



REVIEW

Multi-Omics Biomarkers of Plant Abiotic-Stress Resilience: Discovery, Validation, Integration, and Translational Applications

Ravneet Kaur¹, Nishtha Paul^{1,*}, Vaseem Raja^{2,*}, Natasha Sharma Awasthi²,
Harvinder Kaur Sidhu³ and Khalid Rehman Hakeem^{4,5,*}

¹Department of Biosciences, University Institute of Biotechnology, Chandigarh University, Gharuan, Mohali, Punjab, India

²University Centre for Research and Development, Chandigarh University, Gharuan, Mohali, Punjab, India

³Faculty of Agriculture and Life sciences, Desh Bhagat University, Mandi Gobindgarh, Punjab, India

⁴Department of Biological Sciences, Faculty of Science, King Abdulaziz University, Jeddah, Saudi Arabia

⁵Princess Dr. Najla Bint Saud Al-Saud Center for Excellence Research in Biotechnology, King Abdulaziz University, Jeddah, Saudi Arabia

*Corresponding Authors: Nishtha Paul. Email: p.nish8@gmail.com; Vaseem Raja. Email: wrajamp2009@gmail.com;
Khalid Rehman Hakeem. Email: kur.hakeem@gmail.com

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ABSTRACT: Abiotic stresses such as drought, salinity, extreme temperatures, and heavy metal toxicity severely threaten global agricultural productivity. Recent advances in high-throughput sequencing, mass spectrometry, and computational biology have enabled multi-omics approaches to identify molecular, microbial, and biochemical biomarkers associated with plant stress responses. This review highlights recent progress in the characterization of microbiome signatures, metabolite profiles, epigenetic marks particularly Deoxyribonucleic acid (DNA) methylation loci and transcriptomic markers that define plant resilience under abiotic stress. We further outline a proposed classification framework distinguishing stress indicators, tolerance-associated biomarkers, predictive biomarkers, mechanistic effectors, and intervention targets, and examine how integrative multi-omics platforms, machine-learning-based data integration, synthetic microbial consortia, and genome/epigenome editing are converging to translate candidate biomarkers into actionable tools for marker-assisted breeding, precision agriculture, and microbiome engineering. Despite this progress, cross-platform data heterogeneity, a lack of standardized sampling and analytical pipelines, limited independent field validation across genotypes and environments, and incomplete genomic resources for many crop species continue to constrain reproducibility and real-world deployment. We conclude by highlighting priority directions, standardized multiomics workflows, functional validation through reverse genetics, and interpretable predictive modelling, needed to accelerate the translation of multi-omics biomarkers into climate resilient, sustainably managed crops.

KEYWORDS: Abiotic stress; biomarkers; stress resilience; microbiome; crop improvement

1 Introduction

Plants are continuously exposed to a multitude of abiotic stresses including drought, salinity, heat, cold, Ultra violet (UV) radiation, and heavy metal toxicity that disrupt cellular homeostasis [1]. These stress conditions often lead to physiological dysfunctions, and ultimately lead to significant reductions in agricultural yield and quality [2]. Historically, efforts to enhance stress resilience have depended predominantly on conventional phenotypic selection, a process that is both time-intensive and susceptible to environmental variability. Moreover, these approaches rely upon single-omics approaches, which capture

only individual components, such as transcriptional or metabolic alterations, of a fundamentally interconnected response network [3]. This fragmented view often missed the systemic crosstalk and compensatory mechanisms essential for adaptation. The advent of multi-omics technologies integrating metagenomics, metabolomics, epigenomics, and transcriptomics now provides a promising, holistic understanding of plant stress signalling networks by simultaneously profiling biomarkers across biological scales, from the rhizosphere to the chromatin [4]. This integration can help map the molecular convergence points where microbial interactions, metabolic reprogramming, epigenetic memory, and transcriptional regulation intersect to influence tolerance outcomes [5]. By constructing these system-wide networks, researchers may be able to identify master regulators and early indicators of stress that are not apparent from single-layer analyses. This insight is informing predictive strategies for stress alleviation, including the development of next-generation crops through precision breeding, microbiome engineering, and agronomic interventions suited to a changing climate [6]. The novelty of this review lies in bringing microbial, metabolomic, epigenomic, and transcriptomic biomarkers together across major abiotic stresses within a common framework, while clearly distinguishing their biological roles and applications. We further discuss how multi-omics integration and computational approaches can support biomarker validation and translation from controlled experiments to field-level stress management and crop improvement.

2 Microbial Taxa as Biomarkers for Abiotic Stress Tolerance

Plant-associated microbial communities represent dynamic and functionally responsive biomarkers of abiotic stress, with changes in rhizosphere composition reflecting both environmental selection and plant-mediated recruitment. Across stresses including drought, salinity, temperature extremes, heavy-metal exposure, and disease, specific microbial taxa and functional groups can become consistently enriched and may therefore serve as indicators of stress conditions and plant resilience [7]. Stress colonizers, including *Actinobacteria*, *Clostridia*, *Ralstonia*, *Bradyrhizobium* and *Bacilli*, enrich under multiple stresses and rank highest in predictive importance. Taxon-specific amplicon sequence variants show drought stress-specific amplicon sequence variants concentrating in *Actinobacteria* (48.2%) and *Alphaproteobacteria* (36.5%); salt-specific in *Firmicutes* (16.7%) and *Actinobacteria* (57.7%); and disease-specific in *Proteobacteria* (70.1%). Core microbiota including *Arthrobacter* and *Streptomyces* stabilize networks via stochastic dispersal, contributing 15.6% to beta diversity, while synthetic communities upregulate genes like *FUS3*, boosting biomass under drought or salinity [6–8]. These taxa signal deterministic assembly processes like heterogeneous selection, allowing early detection of stress and plant resilience potential. *Actinobacteria*, particularly *Streptomyces* and *Arthrobacter*, represent important examples of stress-associated microbial biomarkers. Their persistence under low water availability and osmotic stress is associated with metabolic traits that support microbial survival and plant adaptation, including osmolyte metabolism, ACC deaminase activity, secondary metabolite production, and nutrient mobilization [9]. Their resilience and plant-beneficial functions stem from a suite of physiological and biochemical adaptations. These filamentous bacteria are not merely tolerant to low water potential; they actively mitigate plant stress through direct and indirect mechanisms.

Proteobacteria, particularly members of the *Gammaproteobacteria*, constitute another major group of functionally important plant-associated microorganisms. *Pseudomonas*, *Burkholderia*, *Azospirillum*, *Rhizobium*, and *Enterobacter* have been widely associated with plant growth promotion and stress adaptation through diverse functional traits, including siderophore production, phytohormone modulation, nutrient acquisition, antioxidant priming, and regulation of ion homeostasis [10,11].

The class *Gammaproteobacteria*, especially the genera *Pseudomonas* and *Burkholderia*, includes several well-studied PGPR that enhance plant tolerance to abiotic stress [12]. The effectiveness of these PGPRs

is largely attributed to their remarkable metabolic versatility and capacity to synthesize a diverse array of bioactive compounds that modulate plant physiological processes and alter rhizosphere chemistry. Proteobacteria employ a multi-pronged strategy. First, under stress conditions like drought or salinity, iron becomes less bioavailable. *Pseudomonas* spp. secrete high-affinity iron-chelating siderophores. By solubilizing and sequestering Fe^{3+} , they not only fulfil their own iron needs but also increase iron uptake by the plant, which is important for chlorophyll synthesis and electron transport chains, thereby indirectly improving photosynthetic efficiency under stress [12]. Siderophores also help plants against phytopathogens by sequestering iron from pathogen rhizosphere and making it deficit for their growth [13]. Second, certain strains synthesize phytohormones such as auxins (e.g., indole-3-acetic acid, IAA). IAA stimulates root cell division and elongation, leading to root system that can access water from deeper soil layers during drought [14]. Other phytohormones secreted by microbes include gibberellic acids, cytokinins, and abscisic acid [15]. Third, these beneficial microorganisms, including *Pseudomonas*, *Stenotrophomonas*, *Burkholderia*, *Aspergillus*, and *Trichoderma*, help alleviate oxidative damage caused by abiotic stresses by enhancing antioxidant defense systems through the production of antioxidant enzymes and stimulation of the plant's endogenous ROS-scavenging machinery, particularly catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD). These enzymes contribute to the detoxification of excess ROS and thereby protect cellular components from oxidative damage [16,17]. Recent advances involve the use of omics technologies to identify key genes and pathways. For instance, Proteomic study showed that inoculation with *Pseudomonas* alters the expression of stress-responsive proteins viz. SOD, CAT, POD in wheat, enhancing drought tolerance [18]. Furthermore, molecular evidence shows that *Burkholderia* strains can reprogram ion transport and antioxidant polyamine synthesis in tomato plants under salt stress, enhancing salinity tolerance by modulating ion homeostasis [19].

The phylum Proteobacteria is a major group of Gram-negative bacteria that includes key PGPR genera such as *Pseudomonas*, *Azospirillum*, *Rhizobium*, *Burkholderia*, and *Enterobacter*. Polyols including mannitol and trehalose, secreted by certain fungi, function as osmoprotectants by stabilizing cellular membranes and proteins under dehydration stress [20]. Also, fungal secondary metabolites such as ergothioneine, melanin, and phenolic acids counter the oxidative damage by scavenging ROS [21]. Therefore, the metabolic versatility and close associations of microorganisms with plant roots make them instrumental in enhancing plant resilience to various abiotic stresses through direct and indirect mechanisms.

3 Biomarkers for Stress Tolerance in Plants

3.1 Biomarkers for Salt Stress Tolerance

Salinity induces ionic toxicity, osmotic stress, and secondary oxidative damage. Salt-tolerant plants commonly recruit rhizosphere microorganisms capable of surviving under high electrical conductivity and supporting plant adaptation. Bacterial taxa including *Pseudomonas*, *Burkholderia*, *Enterobacter*, *Paenibacillus*, *Bacillus*, *Alcaligenes*, and *Arthrobacter* have been consistently associated with saline environments and may serve as indicators of salt-adapted microbial communities [22]. Their beneficial effects are associated with complementary functions, including EPS production, osmotic adjustment, ACC deaminase activity, nutrient acquisition, and regulation of plant ion homeostasis [23]. Recently it has been demonstrated that the consortium of *Halomonas* (a halophilic *Gammaproteobacterium*) and *Bacillus licheniformis* significantly improved rice growth under high salinity by enhancing K^+/Na^+ homeostasis and upregulating genes for SOS1 and NHX transporters [24]. Similarly, *Oceanobacillus picturae* was identified as a root-associated microbial biomarker in saline soils, with its occurrence associated with reduced sodium accumulation in wheat through spermidine production [25]. The root endophytic fungus *Serendipita indica* is an active

fungal biomarker, as its colonization reprograms the plant transcriptome, enhancing antioxidant defense under salt stress [26,27].

