis to identify the effects of brassinosteroid (BR) signaling in the root via characterization of briTRIPLE mutants at single-cell resolution, and they reported that BR signaling did not influence cellular development or cell proliferation, but rather improved cell division plane orientation and cellular anisotropy.

In the transition from microarrays to RNA-seq, differential gene expression data are usually reported alone as a single-omics study, whereas studies incorporating alternative omics methods such as metabolomics and proteomics commonly anticipate the logical follow-up question of how observed changes are associated with underlying patterns of gene expression [298]. The introduction of single-cell and spatially resolved methods has further exacerbated this difficulty by including additional levels of information which should be considered. The challenge of multi-omics is that adding more data is just as

likely to obfuscate the underlying signal as it is to clarify it. There is also no guarantee that gathering more and different types of data will make a problem easier to solve, and rapid expansion of the omics portfolio brings with it a new set of challenges. Multi-omics data are expensive and difficult to analyze and generate, and the development of new tools will possibly be able to tease out patterns which are missed by current tools [298,626].

14. Conclusions

The recent progress in high-throughput proteomics, genomics, and metabolomics technologies enables the understanding, quantification, and analysis of proteomes, genes, and metabolomes in different tissues and their response to various stresses. The role of genomics technologies in recent years has revolutionized genome sequencing, annotation, and analysis, which has significantly improved information about the plant genetic architecture of environmental adaptation. High-throughput genotyping and phenomics systems, together with genome selection strategies and machine learning, may help breeders to make a rapid evaluation of genetic resources for increasing biotic and abiotic stress tolerance and yield stability. Advances in transcriptomics consist of RNA-seq, alternative splicing analysis, gene co-expression network analysis, functional annotation, IncRNA analysis, and pathway analysis. In recent years, proteomics has emerged as an important tool for understanding stress tolerance in crops, which may allow scholars to identify and quantify differentially expressed proteins in response to various stresses. Modern metabolomics methods such as NMR, MS, and cutting-edge imaging technologies like NanoSIMS have caused better chances for study of crop metabolomes. Plant metabolomics is an important tool for discovering the complex chemical landscape of plants, and by identifying and quantifying metabolites, scholars can gain considerable insights into improving crop varieties, plant physiology, better understanding of how plants interact with the environment, and discovering new medicinal components. The main opportunities for the application of multi-omics studies are yield improvement, nutritional quality, precision breeding, stress resistance, and enhanced trait identification; the main challenges are experimental design, data complexity, integration issues, and transferring data into a biological context, and prospects are sustainable agriculture, personalized agriculture, enhanced breeding programs, increased throughput, and interdisciplinary collaborations. Phenomics may help solve complicated issues about plant physiology, which may need a clear framework to be programmed, as has been achieved for genomics. The main limitations of single-omics techniques are difficult detection of low-abundance proteins and distinguishing between pathogen proteins and hosts in proteomics studies. Not accurate information of transcriptomics studies on protein abundance because regulatory processes like microRNA-mediated control and alternative splicing knowledge. Limitations of metabolomics studies in capturing the full range of metabolites, with shared metabolites between pathogen and host. Although, in recent years, omics technologies have been extensively used for different crops, however, due to the complex biological regulation network, single omics generally fail to illustrate the specific biological phenomena. Integrated omics technologies have shown high potential in crop breeding to bridge the gap between food security and environmental challenges. Future studies should focus more on the role of transgenerational stress memory and epigenetic regulation in upregulating hormonal reactions, as well as the contribution of plant growth-promoting bacteria and AMF. Also, to facilitate more research on crops, considering the ordinary bioinformatics resources available for studying omics datasets is needed. Moreover, future studies should focus on the importance of advances in omics technologies for accelerating crop breeding to cope with the changing climate and increase sustainable food production.

