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REVIEW ARTICLE

Omics approaches - Comprehensive insights for abiotic stress tolerance in horticultural crops

A Bharathi[1*], K S Vijai Selvaraj[2*], J Karthikeyan[2], P Agalya[2] & Rajiv P[3]

[1]Dr M. S. Swaminathan Agricultural College and Research Institute, Eachangkottai 614 902, Tamil Nadu, India
[2]Vegetable Research Station, Palur, Cuddalore 607 102, Tamil Nadu, India
[3]PSG College of Arts and Science, Coimbatore 641 014, Tamil Nadu, India

*Correspondence email - bharathi.a@tnau.ac.in; ksvijaiselvaraj@gmail.com

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Abstract

Abiotic stress tolerance in plants can be better understood and enhanced through the use of omics techniques, which entail the extensive study of biological molecules. Drought, salt, temperature fluctuations and heavy metal toxicity are examples of abiotic stresses that can drastically lower the output of agriculture. Researchers identified the molecular mechanisms behind plant responses to these stresses and created plans for enhancing agricultural stress tolerance by utilizing a variety of omics technologies, including phenomics, proteomics, metabolomics, transcriptomics and genomics. Researchers are now able to clarify the molecular expressions behind the difficult-to-understand plant stress responses because of the advancements in omics methods and technology. CRISPR-Cas9 genome editing has the ability to overexpress resilience factors or wipe out susceptibility genes. Regulatory networks governing stress-adaptive pathways were revealed by RNA-Seq. In order to lessen the consequences of stress, proteomics found proteins that had been activated by post-translational modifications. Osmoprotectants and signaling molecules produced during acclimation were discovered by metabolomics. Stress tolerance marker-trait connections have been found using "quantitative trait locus mapping." Climate resilience can be increased by introducing wild genes into crops. Crosstalks across stress tolerance pathways are being uncovered by combining these omics using systems biology modeling. In order to maintain food and nutritional security, the development of climate-resilient horticultural crops will be supported by ongoing omics developments.

Keywords: abiotic stresses; CRISPR-Cas 9; horticultural crops; Omics; resilience

Introduction

Potentially adverse changes in biological and/or environmental factors that negatively influence the plant growth, development and productivity are referred to as stress (1). Plants are affected by both abiotic stresses caused by drought, heat, cold, salt, heavy metals, etc. and biotic stress caused by fungi, bacteria, viruses, parasites, insects, weeds and native plants due to climate change (2, 3). Climate change is expected to reduce the production of all agricultural crops by 4.5 % to 9 % between 2010 and 2039 (4). Crop yield in the future may be insufficient to feed the world's expanding population (5). It is essential to improve the stress tolerance crop varieties to combat the climate change. Biotic stress resistance is governed by single gene but breeding for abiotic tolerance is more difficult due to the complex nature of plant responses mechanism to the stress.

A new era of effective plant molecular tools for adapting to environmental changes began with the advancement of next-generation sequencing (NGS) and other high-throughput tools, researchers were now able to investigate complex stress responses at a much deeper level. Genomic and transcriptomic studies helped to identify key genes and their regulatory networks that contributed to stress tolerance. These findings could be harnessed to create genetically modified or selectively bred crops with improved resilience. Proteomics, which focused on the entire protein profile, allowed for the identification of stress-responsive proteins and pathways involved in defense mechanisms. For example, proteins involved in cell wall strengthening, osmotic regulation and antioxidant defense could be targeted to enhance stress tolerance in crops like tomatoes, peppers and cucumbers. Metabolomics further expanded this understanding by providing insights into metabolic shifts that occured during stress, revealing potential biomarkers for early detection of abiotic stress, such as drought or salinity. In addition to these traditional omic fields, as shown in Table 1, emerging areas like lipidomics and ionomics are offering new perspectives in understanding how plants managed stress (6). Lipidomics explores how alterations in membrane lipid composition influences cell membrane integrity under stress, while ionomics focuses on the role of ion homeostasis in maintaining cellular functions during exposure to stresses like salt or drought. Both fields provide valuable insights into the physiological adaptations that enable plants to survive in challenging environments.

Furthermore, phenomics, which encompassed the comprehensive measurement of plant traits, became an essential tool for understanding the physical manifestations of stress in plants. By coupling phenomics with genomic data, researchers could

Table 1. Different Omics tools and technologies in abiotic stress (10)