A consistently elevated abundance of *Gammaproteobacteria* relative to *Alphaproteobacteria*, together with the occurrence of established ACC deaminase-producing genera, may represent a characteristic microbial signature associated with active adaptation to salinity stress [28,29]. In saline environments, Actinobacteria play a pivotal role in re-establishing ionic homeostasis and reducing oxidative damage. They help maintain a favorable K^+/Na^+ ratio in plant tissues by regulating ion transporter activity, thereby supporting cellular enzyme function and photosynthetic performance under salinity stress. For instance, *Streptomyces avermitilis* has been reported to markedly enhance the activities of SOD, CAT, and POD in rice plants exposed to salt stress [30]. The production of siderophores under saline conditions also aids in nutrient acquisition, chelating iron to improve its bioavailability despite high sodium interference. Additionally, the synthesis of volatile organic compounds (VOCs) like 2-methyl-1-butanol by *Streptomyces* sp. has been shown to enhance salinity tolerance in *Arabidopsis*. Under saline conditions, Proteobacteria help re-establish ionic homeostasis. They reduce Na^+ uptake and enhance K^+ acquisition in plants, a vital balance for cellular function. They also stimulate the synthesis of compatible solutes (e.g., proline, glycine betaine) in plant tissues [31]. Members of *Pseudomonas* have similarly shown improvements in plant growth, biomass, grain yield, chlorophyll content, and K^+/Na^+ ratios under high salinity [32]. In addition, ACC deaminase-producing *Enterobacter cloacae* ZNP-2 improved biomass and chlorophyll content in wheat under saline conditions, with associated changes in osmolyte status [33].

3.2 Biomarkers for Cold Stress Tolerance

Cold stress disrupts membrane fluidity, nutrient/water uptake, and causes oxidative damage. Psychrotolerant microbes that remain metabolically active at low temperatures are key biomarkers for plant survival in cold climates. *Pseudomonas*, particularly *P. fluorescens*, represents an important bacterial group associated with cold adaptation through production of antifreeze-related compounds and modulation of plant signaling pathways [34]. Furthermore, endophytic bacteria like *Duganella*, *Erwinia*, *Pseudomonas*, and *Rhizobium* from perennial plants in alpine zones confer freezing tolerance in plants. The dominance of pigmented cold-tolerant *Pseudomonas* and the presence of endophytic *Actinobacteria* within root tissues are reliable microbial indicators of ecosystem adaptation to perennial cold. Actinobacteria, especially cold-adapted strains, help plants acclimate through physiological and molecular modulation. They produce cold-active enzymes and anti-freeze compounds that stabilize cellular structures. For example, *Streptomyces* sp. *KK1* isolated from Antarctic soil was shown to produce extracellular anti-freeze glycoproteins that reduced ice crystal formation in the rhizosphere of cold-stressed wheat [35]. Inoculation with these bacteria often leads to increased accumulation of cryoprotectants such as soluble sugars and proline in plant tissues. *Streptomyces albus* inoculation increased sucrose and raffinose accumulation in maize under chilling stress and was associated with reduced electrolyte leakage [36]. Furthermore, Actinobacteria modulate plant hormone signaling, particularly increasing ABA and jasmonic acid (JA) levels, which are important for cold acclimation. Recent transcriptomic studies have shown that beneficial microorganisms can enhance plant freezing tolerance by activating the CBF/DREB regulon and inducing downstream cold-responsive genes such as *COR15a*, thereby improving cellular protection under low-temperature stress [37].

3.3 Biomarkers for Drought Stress Tolerance

Drought stress restricts water and nutrient availability, resulting in hydraulic failure and carbon starvation. It further induces stomatal closure, decreases CO_2 assimilation and photosynthetic efficiency, and

disrupts the structural and functional stability of cellular membranes and proteins, ultimately compromising plant growth and metabolic homeostasis [11]. Microbial communities associated with drought-tolerant plants frequently contain taxa that support root development, water acquisition, osmotic adjustment, and nutrient availability. *Actinobacteriota*, particularly *Streptomyces*, and *Bacillus subtilis* have been associated with drought tolerance and modulation of plant hormonal responses [38]. The most prominent fungal biomarkers are arbuscular mycorrhizal fungi (AMF), particularly *Rhizophagus irregularis*. Their extraradical hyphal networks function as an extension of the root system, enabling plants to access water from fine soil micropores that are otherwise inaccessible to roots [39].

A meta-analysis identified Actinobacteriota as one of the consistently drought-enriched bacterial groups across different plant species [40]. A *Streptomyces*-dominated synthetic microbial community enhanced maize root hydraulics under drought through induction of aquaporin expression [41], while *Ensifer meliloti* improved stress resilience in alfalfa through changes in stress-responsive gene expression and symbiotic performance [42]. A high AMF colonization rate in roots and an elevated abundance of *Actinobacteriota* and ABA-modulating *Bacillus* in the rhizosphere soil are robust microbial predictors of a plant's capacity to withstand prolonged dry periods. Under drought conditions, Actinobacteria and *Streptomyces* employ a multi-faceted strategy to mitigate water deficit in plants. The functional contribution of these microorganisms is associated with improved soil structure, root development, hormonal regulation, and osmotic adjustment. EPS and biofilm formation can improve soil aggregation and water retention, whereas ACC deaminase-producing bacteria can support root development under water limitation. *Pseudomonas* spp. have been associated with improved drought tolerance through ACC deaminase activity (Fig. 1) [43]. Chukwuneme et al. [44] demonstrated that ACC deaminase-producing *Streptomyces* S30 enhanced root architecture and biomass in maize under water-limited conditions. Beneficial *Streptomyces* spp. can also increase proline and glycine betaine accumulation in drought-stressed plants [45]. Similarly, *Azospirillum brasilense* promotes root hair and lateral root development, increasing the capacity for water uptake [46]. *Paenibacillus polymyxa* improved drought tolerance in *Arabidopsis thaliana* through increased expression of *ERD15* [47]. Culturomic studies have further identified stress-specific microbial communities associated with regulation of genes such as *FUS3*, photosynthetic performance, biomass production, and ABC transporter activity under drought and salinity [7,48]. These findings support the use of microbial community composition together with functional and physiological measurements as indicators of drought resilience [49].

3.4 Biomarkers for Heavy Metal Stress Tolerance

Heavy metals exert phytotoxic effects by disrupting enzyme function, inducing excessive ROS production, and interfering with the uptake and homeostasis of essential nutrients. Consequently, metalliferous soils harbor microbial communities enriched in taxa possessing diverse genetic, biochemical, and physiological mechanisms that enable them to tolerate and survive elevated concentrations of heavy metals. Metal resistant classes Gammaproteobacteria and Betaproteobacteria are universal bacterial biomarkers. They possess efflux pumps, metallothioneins, and metal-binding siderophores [50]. *Variovorax paradoxus* has been identified as a biomarker in cadmium-contaminated rice paddies because of its capacity to transform rhizospheric Cd^{2+} into less bioavailable forms [51]. Similarly, *Enterobacter* has been associated with arsenic detoxification through expression of the *ars* operon and reduced As(III) accumulation in rice grains [52]. In legumes, metal-tolerant *Bradyrhizobium* represents an important microbial partner, whereas *Trichoderma harzianum* and the AMF *Funneliformis mosseae* contribute to metal sequestration and immobilization [53]. Actinobacteria, including *Streptomyces*, are particularly relevant because their cell-wall components can bind metal ions, while biosorption, bioprecipitation, and siderophore production

can reduce metal availability. Beneficial rhizobacteria can additionally stimulate plant metallothioneins and phytochelatin synthase, supporting intracellular metal sequestration and detoxification [54]. Co-inoculation of *Streptomyces augustomyceticus* ST6 with AMF increased glutathione reductase and ascorbate peroxidase activities in arsenic-stressed rice and reduced oxidative damage [55]. *Burkholderia* and *Pseudomonas* have similarly been associated with reduced metal uptake and improved plant growth in contaminated soils [56]. Therefore, enrichment of metal-resistant microbial groups, together with genes and traits involved in metal immobilization, transformation, and plant detoxification, represents a useful biomarker framework for heavy-metal tolerance (Fig. 1).

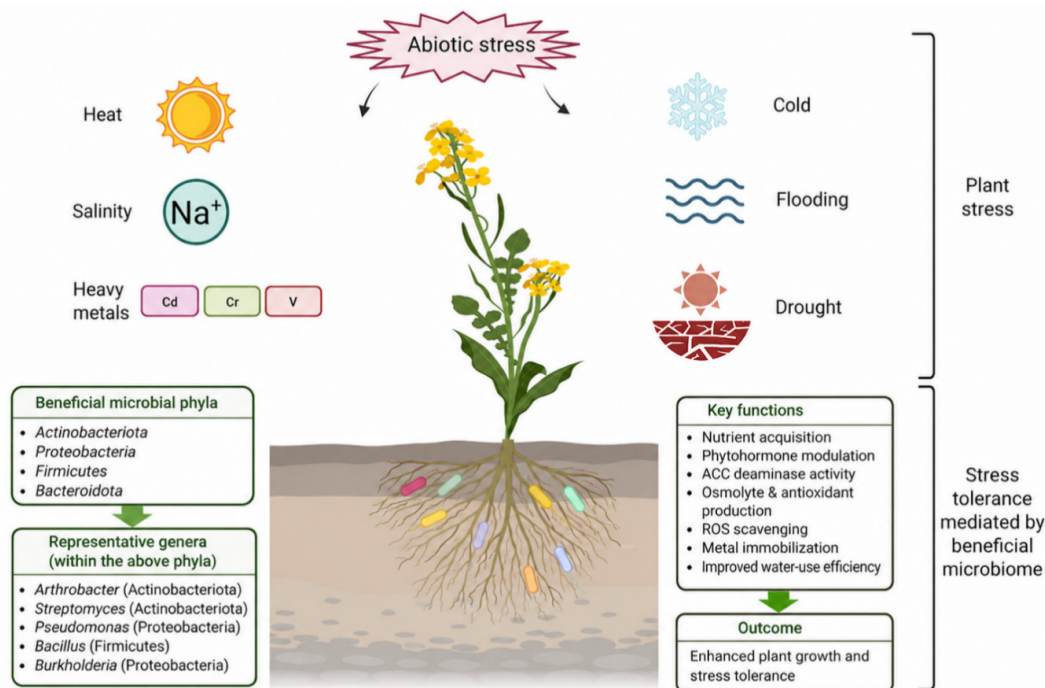


Figure 1: Beneficial plant-associated microbiome-mediated tolerance to abiotic stresses. The schematic illustrates major abiotic stresses, including heat, salinity, heavy metals (Cd, Cr, and V), cold, flooding, and drought, and their interactions with beneficial rhizosphere microorganisms. Representative bacterial phyla and genera associated with stress tolerance are shown, along with key microbial functions such as nutrient acquisition, phytohormone modulation, ACC deaminase activity, osmolyte and antioxidant production, ROS scavenging, metal immobilization, and improved water-use efficiency. These microbial activities collectively contribute to enhanced plant growth and improved tolerance to abiotic stress.