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Abbreviations

The following abbreviations are used in this manuscript:

ROS	Reactive Oxygen Species
LEA	Late Embryogenesis Abundant
ABA	Abscisic Acid
IPM	Integrated Pest Management
RNAi	RNA Interference
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
ET	Ethylene
SA	Salicylic Acid
JA	Jasmonic Acid
GS	Genomic Selection
MAS	Marker-Assisted Selection
BCMV	Bean Common Mosaic Virus
BCMNV	Bean Common Mosaic Necrosis Virus
HP	*Hypericum perforatum*
IAA	Indole 3 Acetic Acid
MDA	Malondialdehyde
ACC	1-aminocyclopropane-1-carboxylic acid
scMulti-omics	Single-cell multi-omics
PSII	Photosystem II
PGPM	Plant Growth-Promoting Microorganism
CIPKs	Coordinated Action of a Family of Twenty-Six Protein Kinases
TFs	Transcription Factors
ID	Intrinsic Disorder
AOX	Alternative Oxidase
SOS	Salt Overly Sensitive
CBF	C-Repeat Binding Factor
ZFNs	Zinc Finger Nucleases
TALENs	Transcription Activator-Like Effector Nucleases
DBD	DNA-Binding Domain
DSBs	Double-Stranded Breaks
HDR	Homology-Directed Recombination
UV	Ultraviolet
F3H	Flavonoid 3-hydroxylase
FLS	Flavonol Synthase
POD	Peroxidase
DFR	Dihydroflavonol Reductase
APX2	Ascorbate Peroxidase 2
GST	Glutathione S-Transferase
COMT	Caffeic Acid O-Methyltransferase
AITR	ABA-Induced Transcription Repressors

GWAS	Genome-Wide Association Studies
QTLs	Quantitative Trait Loci
CAT	Catalase
OST2	Open Stomata 2
siRNA	Small Interfering RNA
RAPD	Random Amplified Polymorphic DNA
qRT-PCR	Quantitative Real-Time PCR
TWAS	Transcriptome-Wide Association Studies
SBE	Starch Branching Enzyme
PTMs	Post-Transcriptional Modifications
shRNA	Short Hairpin RNA
VIGS	Virus-Induced Gene Silencing
TALENs	Transcriptional Activator-Like Effector Nucleases
SOD	Superoxide Dismutase
ISSR	Inter Simple Sequence Repeat
SSR	Simple Sequence Repeats
MBD	Methyl-CpG Binding Domain
CUT&Tag	Cleavage under Targets and Tagmentation
scRNA-seq	Single-Cell RNA Sequencing
PTEs	Potentially Toxic Elements
ChIP-seq	Chromatin Immunoprecipitation Sequencing
PAMPs	Pathogen-Associated Molecular Patterns
AFLP	Amplified Fragment Length Polymorphism
SNP	Single Nucleotide Polymorphism
DArt	Diversity Arrays Technology
ETI	Effector-Triggered Immunity
PTI	Pattern-Triggered Immunity
ESTs	Expressed Sequence Tags
DEGs	Differentially Expressed Genes
GS	Glutamine Synthetase
HTP	High-Throughput Phenotyping
LC-MS	Liquid Chromatography-Mass Spectrometry
PPI	Protein-Protein Interaction
DIGE	Differential Gel Electrophoresis
iTRAQ	Isobaric Tags for Relative and Absolute Quantification
MALDI-TOF	Matrix-Assisted Laser Desorption and Ionization Time of Flight
MudPIT	Multidimensional Protein Identification Technique
HPLC-MS	High Performance Liquid Chromatography Mass Spectrometry
LAESI	Laser Ablation Electrospray Ionization
CNNs	Convolutional neural networks
AI	Artificial intelligence
CSI-OC	Control-Stress Data Integration with Overlapping Clustering
DAPs	Differentially Abundant Proteins
PR	Pathogenesis-Related
NGS	Next generation sequencings
FTIR	Fourier Transform Ion Resonance
GRNs	Gene Regulatory Networks
SIMS	Secondary Ion Mass Spectrometry
LDI	Laser Desorption/Ionization
DESI	Desorption Electrospray Ionization
GeLC	Gel-Enhanced Liquid Chromatography
NMR	Nuclear Magnetic Resonance
TMT	Tandem Mass Tag
MS	Mass Spectrometry

CE-MS	Capillary Electrophoresis Mass Spectrometry
GC-MS	Gas Chromatography Mass Spectrometry
P5CS	Pyrroline-5-Carboxylate
PRR	Pattern Recognition Receptor
SWATH-MS	Sequential Window Acquisition of all Theoretical Fragment Ion Spectra-Mass Spectrometry
DEPs	Differentially Expressed Proteins
MSI	Metabolomic Standard Initiative

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