3.5 Biomarkers for Heat Stress Tolerance

Rising temperatures and more frequent heatwaves associated with climate change are becoming important constraints on global crop productivity. Increased temperatures not only affect the efficiency of photosynthesis, but also can cause changes in cell membranes, denature proteins, affect reproductive development, and cause overproduction of ROS, which ultimately lead to reduced yield and quality of crops [57,58]. It was found that the structure of plant associated microbial communities is highly altered under high temperature conditions, with enrichment of thermotolerant taxa of bacteria and fungi that serve as good microbial biomarkers of heat adaptation. Through multi-omics approaches, these microbial biomarkers have not only been identified as indicators of the plant's stress status, but also have been shown to actively contribute to the enhancement of thermotolerance in a coordinated metabolic and

signalling network [59,60]. *Bacillus*, *Pseudomonas*, *Paenibacillus*, *Sphingomonas*, and *Paraburkholderia* are consistently selected genera that are enriched in the heat-stressed rhizospheres as bacterial biomarkers [60]. These microorganisms help in boosting plant productivity by synthesizing heat-stable phytohormones, exopolysaccharides (EPS), osmoprotectants, siderophores, and ACC deaminase, which helps in sustaining root growth and minimizing the accumulation of ethylene under stress conditions [61]. The metagenomic studies revealed that thermotolerant *Bacillus velezensis* and *B. subtilis* induce antioxidant enzymes and improve osmotic regulation in the cell under high temperatures thus increasing photosynthetic efficiency and membrane stability [60,62]. Tyagi et al. [63] reported that the greening of *Serendipita indica* during heat stress was accompanied by the activation of genes encoding HSP70, HSP90 and antioxidant proteins, which led to better retention of membrane integrity and chlorophyll. Likewise, *Trichoderma* spp. induce systemic thermotolerance by regulating the signaling pathway of salicylic acid, jasmonic acid and abscisic acid while enhancing carbon metabolism and ensuring the stability of photosystem II [64]. The heat-induced microbial biomarkers are involved in the regulation of various interconnected physiological processes at the molecular level. In recent years, various multi-omics studies have greatly enriched our knowledge of heat-responsive microbial biomarkers. Integrated metagenomic and metatranscriptomic, metabolomic and transcriptomic analyses have shown the activation of genes involved in ROS detoxification, protein folding, carbon metabolism, biosynthesis of compatible solutes and phytohormone signalling by thermotolerant microbial communities [64]. Given that these cover microbial and plant variability, machine learning based integration has led to discovery of conserved microbial signatures that accurately predict plant thermotolerance in different species and environments [59]. These also can help identify microbial functional traits that do not change with changing climatic conditions, which can enhance the reliability of biomarkers [59].

3.6 Biomarkers for Flooding/Waterlogging Stress Tolerance

Flooding and waterlogging severely constrain plant growth by creating hypoxic or anoxic conditions in the rhizosphere, which impair root respiration, nutrient uptake, photosynthetic activity, and energy metabolism [65]. Extended hypoxia also leads to the accumulation of ROS, production of ethylene and a marked metabolic reprogramming which are responsible for the decrease in plant productivity [66]. Flooding results in a dramatic shift in the root microbiome, from aerobic to facultative and obligate anaerobic taxa, which occurs much more rapidly than any other stress factor, such as drought or salinity [67]. Thus, compositional changes in the microbial communities have become an important indicator of plant adaptation to water logging conditions. Root metabolic homeostasis, antioxidant defence, nutrient cycling and hormone signalling are regulated by beneficial microbiomes, which help mitigate hypoxia-induced damage [68]. In the case of bacteria, individuals of the genera *Bacillus*, *Pseudomonas*, *Herbaspirillum*, *Serratia*, *Achromobacter*, and *Ochrobactrum* have been consistently associated with improved flooding tolerance [69]. Useful fungal biomarkers consist of *Trichoderma*, *Penicillium* and some endophytic fungi that are beneficial in maintaining root integrity, controlling opportunistic pathogens and providing stress resistance in hypoxic environments. However, long-term flooding typically results in a reduction in colonization by AMF because fungal hyphal growth and spore germination is limited by the lack of oxygen. Hence, if the beneficial fungal endophytes remain in the flood water, this may indicate the stability of an intact root microbiome that will enable recovery after flooding [68]. The microbial community's responses to flooding have been studied and greatly aided by recent advances in metagenomics, metatranscriptomics, transcriptomics, and metabolomics [70]. The multi-omics integration has led to the identification of microbial genes involved in anaerobic metabolism, ACC deaminase activity, ROS detoxification, nitrogen cycling, and phytohormone biosynthesis in water-logged soils [71]. Increasingly, these datasets are being

combined and analyzed using machine learning algorithms to search for conserved patterns of microbes that can predict the resistance to flooding across different species. Majority of the candidate biomarkers are not yet validated under field conditions to be used in crop improvement [72]. Although there has been good progress, very few microbial biomarkers of flooding have been validated in a variety of genetic backgrounds and agroecological zones. Standardized sampling procedures, independent validation, multi-location field trials, causal functional characterization and interpretable predictive models with multi-omics datasets are suggested directions for future research [73]. This will help the development of strong microbial markers to breed flood-tolerant cultivars and strategies for sustainable crop production under the current climate of more frequent flooding events [74].

3.7 Biomarker for UV Stress

UV radiation, especially UV-B (280–315 nm), is a growing environmental stress that causes damage to the DNA, lipids, proteins and overproduction of reactive oxygen species (ROS) causing plant growth inhibition [75]. Plants in turn recruit a unique microbial community to act as protective biomarkers against UV-induced oxidative stress. Microbiome studies have reported the enrichment of pigmented bacteria, able to synthesize carotenoids, melanin, scytonemin and mycosporine-like amino acids (MAAs), after exposure to UV radiation, which are responsible for absorbing radiation and protecting the microbial cells and tissues of the host [76,77]. Increased UV-B exposure consistently results in increased levels of the bacterial biomarkers *Deinococcus*, *Sphingomonas*, *Hymenobacter*, *Methylobacterium*, *Bacillus* and *Arthrobacter*. These microorganisms have efficient DNA repair systems and antioxidant effects, which limit oxidative damage. *Deinococcus* spp. are also used as biomarkers due to their ability to readily overcome DNA damage caused by UV radiation through efficient homologous recombination and nucleotide excision repair pathways [78]. Similarly, *Sphingomonas* spp. promote the expression of flavonoids and promote antioxidant metabolism in host plants with a decrease in ROS accumulation and an increase in the photosystem stability [79]. Fungal biomarkers include melanized fungi, such as *Cladosporium*, *Alternaria*, *Epicoccum* and beneficial endophytes such as *Serendipita indica* and *Trichoderma harzianum* that activate phenylpropanoid metabolism, consequently increasing the production of flavonoids and anthocyanins and improving UV tolerance [80]. Using integrated metagenomic, transcriptomic and metabolomic analyses, microbial genes related to carotenoid biosynthesis, photolyase activity, DNA repair, ROS detoxification and phenolic metabolism were identified as reliable biomarkers of UV adaptation [81]. Multi-omics data also suggest that beneficial microorganisms induce coordinated activation of the flavonoid biosynthesis, glutathione metabolism and UVR8-mediated signalling pathways in plants [59]. These conserved molecular signatures offer potential biomarkers for UV resistance monitoring in a range of crop plants. But additional testing is needed under field conditions and various radiation exposures before they can be used in breeding and precision agriculture [62].

3.8 Alkalinity Stress Tolerant Biomarkers

The alkalinity stress differs from salinity stress as it is a high pH with the presence of excess carbonate and bicarbonate ions and it significantly reduces the availability of nutrients, especially iron, zinc, phosphorus and manganese [82]. Alkalinity is one of the least studied abiotic stresses from microbiomes perspective due to its impact on root architecture, membrane transport, and photosynthesis (higher pH levels). The alkaline soils are also characterized by unique microbial community that can maintain the rhizosphere pH homeostasis and enhance nutrient uptake, which makes them potential microbial markers of stress tolerance to alkaline stress [83].

The common bacteriological markers are *Bacillus*, *Paenibacillus*, *Pseudomonas*, *Microbacterium*, *Arthrobacter* and *Nocardioides*, which promotes the production of organic acids, siderophores and phosphatases in alkaline soil to enhance the solubility of nutrients [84]. They release gluconic acid and citric acid, lowering the pH of the rhizosphere, and also help enhance the availability of iron and phosphorus [85]. In specific, *Paenibacillus polymyxa* is recognized as a powerful biomarker due to its capability to control the pH of the rhizosphere and to increase the uptake of nutrients under sodic conditions [86]. The fungi considered to be the biomarkers include *Trichoderma*, *Penicillium*, *Aspergillus* and arbuscular mycorrhizal fungi which enhance nutrient uptake by improving root absorptive capacity and increasing uptake of phosphorus and micronutrients [87]. These fungi also mediate the antioxidant metabolism as well as osmotic adjustment, which helps to minimize the phytotoxic response of alkaline soils [88].

The rhizospheres enriched with alkaline soils showed higher abundance of microbial genes related to proton transport, organic acid biosynthesis, chelation of iron, phosphate solubilization and nitrogen metabolism. Further, transcriptomic analyses show that nutrient transporter genes, H^+ -ATPases and antioxidant pathways are activated after microbial colonization [83]. The molecular signatures are interesting as potential markers for selecting alkaline-tolerant crop plant genotype and developing microbial inoculants for alkaline soils. However, extensive testing and validation in a range of soil and climatic conditions is still under way [89].

3.9 Biomarkers for Combined Abiotic Stresses

Abiotic stresses in natural ecosystems are rarely encountered alone. Instead, it is the combination of drought, heat, salinity, flooding, nutrient deficiency or heavy metals that produces different responses that are not predictable from their individual studies [90]. Therefore, it is important to recognize that the microbial biomarkers detected under one stress may not be reliable to assess plant performance under combined stresses [91]. In recent years, multi-omics research has shown that combined stresses recruit specialized microbial consortia as opposed to specific taxa, which necessitates identification of system-level biomarkers that combine microbial composition with plant metabolic responses [92]. *Bacillus*, *Pseudomonas*, *Streptomyces*, *Variovorax*, *Sphingomonas* and *Rhizophagus irregularis* are consistently found to be enriched in multiphasic stress condition. These microbes can influence a wide range of stress protection mechanisms, including the regulation of antioxidant defence, phytohormone signalling, osmolyte accumulation, ion homeostasis and nutrient acquisition, offering broad-spectrum stress protection [93]. These microbial communities do not operate individually, but rather synergistically in the sense that the metabolic cross-feeding and complementary stress-response pathway of each one complement and enhance the other [94].

Combined stress activates conserved microbial functions such as ACC deaminase activity, exopolysaccharide biosynthesis, ROS detoxification, production of heat shock proteins, synthesis of osmoprotectant, and biosynthesis of secondary metabolites (Fig. 1) as shown by integrated metagenomic, metatranscriptomic, proteomic and metabolomic analysis [49]. Microbial co-occurrence modules were also identified as more reliable biomarkers than individual microbial taxa, highlighting their potential utility as robust indicators of plant responses to combined stress conditions (Table 1), as they are relatively stable in face of changing environmental conditions, through network analysis [95]. Therefore, future identification of new biomarkers should be based on community level and function based biomarkers based on AI and machine learning approaches instead of the discovery of single microbial species [96]. Microbiome composition can be used to complement transcriptomic, metabolomic and phenomic datasets to develop predictive biomarker models for facilitating breeding for climate resilience, precision agriculture, and microbiome engineering [97]. These biomarkers need to be validated independently on various crop species, environments, and combined stress scenarios, before they can be implemented in agricultural practices [97].

Table 1: Microbial taxa as biomarkers for abiotic stress tolerance.

Abiotic Stress	Plant Species	Microbial Taxon (Biomarker)	Sampled Compartment	Biomarker Change	Key Mechanism	Evidence Type/Representative Reference/Stress Condition	References
Salt stress	Rice	<i>Pseudomonas</i> sp. (Gammaproteobacteria)	Rhizosphere/soil	↑ Enrichment	ACC deaminase, EPS, osmoprotectants	Microbiome profiling + functional/PGPR evidence; salt-stressed rice; enrichment associated with improved ionic/osmotic stress tolerance	[98]
	Rice	<i>Halomonas</i> sp. & <i>Bacillus licheniformis</i> (Firmicutes)	Rhizosphere	↑ Consortium	K ⁺ /Na ⁺ homeostasis	Culture-dependent inoculation/consortium study; saline conditions; improved ionic balance and plant growth	[99]
	Wheat	<i>O. picturae</i> (Firmicutes)	Root/rhizosphere	↑ Colonization; ↓ Na ⁺	Spermidine/polyamines	Inoculation + physiological/biochemical evidence; salt-stressed wheat; reduced Na ⁺ accumulation and enhanced polyamine metabolism	[100]
Cold stress	Arabidopsis/Maize	<i>Serendipita indica</i> (Basidiomycete)	Root endosphere	↑ Colonization; ↑ ROS defense	Antioxidant defense; transcriptome reprogramming	Endophyte inoculation + transcriptomic/physiological evidence; salinity stress	[101]
	Maize/Wheat	<i>Pseudomonas fluorescens</i> (Gammaproteobacteria)	Rhizosphere	↑ Colonization; ↑ VOCs	Antifreeze-related responses; VOCs including 2,3-butanediol	PGPR inoculation + metabolite/VOC evidence; cold stress	[102]
	Maize	Psychrotolerant <i>Pseudomonas</i> sp. (Gammaproteobacteria)	Root/rhizosphere	↑ Abundance; ↑ proline/sugars	Osmoprotectant synthesis	Microbiome/culture-based evidence + physiological measurements; low-temperature stress	[102]
	Arabidopsis	<i>Serendipita indica</i> (Basidiomycete)	Root endosphere	↑ Colonization; ↑ freezing tolerance	CBF transcription factors; COR genes	Endophyte inoculation + gene-expression evidence; freezing/cold stress	[103]
	Wheat/Barley	Endophytic Actinobacteria	Endosphere	↑ Colonization; ↑ COR genes	Cryoprotective EPS; COR induction	Endophyte isolation/inoculation + molecular evidence; cold stress	[104]
	Multiple crops	Actinobacteriota	Rhizosphere/soil	↑ Enrichment	Soil structure; water retention	Comparative rhizosphere microbiome profiling across drought-stressed soils; drought-associated enrichment	[105]
Drought stress	Rice/Sorghum	<i>Bacillus subtilis</i> (Firmicutes)	Rhizosphere	↑ abundance/activity; ↑ ABA/aquaporin responses	ABA modulation; aquaporin regulation	PGPR inoculation + physiological/transcriptomic evidence; water-deficit/drought stress	[106,107]

Table 1: *Cont.*

Abiotic Stress	Plant Species	Microbial Taxon (Biomarker)	Sampled Compartment	Biomarker Change	Key Mechanism	Evidence Type/Representative Reference/Stress Condition	References
Heavy-metal stress	Rice/Multiple crops	Gammaproteobacteria & Betaproteobacteria	Rhizosphere/endosphere	↑ Enrichment under stress	Efflux pumps, metallothioneins, siderophores	Comparative microbiome profiling + functional-gene evidence; Cd/Pb/other metal-contaminated soils	[106]
	Rice	<i>Variovorax paradoxus</i> (Betaproteobacteria)	Rhizosphere soil	↑ Abundance; ↓ Cd bioavailability	Cd immobilization through precipitation, adsorption and bioaccumulation	Isolation/culture + inoculation/bioremediation evidence; Cd-contaminated soil. Important: Cd immobilization should not be described as oxidation to CdO without direct mineralogical evidence	[108]

Note: ↑: Enhanced; ↓: Reduced.

4 Biomarker Classification in Abiotic Stress in Plants

Plant stress biology, multi-omics and artificial intelligence technologies have greatly extended the number of biological entities suggested as stress markers for abiotic stress [92]. The definition of biomarker, however, is frequently used to refer to stress-responsive genes, proteins, metabolites, microorganisms, enzymes, and physiological characteristics, although these are all biologically different [62]. This indiscriminate use may make it difficult to interpret the results of experiments and to create strong diagnostic and translational tools. The need to consider the biomarkers based on their role in the biological system, their predictivity, and their easy applicability beyond their responsiveness to stress factors were reported by [83].

4.1 Stress Indicators

Stress indicators are measurable biological responses which indicate abiotic stress, but which don't necessarily provide a direct contribution to abiotic stress tolerance. The main use of these markers is to monitor plant health and determine the stress levels. Many physiological parameters, such as chlorophyll fluorescence (Fv/Fm), relative water content, electrolyte leakage, stomatal conductance and photosynthetic efficiency, along with biochemical parameters including ROS, hydrogen peroxide (H₂O₂), malondialdehyde (MDA), and electrolyte leakage, are used as diagnostic tools for oxidative and cellular damage [109]. These parameters are considered as a result of stress exposure, and are generally used to get an idea of stress adaptation rather than as stressors themselves [110].

4.2 Tolerance-Associated Biomarkers

Tolerance-associated biomarkers are biological characteristics that are related to greater stress resilience consistently, across genotypes, environments and developmental stages [97]. They are not stress indicators, but are associated with adaptive responses that will enhance plant performance when challenged by adverse conditions [111]. They comprise antioxidant enzymes, such as SOD, CAT, APX, GR, osmoprotectants such as proline, glycine betaine, soluble sugars, late embryogenesis abundant (LEA) proteins, heat shock proteins (HSPs), and stress-responsive transcription factors, including DREB, NAC, WRKY and bZIP families [112]. Other beneficial microorganisms from the rhizosphere such as *Arthrobacter*, *Streptomyces*, *Bacillus* and *Pseudomonas* species have also been identified as tolerance-associated biomarkers due to their enrichment often being linked to increased stress tolerance [113].

4.3 Predictive Biomarkers

Predictive biomarkers are molecular, microbial, or physiological signatures that can predict the occurrence of stress, the severity of stress or plant performance, prior to the appearance of visible stress symptoms. The combination of genomics, transcriptomics, proteomics, metabolomics, microbiomics, remote sensing and machine learning technologies have led to the rapid identification of predictive biomarkers. Predictive models generally combine multiple variables to come up with a very accurate stress classification, as opposed to using a single molecule. To illustrate, machine learning models like Random Forest have shown the ability to accurately predict different stress scenarios with rhizosphere microbial signatures, highlighting the potential of microbiome-based biomarkers in precision agriculture and early stress detection [94]. In a similar way, metabolomic and transcriptomic signatures are also increasingly being used in predictive models used for crop phenotyping and breeding.

4.4 Mechanistic Effectors

Mechanistic effectors are biological components which are actively involved in the perception of stress, the spread of this perception from cell to cell, and the adaptation to stress, and therefore are not simply a measure of exposure to stress [114]. They include genes, regulatory proteins and phytohormones, transporters and enzymes and microbial metabolites which directly affect plant physiology in response to stress [115,116]. Some of these include ABA signalling components (PYR/PYL receptors, SnRK2 kinases), calcium dependent protein kinases (CDPKs), mitogen activated protein (MAPK) cascades, ROS scavenging enzymes, ion transporters like HKT and NHX, aquaporins, heat shock proteins, and beneficial microbial metabolites involved in hormone homeostasis or antioxidants production. Mechanistic effectors are important targets for functional validation, as they provide valuable insights into the molecular mechanisms underlying plant adaptation, and are causally involved in stress tolerance [117].

4.5 Intervention Targets

Intervention targets are validated targetable biomarkers that can be manipulated when working on breeding, genome editing, microbial inoculation, application of biostimulants or agronomic management to enhance crop resilience [118]. Intervention targets have been shown to have functional significance and can be used to enhance stress tolerance, as opposed to predictive biomarkers [119]. The development of genome editing technologies (CRISPR/Cas), synthetic microbial communities, RNA-based technologies and biostimulant development have paved the way for new possibilities for translating biomarker discoveries into real applications in agriculture [92]. Potential targets for developing stress-mitigation strategies include stress-responsive transcription factors, ion transporters, antioxidant enzymes, microbial consortia, and key metabolic pathways. Experimental studies have demonstrated that manipulating these targets can enhance plant growth, physiological performance, and stress tolerance under diverse abiotic stresses, including drought, salinity, heat, cold, and heavy metal toxicity [120].

The development of a uniform classification system for plant stress biomarkers will help to increase the uniformity within experimental studies and aid in the validation of plant stress biomarkers for use in agriculture [121]. Future studies should focus on the merging of multi-omics data with AI to identify biomarkers which are correlated with stress but not causally involved, or appropriate for intervention. This hierarchical approach will help the development of reliable diagnostic platforms, precision breeding strategies and microbiome-assisted technologies for climate-resilient crop production, and increase the translation potential of plant stress biomarker research [122].

5 Microbial Taxa as Functional Biomarkers in Plant Abiotic Stress Tolerance

Plant-associated microbiomes are dynamic consortia whose composition and activity can directly determine host resilience to environmental stressors. Specific microbial taxa serve as functional biomarkers not merely through their presence or abundance, but through their mechanistic, biochemical contributions to plant physiology. These functions are measurable and indicative of a microbiome's capacity to enhance host tolerance. Four key biomarker functions include: enhancing osmotic adjustment, modulating hormone signaling, boosting antioxidant capacity, and regulating ion homeostasis, each facilitated by distinct microbial metabolic pathways.

5.1 Enhancing Osmotic Adjustment via Compatible Solute Production

A primary biomarker function of beneficial microbiota is the synthesis and provision of osmolytes, the small, highly soluble organic compounds that stabilize proteins and cellular structures under osmotic

stress. Microbial production of trehalose, glycine betaine, and proline directly influences the plant's osmotic adjustment capacity, a critical trait for maintaining turgor and cellular function during drought and salinity [123].

Trehalose, a non-reducing disaccharide, is a well-documented osmoprotectant produced by diverse bacteria (e.g., *Rhizobium*, *Pseudomonas*) and fungi (*Trichoderma*, *Glomus*). It acts as a molecular chaperone, preventing protein denaturation and membrane fusion. A study on *Arabidopsis thaliana* inoculated with a trehalose-producing *Pseudomonas putida* strain demonstrated a significant increase in endogenous trehalose levels in plant tissues, which correlated with improved relative water content and biomass under severe drought, compared to plants inoculated with a trehalose-deficient mutant [124]. Glycine betaine (GB) is another potent osmolyte synthesized by bacteria such as *Bacillus* and *Arthrobacter*. Its role involves protecting the photosynthetic apparatus. Research on maize showed that inoculation with GB-producing *B. subtilis* led to the accumulation of GB in leaves, which was directly linked to higher photosynthetic efficiency and reduced electrolyte leakage under saline conditions [125]. Proline, an amino acid, is a major osmolyte and antioxidant. While plants synthesize proline under stress, rhizosphere microbes like *Azospirillum brasilense* can significantly augment its pool. A meta-analysis confirmed that microbial proline production is a consistent biomarker for improved drought tolerance, with the effect size correlating strongly with the microbial proline synthesis gene (*proBA*) abundance in the rhizosphere [126]. The microbial contribution to the plant's osmolyte pool is thus a quantifiable biomarker, detectable via metabolite profiling or the presence of microbial biosynthetic genes.

5.2 Modulating Plant Hormone Signaling (IAA, ABA, GAs)

Plant hormonal balance is a master regulator of stress responses, and microbial taxa serve as key extrinsic modulators of this signaling network. By producing, degrading, or altering the sensitivity to phytohormones, microbes act as living biomarkers for a plant's altered physiological state, shifting it from survival-focused to growth-tolerant.

Auxin (IAA) production is a hallmark of many PGPR (e.g., *Pseudomonas*, *Enterobacter*, *Azospirillum*, *Bacillus*, *Stenotrophomonas*, *Burkholderia*). Microbial IAA influences root architecture, promoting lateral root and root hair development, which expands the soil exploration volume for water and nutrients under stress. IAA-overproducing transgenic *Pseudomonas simiae* strain in wheat demonstrated that increased root system depth and density from microbial IAA led to a 40% higher soil water extraction during a terminal drought period [127]. Conversely, microbes can also modulate the stress hormone abscisic acid (ABA). While ABA triggers stomatal closure to conserve water, excessive levels can inhibit growth. Certain bacteria, like *Azospirillum*, can lower plant ABA levels, mitigating overreaction. *Azospirillum baldaniorum* Sp245 downregulated key ABA biosynthesis genes in rice roots under drought, reducing ABA accumulation and allowing for more balanced growth-stress trade-offs [128]. Furthermore, microbes influence gibberellins. *Burkholderia* and *Bacillus* species can produce GAs that counteract the growth-retarding effects of stress. A report on salt-stressed tomato plants showed that inoculation with a GA-producing *Burkholderia cepacia* strain restored endogenous GA levels, reversed salt-induced hypocotyl elongation inhibition, and improved biomass, highlighting microbial GA as a biomarker for growth maintenance under stress [129]. The quantification of microbial hormone synthesis genes (e.g., *ipdC* for IAA) or the resulting plant transcriptional changes serves as a functional biomarker for this microbiome-mediated priming [38].

5.3 Improving Antioxidant Capacity via Enzyme Production

Abiotic stresses induce oxidative damage through the accumulation of ROS (Fig. 2). A critical biomarker function of stress-resilient microbiomes is their ability to enhance the host's antioxidant capacity, both directly by secreting ROS scavenging enzymes and indirectly by upregulating the plant's own antioxidant system.

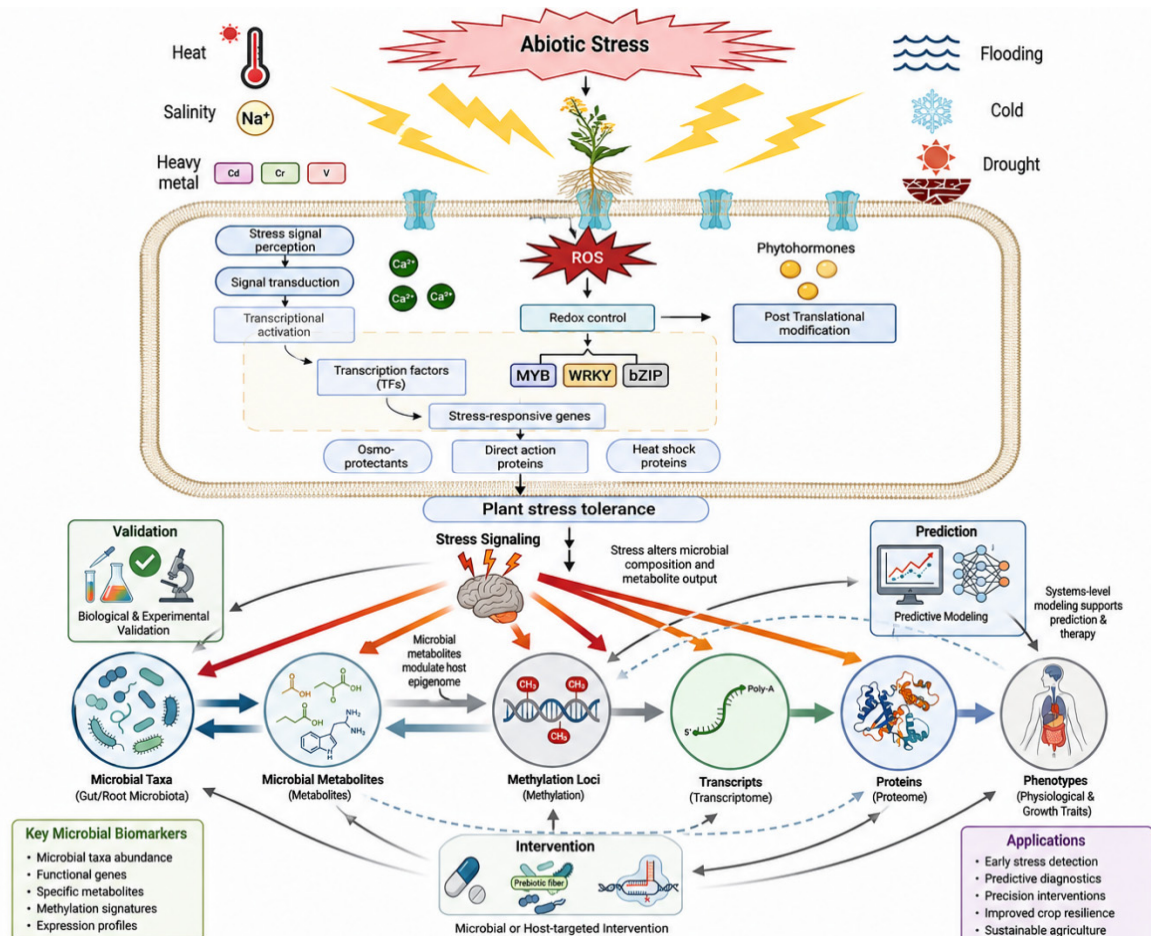


Figure 2: Integrative plant response network to abiotic stress, linking environmental triggers to molecular pathways, transcription factors, and protective mechanisms for enhanced tolerance.

Key microbial antioxidant enzymes include SOD, which converts superoxide radicals to H_2O_2 ; and CAT and POD, which then detoxify H_2O_2 . For instance, the endophytic fungus *Piriformospora indica* is renowned for its strong CAT and SOD activity. A study demonstrated that co-cultivation with *P. indica* significantly increased the activity of these enzymes in barley leaves under salt stress, which was directly correlated with a 50% reduction in lipid peroxidation (as measured by malondialdehyde content) compared to uninoculated plants [130]. Similarly, bacteria like *Bacillus amyloliquefaciens* can systemically induce the plant's antioxidant pathway [131]. A proteomic analysis of drought-stressed rice revealed that inoculation with *B. amyloliquefaciens* SB-9 led to the upregulation of over 15 plant-encoded antioxidant proteins, including ascorbate peroxidase and glutathione S-transferase, creating a more robust defensive network against ROS. This enhancement of the plant's endogenous enzymatic antioxidant machinery is a more sustainable biomarker than direct microbial enzyme secretion, as it represents a primed, systemic state.

5.4 Enhancing Ion Homeostasis under Salinity by Regulating Na^+/K^+ Transport

Salinity tolerance is fundamentally linked to the maintenance of a high cytosolic K^+/Na^+ ratio. Specific microbial taxa function as biomarkers for improved ion homeostasis by directly or indirectly regulating the expression and activity of key plant ion transporters involved in Na^+ exclusion and K^+ retention [132].

Mechanistically, microbes can enhance the activity of the plant's Na^+/H^+ Antiporters (e.g., *SOS1*) located at the root plasma membrane, which efflux Na^+ back into the soil. A 2020 study on wheat inoculated with the bacterium *Dietzia natronolimnaea* found that the bacterium upregulated the expression of *AtSOS1* and *AtNHX1* (a tonoplast-located Na^+/H^+ antiporter for vacuolar sequestration). This dual action led to lower Na^+ and higher K^+ accumulation in shoots, a direct biomarker of improved homeostasis [22]. Furthermore, microbes like *B. subtilis* can influence High-Affinity Potassium Transporters (e.g., *HAK5*). Cucumber under salinity showed that a *B. subtilis* strain increased the transcript level of *CsHAK5*, improving K^+ uptake efficiency even in high Na^+ environments, thereby protecting the plant from K-deficiency-induced metabolic dysfunction [133]. The microbial regulation of these transporter genes can be used as a transcriptional biomarker, where the expression level of *SOS1* or *HAK5* in plant roots in response to specific microbial inoculation predicts the degree of salinity tolerance.

6 Epigenetic Biomarkers: DNA Methylation Loci in Stress Memory

Recent studies utilizing whole-genome bisulfite sequencing (WGBS) have revealed that abiotic stress triggers dynamic, context-dependent changes in DNA methylation across all sequence contexts (CG, CHG, and CHH). These modifications are particularly concentrated in the promoters of stress-responsive genes and within transposable elements (TEs), where they act to stabilize the genome and modulate transcriptional plasticity (Fig. 2). For instance, drought stress induces hypermethylation in the CHH context within TE bodies to suppress their reactivation, while causing targeted hypomethylation in the promoters of key transcription factors [134]. These stress-induced epigenetic signatures are not merely transient; specific methylation loci can serve as durable molecular biomarkers for stress memory and tolerance. In drought priming, for example, a phenomenon called “drought memory” is associated with sustained hypermethylation in the CHH context at the promoters of ABA-responsive genes like *ABI1* and *RD29A*, which correlates with a faster and stronger transcriptional response upon recurrent stress [15].

Stress memory should be distinguished from intergenerational and transgenerational inheritance because these phenomena operate over different biological timescales. Stress memory generally refers to the persistence of altered physiological, molecular, or epigenetic responsiveness within the previously exposed plant, such that a subsequent stress episode elicits a faster, stronger, or otherwise modified response. This memory may involve chromatin remodelling, DNA methylation, histone modifications, transcriptional changes, regulatory RNAs, metabolic states, or hormone-mediated priming, and does not necessarily involve transmission to progeny. Thus, persistence of a stress-associated molecular signature within an individual plant should not by itself be interpreted as heritable inheritance [135].

Intergenerational effects refer to the detection of a stress-associated phenotype or molecular state in the immediate offspring generation following parental exposure. In plants, such effects can reflect transmission of epigenetic information, but they may also arise from parental physiological effects, altered seed provisioning, maternal tissues, or other factors associated with the parental environment (Fig. 2). Therefore, an altered F1 phenotype following parental stress exposure is not, by itself, sufficient evidence for true transgenerational inheritance. In contrast, transgenerational inheritance requires persistence of the environmentally induced phenotype or molecular state beyond generations that were directly exposed to the original stress or otherwise affected by the parental environment. Consequently, claims of transgenerational

inheritance require multigenerational experimental designs capable of separating inherited information from direct exposure and parental effects [135,136].

Similarly, comparative methylome analyses of salt-tolerant and sensitive genotypes have identified consistent methylation polymorphisms (CMPs) as biomarkers for salinity tolerance. Key markers often include hypomethylation in the CG context within the promoters or introns of high-affinity potassium transporter (*HKT1*) and sodium/hydrogen exchanger (*NHX*) genes, which is linked to their sustained expression and improved ionic homeostasis [137]. Conversely, heat stress frequently induces active demethylation via ROS1-family glycosylases, leading to hypomethylation in the promoters of heat shock protein (HSP) genes such as *HSP70* and *HSP90*. This epigenetic derepression facilitates rapid gene activation and is a reliable biomarker for thermotolerance acquisition in crops like tomato [138]. Importantly, these condition-specific epigenetic marks provide a molecular archive of past stress exposure and can be leveraged for epigenetic selection in breeding programs, aiming to develop elite cultivars with pre-conditioned, heritable stress resilience [139].

6.1 Intergenerational and Transgenerational Epigenetic Effects: Evidence and Applications

Stress-associated epigenetic changes detected in progeny should be interpreted according to the generation in which they are observed and the extent to which direct parental effects have been excluded [136]. When the immediate offspring generation exhibits altered stress responses following parental exposure, the phenomenon is generally described as an intergenerational effect. Such effects may involve transmitted DNA methylation, histone modifications, small RNAs, altered parental provisioning, or developmental effects associated with the parental environment [139,140]. They therefore should not automatically be considered evidence of stable transgenerational inheritance. By contrast, true transgenerational inheritance requires persistence of the stress-associated phenotype or molecular signature in generations that were not directly exposed to the original stress and in which alternative parental or developmental explanations have been adequately controlled [133,136].

In plants, this distinction is particularly important because environmental exposure can affect reproductive tissues and developing embryos, while epigenetic states may also undergo resetting or remodelling during reproduction and early development. Consequently, the detection of a stress-associated DNA methylation pattern in F1 progeny demonstrates transmission to the offspring but does not necessarily establish stable transgenerational inheritance [141]. Stronger evidence requires demonstration of persistence across additional generations together with appropriate control of maternal effects, seed provisioning, genetic segregation, microbiome transmission, and continued environmental exposure [142]. Thus, stress-associated methylation loci should initially be described as candidate epigenetic memory or inheritance biomarkers unless their persistence and functional contribution have been demonstrated across the appropriate generations.

Accumulating evidence from the literature confirms that a subset of environmentally induced DNA methylation changes can escape epigenetic reprogramming during reproduction, thereby contributing to the establishment of heritable transgenerational epigenetic memory. This is characterized by offspring displaying enhanced stress tolerance such as improved water-use efficiency or salinity resilience even in the absence of the initial stress exposure experienced by the parental generation [143]. The heritable marks are often stabilized in the form of CHH methylation at specific genomic loci, particularly within promoter regions of stress-responsive genes or at silenced transposable elements, which act as an epigenetic blueprint for rapid gene regulation [144]. For instance, altered DNA methylation patterns and stress responsive phenotypes have been reported in progeny of plants exposed to drought and other abiotic stresses [145].

Such observations provide evidence for intergenerational transmission of stress-associated molecular states. However, their interpretation as true transgenerational inheritance requires careful consideration of the generation examined and of parental, maternal, seed-associated, and environmental effects [146]. Accordingly, methylation changes detected in offspring should be considered candidate inherited epigenetic biomarkers unless their persistence has been demonstrated in subsequent non-exposed generations and linked functionally to the observed stress phenotype [131]. Stable epigenetic variants, including epialleles, provide important candidates for studying heritable variation in stress responses. However, the presence of an epiallele does not necessarily establish that it was induced by a previous environmental stress or that it represents transgenerational stress memory. Demonstrating a causal relationship requires evidence that the epigenetic state is stable across the relevant generations, is associated with a reproducible phenotype, and is distinguishable from underlying genetic variation. Such validated epialleles could nevertheless provide useful biomarkers for epigenetic selection and breeding for stress resilience [136,147].

Recent advances in plant epigenetics are actively being translated into applied strategies for stress alleviation through three primary pathways. Epigenome editing is an emerging approach in precision breeding, coupling a catalytically inactive CRISPR-Cas9 (dCas9) system with epigenetic effectors such as the mammalian demethylase TET1 or methyltransferase DNMT3A, researchers can potentially modify the epigenetic status of stress-responsive loci. For instance, targeted demethylation of the promoter for the *OsDREB1a* gene in rice using dCas9-TET1 led to its constitutive expression and significantly enhanced drought and salinity tolerance without altering the DNA sequence. Complementing this, the identification of epigenetic quantitative trait loci (epi-QTLs) through integrated methylome and phenome analysis has uncovered stable, heritable methylation variants linked to yield under stress. These epi-QTLs serve as novel biomarkers for epigenome-assisted breeding, allowing for the selection of lines with favorable epigenetic alleles that confer metabolic plasticity and resilience, thus adding a new dimension to marker-assisted selection programs [139]. Furthermore, the use of chemical epigenetic modifiers offers a scalable priming approach. Compounds such as DNA methyltransferase inhibitors (e.g., zebularine) or histone deacetylase inhibitors (e.g., trichostatin A) can be applied to seeds or seedlings to globally remodel the epigenome, resulting in enhanced stress-responsive gene expression and improved tolerance to subsequent abiotic challenges in crops like maize and tomato [148]. Together, these strategies from precise editing and molecular breeding to chemical priming, provide a multifaceted toolkit to epigenetically engineer or select for crops with durable, climate-resilient phenotypes.

6.2 Transcriptomic Biomarkers: Gene Expression Signatures and Regulatory RNAs as Biomarkers

High-resolution transcriptomic analyses have identified a conserved core set of stress-responsive transcription factors (TFs) whose expression dynamics serve as robust biomarkers for the onset, severity, and type of abiotic stress. Key transcriptional markers prominently include members of the DREB/CBF, NAC, MYB, WRKY, and bZIP families, which act as master regulators orchestrating complex adaptive responses [149]. For instance, the rapid induction of DREB2A and CBF1/3 expression is a canonical biomarker for dehydration and cold stress, respectively, triggering a cascade of genes involved in cellular protection [150]. Similarly, specific NAC TFs (e.g., *ANAC019*, *RD26*) and WRKY factors are established transcriptional signatures for salinity and drought, directly binding to promoters of genes responsible for osmotic adjustment and senescence regulation [151].

These TFs function as central hubs, regulating downstream tolerance pathways by modulating the expression of genes involved in osmotic balance, ROS detoxification, and ion homeostasis [152]. The combinatorial expression patterns of these TF families provide a precise, multi-dimensional transcriptomic

signature that can diagnose stress states and predict phenotypic resilience, forming a critical foundation for the development of diagnostic tools and the engineering of synthetic gene circuits for enhanced stress tolerance [89]. Beyond protein-coding transcripts, a sophisticated layer of gene regulation is mediated by non-coding RNAs (ncRNAs), which have emerged as potent, dynamic biomarkers for abiotic stress.

Specific stress-responsive microRNAs (miRNAs) serve as important molecular indicators of stress type and severity in plants. Among these, miR398 is widely recognized as a conserved oxidative stress-responsive miRNA; its rapid downregulation under stress conditions enhances the expression of copper/zinc superoxide dismutases (*CSD1* and *CSD2*), thereby improving reactive oxygen species (ROS) scavenging and oxidative stress tolerance in plants [153]. Conversely, Stress-responsive microRNAs such as miR159 and miR396 play important roles in regulating plant adaptation to drought and salinity stress and are considered potential biomarkers of ABA-mediated stress responses. miR159 regulates ABA signaling through the targeting of MYB transcription factors, while miR396 modulates Growth-Regulating Factors (GRFs) to suppress leaf growth and redirect energy and resources toward stress tolerance under unfavorable environmental conditions. Furthermore, long non-coding RNAs (lncRNAs) and circular RNAs (circRNAs) are now recognized as important components of stress-responsive regulatory networks. These RNAs function as competitive endogenous RNAs (ceRNAs), acting as molecular sponges that sequester miRNAs to modulate the expression of their target mRNAs. For example, specific salt-induced lncRNAs in cotton and rice can sponge miR169, thereby upregulating the expression of the nuclear factor YA transcription factor, which enhances drought tolerance [154]. Additionally, Stress-responsive circRNAs and lncRNAs play important regulatory roles in plants by modulating gene expression through interactions with chromatin remodelers, transcription factors, and RNA-binding proteins, thereby influencing transcriptional activity and mRNA stability under adverse environmental conditions. The expression patterns of these regulatory RNAs thus offer a high-resolution, early-warning biomarker system with immense potential for developing diagnostic tools and engineering RNA-based resilience.

6.3 RNA-Based Stress Mitigation

RNA-based technologies have emerged as novel toolkits for crop stress mitigation, leveraging knowledge of transcriptomic biomarkers. A primary application is the exogenous application of engineered RNAs, such as spray-induced gene silencing (SIGS). In this approach, exogenous application of double-stranded RNAs (dsRNAs) targeting key virulence-related genes in fungal pathogens has emerged as a promising eco-friendly approach for disease management in crops. Recent studies have demonstrated that spray-induced gene silencing (SIGS) using dsRNAs against *Fusarium graminearum* effectively reduces Fusarium head blight infection and mycotoxin accumulation in wheat, providing a sustainable alternative to conventional fungicide-based control strategies.

Secondly, RNA interference (RNAi)-based silencing of stress-sensitive genes provides a strategy to reprogram plant responses. For example, targeted suppression of negative regulatory genes, including PP2Cs and ethylene-responsive transcription factors, through transgenic approaches or virus-induced gene silencing (VIGS) has been reported to improve drought and salinity tolerance by maintaining the activation of key stress-responsive signaling pathways, thereby enhancing stress adaptation and survival in crops such as rice [155]. Finally, transcriptome sequencing facilitates the discovery of transcriptome-derived SNP markers, which are often more functionally informative than anonymous genomic SNPs. These markers, identified through allele-specific expression (ASE) analysis or expression quantitative trait loci (eQTL) mapping, are tightly linked to regulatory variation underlying stress resilience. Integrating these expression-

associated SNPs into genomic selection models has improved the predictive accuracy for complex traits like heat tolerance in maize, thereby accelerating the breeding of climate-resilient varieties [156].

7 Integrative Multi-Omics Platforms for Biomarker Discovery

Integrative multi-omics platforms are contributing to biomarker discovery by providing a systems-level understanding of plant stress responses, extending beyond single-layer snapshots to capture dynamic, interconnected regulatory networks. Combining data from the microbiome, metabolomics, methylomics, and transcriptomics, researchers can uncover causative relationships and identify master regulatory hubs. For example, integration of rhizosphere microbiome profiling with root metabolomics has identified specific hub genes linking microbial activity to plant metabolism, such as transporters and flavonoid biosynthesis genes whose expression correlates with beneficial *Pseudomonas* colonization and subsequent accumulation of stress mitigating salicylic acid and lignans [157]. Furthermore, simultaneous methylome and transcriptome sequencing (Methyl-RNAseq) elucidates the direct crosstalk between DNA methylation and transcription under stress. This approach has revealed that stress-induced demethylation at enhancer-like regions upstream of key NAC transcription factors precedes their transcriptional activation, establishing a clear epigenetic-genic cascade essential for osmotic adjustment [158]. One promising direction for integration may be the construction of probabilistic networks capable of yielding network level biomarkers that could help predict stress tolerance. These biomarkers are not single molecules but robust modules, such as a co-expression network linking a specific root exudate metabolite, a bacterial taxon's abundance, and the methylation state of a WRKY transcription factor's promoter. Such integrative modules have proven more accurate in predicting composite phenotypes like yield stability under drought than any single-omics biomarker class, providing a good tool for predictive breeding and microbiome engineering [4,159].

Computational Approaches

The effective interpretation of vast multi-omics datasets necessitates advanced computational approaches that transform complex data into actionable biological insights. Machine learning (ML) algorithms, particularly ensemble methods like Random Forest and deep learning models such as convolutional neural networks (CNNs), have become valuable for biomarker prioritization. These models can integrate heterogeneous data—ranging from metabolite abundances to chromatin accessibility—to identify minimal biomarker panels with high predictive power for phenotypes like drought tolerance or nutrient-use efficiency, surpassing traditional statistical methods [160]. Complementing ML, network modelling techniques, including weighted gene co-expression network analysis (WGCNA) and Bayesian network inference, are critical for identifying regulatory hubs. These hubs represent genes, metabolites, or microbial taxa that exert disproportionate influence over the entire stress-response system. For instance, integrative network analysis of rice under combined heat and drought stress pinpointed a small set of transcription factors and primary metabolites as central coordinators of both metabolic flux and transcriptional reprogramming [161]. Furthermore, multi-omics quantitative trait locus (mQTL) mapping integrates genomic loci with variation in transcript, protein, metabolite, or methylation levels. This approach dissects the genetic architecture of complex traits by revealing cis- and trans-acting loci that control molecular phenotypes, effectively linking causative genetic variants to their functional molecular outcomes. Recent mQTL studies in wheat and maize have successfully identified key regulatory hotspots on chromosomes that control networks of stress-responsive genes and metabolites, providing breeders with high-value targets for genomic selection [162]. Collectively, these computational pipelines function as an integrated analytical engine that

distills complex multi-omics datasets into predictive insights into stress resilience, thereby facilitating the precise engineering and selection of stress-resilient plants.

8 Multi-Omics-Guided Strategies for Abiotic Stress Alleviation

Multi-omics-guided strategies are transforming plant–microbe interactions from a predominantly observational field into one of rational design, enabling holistic plant–microbe engineering for targeted abiotic stress alleviation [163]. A key approach involves the design of synthetic microbial consortia informed by integrated multi-omics datasets. By combining metagenomic, metatranscriptomic, and metabolomic analyses of the rhizosphere under stress conditions, researchers can identify keystone microbial taxa whose abundance and functional activity correlate strongly with plant fitness and stress resilience [164,165]. These keystone taxa are often associated with the biosynthesis of beneficial metabolites and enzymes, including ACC deaminase, auxins, and osmoprotectants, which collectively modulate plant hormone balance, root architecture, and stress-responsive signaling pathways [166].

Microbial consortia, composed of complementary strains exhibiting cross-feeding and synergistic interactions, have demonstrated superior and more consistent performance in enhancing drought and salinity tolerance in crops such as maize and tomato compared to single-strain inoculants [167,168]. Concurrently, advances in multi-omics approaches are informing the development of next-generation biofertilizers enriched with stress-modulating metabolites. Proteomic and metabolomic analyses of effective PGPR secretions have identified specific microbial metabolites, including polyamines such as spermidine and VOCs such as 2,3-butanediol, which directly trigger systemic resistance, osmotic adjustment, and antioxidant defense responses in plants [169,170]. Formulating biofertilizers with these live microbial inoculants alongside their characterized and stabilized metabolite blends enhances product efficacy and reliability, providing a dual-action strategy that primes plant defense mechanisms while simultaneously improving nutrient acquisition [24,60]. This integrative engineering paradigm, which conceptualizes the plant and its associated microbiome as a unified meta-organism, leverages multi-omics insights to develop resilient agricultural systems capable of mitigating abiotic stress from the soil upward [59].

9 Predictive Breeding, Genome and Epigenome Editing

The integration of multi-omics data is contributing to advances in predictive breeding by extending genomic selection toward a more comprehensive framework in which biomarkers from multiple molecular layers can support parental selection and trait introgression [171]. This approach leverages multi-omics biomarkers (Table 2) to select parents with high resilience by building predictive models that correlate molecular profiles such as stress-responsive metabolite abundances, favorable epigenetic states, or robust transcriptional signatures with superior field performance under abiotic stress [112]. For instance, integrating metabolomic data with yield stability indices in wheat has enabled the identification of elite parental lines with inherently high levels of osmoprotectants and antioxidants, which reliably transmit enhanced drought tolerance to progeny [172]. Importantly, modern selection indices are now incorporating epigenetic and transcriptomic markers alongside traditional genetic markers. Stable or potentially heritable stress associated epialleles, identified through methylome analysis and subsequently validated for stability and inheritance, and expression QTLs (eQTLs) linked to the constitutive upregulation of key transcription factors like *DREB1A*, serve as powerful proxies for stable, pre-adapted phenotypes.

Table 2: Comparative overview of major omics layers used for the identification, validation, and application of biomarkers associated with plant stress resilience. The table summarizes key biomarker classes, analytical platforms, biomarker outputs, validation requirements, functional relevance to stress responses, potential intervention and crop-improvement applications, major limitations, field readiness, and representative plant studies across microbiome, metabolomics, epigenomics, transcriptomics, and integrative multi-omics approaches.

Omics Layer	Key Biomarker Classes	Analytical Platform	Biomarker Output	Validation Criteria	Stress Relevance & Function	Intervention/ Application	Main Limitation	Field Readiness	Representative Plant References
Microbiome (Metagenomics/Metatranscriptomics)	Keystone/beneficial microbial taxa (<i>Pseudomonas</i> , <i>Bacillus</i> , <i>Streptomyces</i>), AM fungi; functional genes associated with ACC deaminase, N fixation and P solubilization	16S rRNA sequencing, ITS sequencing, shotgun metagenomics, metatranscriptomics	Differential microbial taxa; functional gene abundance/expression; microbial co-occurrence and interaction networks	Independent field validation; reproducibility across soils/seasons; microbial isolation/inoculation assays; plant-growth validation	Rhizosphere restructuring; nutrient acquisition; phytohormone regulation; ACC-deaminase-mediated ethylene modulation; improved stress tolerance	Microbial inoculants, synthetic microbial consortia, biofertilizers, seed coating and microbiome engineering	Strong environmental dependence; microbiome composition and function vary with soil, genotype, climate and management; field consistency remains challenging	Medium–High	[173,174]
Metabolomics	Proline, glycine betaine, trehalose, ascorbate, glutathione, flavonoids, ABA, JA and VOCs	LC–MS/MS, GC–MS, UHPLC–MS, NMR	Differential metabolites; targeted metabolite concentrations; metabolic fingerprints; pathway enrichment	Targeted metabolite confirmation; authentic/isotope-labelled standards; independent biological validation; multi-environment validation	Osmotic adjustment; ROS detoxification; membrane protection; redox homeostasis; hormone signalling; metabolic reprogramming	Metabolite-based diagnostics; exogenous metabolite application; metabolic engineering; selection of stress-associated metabolic markers	High metabolic plasticity; strong genotype, tissue, developmental-stage and environmental dependence; metabolite identification can be ambiguous	Medium–High	[175,176]
Epigenomics (Methylomics)	DNA methylation in CG, CHG and CHH contexts; differentially methylated regions; stress-associated epialleles; transposable-element methylation	Whole-genome bisulfite sequencing (WGBS), RRBS, nanopore methylation sequencing	Differentially methylated regions (DMRs); methylation profiles; stress-associated epigenetic signatures	Bisulfite/targeted methylation validation; association with gene expression; stability across generations where relevant; functional validation	Regulation of stress-responsive genes; genome stability; transposable-element silencing; stress memory and acclimation	Epigenetic breeding; epigenome editing; chemical priming; stress-memory-based crop improvement	Epigenetic marks can be tissue-, genotype- and environment-dependent; inheritance and stability across generations require rigorous validation	Medium	[154,177]

Table 2: *Cont.*

Omics Layer	Key Biomarker Classes	Analytical Platform	Biomarker Output	Validation Criteria	Stress Relevance & Function	Intervention/ Application	Main Limitation	Field Readiness	Representative Plant References
Transcriptomics	Stress-responsive TFs (DREB/CBF, NAC, WRKY, MYB, bZIP); miRNAs; lncRNAs; circRNAs	RNA-seq, small-RNA sequencing, long-read Iso-Seq, qRT-PCR	Differentially expressed genes (DEGs); regulatory RNA profiles; co-expression modules; candidate stress-responsive TFs	qRT-PCR validation; mutant/ overexpression/ complementation assays; independent genotype validation; physiological/phenotypic association	Antioxidant defence; osmolyte synthesis; hormone signalling; photosynthesis; ROS detoxification; transcriptional reprogramming	Marker-assisted breeding; candidate-gene selection; RNAi/SIGS; gene editing; functional validation of stress regulators	Transcript abundance does not necessarily predict protein abundance, metabolite levels or phenotype; strong temporal/tissue specificity	High	[149,178,179]
Integrative Multi-omics	Multi-omics QTLs; cross-omics network hubs; candidate causal regulators; AI/ML-derived predictive biomarkers	Integrated genomics, transcriptomics, proteomics, metabolomics and microbiome profiling; network analysis; machine learning	Multi-layer biomarker panels; regulatory networks; candidate causal hubs; predictive models	Independent multi-environment validation; external datasets; functional validation; predictive performance testing	Identifies interactions among genetic, transcriptional, metabolic and microbial layers and improves mechanistic resolution of complex stress phenotypes	Precision breeding; genomic selection; systems biology; digital agriculture; stress-resilient crop development	High computational complexity; data integration and normalization challenges; large datasets; limited standardized pipelines; causality remains difficult to establish	Medium	[180,181]

Epigenetic and other non-genetic markers capture environmentally driven phenotypic variation and adaptive plasticity that are not fully explained by DNA sequence alone, thereby enhancing the accuracy of genomic estimated breeding values (GEBVs) for complex agronomic traits such as heat tolerance, drought adaptation, and nutrient-use efficiency in crops under changing climatic conditions. By employing these multi-omics biomarkers in early-generation screening, breeders can make more informed crosses, reduce the dependency on extensive field phenotyping, and significantly accelerate the development of climate-resilient cultivars with built-in molecular fortification (Table 2).

The advent of precision genome and epigenome editing technologies has enabled targeted engineering of plant stress resilience by directly manipulating its molecular blueprints. This includes the engineering of key metabolite pathways, such as enhancing proline biosynthesis. By using CRISPR-Cas9 to knock out the proline degradation enzyme *ProDH* or to introduce feedback-insensitive alleles of the rate-limiting enzyme *P5CS*, researchers have successfully generated rice and tomato lines with constitutively elevated proline levels, leading to demonstrable improvements in drought and salinity tolerance through enhanced osmotic adjustment and ROS scavenging [182]. Beyond the genome sequence, editing specific methylation loci controlling stress memory offers a novel strategy. Epigenome editing tools like CRISPR-dCas9 fused to DNA demethylases (TET1) or methyltransferases (DNMT3A) allow for the precise erasure or establishment of methylation marks at promoters of stress-responsive genes. For example, targeted demethylation of the *OsDREB1a* promoter in rice created a heritable epiallele with enhanced transcriptional activity, resulting in a primed state that confers improved drought tolerance across generations without altering the DNA sequence [183]. Furthermore, modifying master transcription factors (TFs) that regulate large gene networks provides a systems-level intervention. CRISPR-based promoter engineering or coding sequence optimization of central TFs such as members of the DREB, NAC, or AREB families can amplify their expression or alter their activity, thereby activating entire downstream networks responsible for osmolyte synthesis, antioxidant production, and stomatal regulation [54]. These editing strategies, by fine-tuning metabolic flux, epigenetic memory, and transcriptional hierarchies, represent a direct and highly specific route to developing crops with designed resilience to abiotic stress.

10 Limitations and Challenges in Translating Biomarkers from Controlled Laboratory Settings to Field Applications

Despite the considerable potential of molecular, physiological, and multi-omics biomarkers for improving the prediction of plant responses to abiotic and biotic stresses, their translation from controlled laboratory or greenhouse conditions to heterogeneous field environments remains a major challenge [49]. Laboratory experiments generally provide highly controlled conditions in which individual stress factors, genotypes, microbial inoculants, and environmental variables can be precisely manipulated. In contrast, field environments are characterized by simultaneous and fluctuating stresses, spatial and temporal heterogeneity, differences in soil properties, plant developmental stages, microbial communities, and unpredictable weather conditions [184]. Consequently, biomarkers identified under controlled conditions may show reduced sensitivity, specificity, or reproducibility when applied across diverse agricultural environments. A biomarker that reliably predicts drought, salinity, nutrient deficiency, or pathogen responses under experimental conditions may therefore not necessarily retain the same predictive value under field conditions where multiple stressors interact [185].

A further limitation is the context dependency of biomarker expression. Many molecular markers, including stress-responsive transcripts, proteins, metabolites, and phytohormones, exhibit strong genotype-, tissue-, developmental-, and environment-specific responses [186]. The same biomarker may be induced by

different stresses or may respond differently depending on stress intensity and duration. Such pleiotropic responses can reduce biomarker specificity and complicate the establishment of universal diagnostic thresholds [187]. Moreover, the considerable natural variation among cultivars and growing environments necessitates validation using independent field populations before biomarkers can be considered robust enough for agricultural decision-making. Integrating environmental metadata, phenotypic measurements, soil characteristics, and climatic variables with molecular biomarkers will therefore be important for developing predictive models that are transferable across locations and seasons [188].

10.1 Technical Bottlenecks in Multi-Omics Integration

The integration of genomics, transcriptomics, proteomics, metabolomics, epigenomics, microbiomics, and phenomics offers good opportunities to identify robust biomarker signatures. However, multi-omics integration remains technically and computationally demanding [189]. The different omics platforms generate datasets with substantially different scales, distributions, dimensionalities, detection limits, and sources of technical variation. Batch effects, missing values, differences in sequencing depth or analytical sensitivity, and inconsistencies among experimental platforms can introduce substantial bias and make direct comparison difficult [190]. In addition, high-dimensional datasets frequently contain many more variables than biological samples, increasing the risk of overfitting and generating apparently strong associations that may not be reproducible in independent datasets.

Another important bottleneck is the difficulty of establishing causal relationships among biomarkers. Correlation across transcriptomic, proteomic, metabolomic, and phenotypic datasets does not necessarily indicate that a particular molecular feature directly controls the stress response. Multi-omics networks may contain thousands of statistically significant associations, making it difficult to distinguish causal regulators from downstream consequences or stress-associated signatures [191]. The development of standardized analytical pipelines, interoperable databases, appropriate normalization procedures, and biologically informed machine-learning approaches is therefore critical. Importantly, predictive models should be subjected to independent cross-environment and cross-genotype validation rather than evaluated solely on the dataset used for model development. Explainable artificial intelligence and network-based approaches may further improve biological interpretation by identifying molecular features that consistently contribute to stress prediction across environments [192].

10.2 Economic Feasibility and Practical Deployment

The economic feasibility of biomarker-based applications represents another major barrier to their widespread adoption. Advanced omics technologies often require expensive instrumentation, specialized laboratory infrastructure, skilled personnel, sample processing, and substantial computational resources [193]. Although the cost of sequencing and other high-throughput technologies continues to decline, comprehensive multi-omics profiling of large numbers of field samples remains considerably more expensive than conventional agronomic or physiological measurements. Consequently, the practical value of a biomarker must be evaluated not only according to its biological accuracy but also according to its cost per sample, analytical turnaround time, scalability, and potential economic benefit to farmers and breeding programs [194].

For field-level implementation, complex multi-omics assays may need to be converted into simpler, rapid, and inexpensive diagnostic platforms. Once robust biomarkers have been validated, targeted assays such as quantitative PCR, targeted metabolite detection, immunoassays, biosensors, or portable sequencing technologies could provide more economically feasible alternatives to whole-omics profiling [195]. A

tiered strategy may therefore be particularly effective, in which multi-omics approaches are initially used for biomarker discovery and validation, followed by development of a small panel of highly informative markers suitable for routine screening [196]. Cost–benefit analyses should consider not only assay costs but also the potential savings associated with early stress detection, optimized irrigation and fertilizer application, improved disease management, reduced crop losses, and accelerated breeding [197].

11 Conclusion and Future Perspectives

Integrated multi-omics approaches have greatly enhanced our ability to understand plant responses to abiotic stress by providing insights into the complex interactions among the genome, epigenome, transcriptome, proteome, metabolome, microbiome, and phenome. Cross-omics integration provides a more holistic framework for identifying robust biomarkers and elucidating the molecular networks governing stress perception, signaling, metabolic reprogramming, and adaptation than single-omics approaches. The integration of transcriptomic, proteomic, and metabolomic datasets has provided some of the strongest evidence for identifying consistent stress-responsive markers, while the incorporation of epigenomic and microbiome data has further advanced our understanding of stress memory and plant resilience. Despite these advances, several challenges continue to limit the practical application of multi-omics biomarkers. Variability in experimental design, sampling strategies, and analytical protocols, together with data heterogeneity, incomplete genomic resources for many crops, and limited independent validation of candidate biomarkers, can compromise their reproducibility and transferability. Moreover, most candidate biomarkers have been evaluated primarily under controlled laboratory conditions, whereas relatively few have been validated across diverse field environments, geographic locations, and growing seasons. Future research should therefore prioritize the development of standardized sampling and data-integration protocols, independent validation across diverse genetic backgrounds and environments, and causal functional studies using genome editing and reverse-genetics approaches. Greater emphasis should also be placed on developing transparent and interpretable predictive models capable of integrating heterogeneous multi-omics datasets. These advances will accelerate biomarker validation and facilitate their application in marker-assisted breeding, precision agriculture, and the development of climate-resilient crops, thereby contributing to sustainable agricultural production under changing environmental conditions.

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