Sl.No.	Omics tools	Technologies used
1.	Genomics	Ilumina (MiniSeq, MiSeq, Next-generation sequencing (NGS) includes Roche Platforms (GS Jr, GS FLX+), SOLID and Ion Torrent, HiSeq and NovaSeq), PacBio (RSII and Sequel), OxNano (MiniON and GridION/ Prome-thION); additionally, there is a bead-based flow cytometric method and expressed sequence tag (EST) analysis
2.	Proteomics	Extraction and purification of proteins; 1-D and 2-D PAGE; reversed-phase high-performance liquid chromatography (RPLC); MALDI-TOF-MS/ MS; ESI-TOF-MS/MS; X-ray crystallography; nuclear magnetic resonance (NMR) spectroscopy; MS/MS-based isotope-coded affinity tags (ICAT) and isobaric tag for relative and absolute quantitation (iTRAQ) and multidimensional protein identification technology (MudPIT)
3.	Transcriptomics	RNA-Seq; expressed sequence tags (ESTs); cDNA-AFLP; RFLPcoupled domain-directed differential Display; microarray and various next generation sequencing (NGS) platforms such as Roche Platforms (GS Jr, GS FLX+), Ilumina (MiniSeq, MiSeq, HiSeq and NovaSeq), SOLID and Ion Torrent, PacBio (RSII and Sequel), OxNano (MiniON and GridION/ Prome-thION)
4.	Metabolomics	high-performance thin-layer chromatography (HPTLC); Thin-layer chromatography (TLC); high-performance liquid chromatography (HPLC); liquid chromatography-mass spectrometry (LC-MS); gas chromatography-mass spectrometry (GC-MS); capillary electrophoresis-mass spectrometry (CE-MS); nuclear magnetic resonance (NMR); Fouriertransform infrared (FT-IR) spectroscopy
5.	Plant Glycosmis	Chromatographic techniques – LC, HPLC; MALDI-mass spectrometry – MALDI-TOF-MS/MS; tandem mass spectrometry; Fourier-transform ion cyclotron mass spectrometry (FT-ICR-MS); ESI-mass spectrometry – LC-ESI-MS/MS; NMR spectroscopy – gCOSY, TOCOSY; Microarray – carbohydrate microarray, Neoglycolipid (NGL)-based oligosaccharide microarray, lectin microarray, glycogene microarray
6.	Plant lipidomics	ion trap mass spectrometer; Liquid chromatography-mass spectrometry (LC-MS); triple quadrupole; direct-infusion ESI-based MS MALDI-TOF MS; Fourier-transform mass spectrometer (FT-MS);
7.	Phenomics	Technologies employed in transcriptomics, metabolomics and genomics
8.	Metatranscriptomics	Technologies employed in genomics and transcriptomics
9.	Cytogenomics and mutagenomics	Technologies employed in genomics; TILLING
10.	Plant miRNomics	Tools utilised in genomics and transcriptomics
11.	Plant secretomics	Tools utilised in genomics, proteomics and metabolomics
12.	Signalomics	Tools utilised in genomics, proteomics and metabolomics
13.	Thiolomics	Tools utilised in genomics, proteomics and metabolomics
14.	Transplastomics and chloroplastomics	Tools utilised in genomics, proteomics and transcriptomics
15.	Plant mitochodriomics	Tools utilised in genomics, proteomics and metabolomics
16.	Micromorphomics	Tools utilised in genomics, proteomics and metabolomics
17.	Microbiomics in plants	Tools utilised in genomics
18.	Cryobionomics	Tools utilised in genomics, proteomics and metabolomics

develop predictive models that linked genotypic variation to stress tolerance phenotypes. This is particularly important for horticultural crops, as morphological traits such as root architecture, leaf area and stomatal density could significantly influence how plants coped with water and nutrient deficiencies.

The successful adaptation to abiotic stress conditions in the post-genomic era was facilitated by swift progress and breakthroughs in "omics" technologies. Molecular profiling advanced sequencing methods, integration of molecular and physiological data through modelling and correlation of these discoveries with plant establishment. These advancements played a crucial role in achieving resilience and efficiency in the face of challenging environmental conditions (7). Incorporating these omics technologies into plant breeding programs opened the door to more precise, accelerated breeding strategies, ultimately leading to the development of crop varieties that were not only high-yielding but also resilient to the adverse effects of climate change. Through these integrated omics approaches, horticultural crops could engineered or selected for improved tolerance to multiple abiotic stresses, paving the way for sustainable agriculture in the face of a rapidly changing climate.

Abiotic stress in horticultural crops

Under these Abiotic stress factors, plants frequently experienced oxidative stress, resulting in an excess reactive oxygen species (ROS) release which damaged cells. In due course, this stress resulted in deterioration in productivity of the crop. Lowering the productivity led to turbulence in the food security, economic stability and ecological balance (8). Drought stress was characterized by restricted water availability, which resulted in altered plant hormone levels, decreased stomatal conductance and worse photosynthesis.

These persecutions in plant metabolism caused a plant to produce restricted leaf area with weakened root structure, which led to stunted stature of the crop (9). Temperature extremes, either hot or cold, could have resulted in reduced yields, with losses varying between 10 %-40 % or even higher. The extent of the stress impact depended on crop habit and depth of the stress conditions. In addition, the adverse effects on plant growth and development often resulted from soil contamination, leading to elevated levels of heavy metal toxicity. Cadmium (Cd), lead (Pb) and mercury (Hg) are some heavy metals which can be absorbed by plant tissues. These metals impacted various cellular functions, resulting in oxidative stress, inhibition of enzymes and reduced absorption of nutrients (10).

Genomics

Genomics is a cutting-edge field that delves into the study of the complete genetic makeup of plants. It involves unravelling the complex DNA sequences, genes and genetic variations within plant species to understand their growth, development, evolution and interaction with the environment. Depending on its methods and results, genomics can be divided into three main categories: structural genomics, functional genomics and comparative genomics (11). The characterization of gene functions and their interactions within a regulatory network was the focus of functional genomics. Identification of gene functions, gene inactivation or editing and gene over expression came under functional genomics (12). RNAi technology was utilised for functional research and gene inactivation (13). Viral-induced gene silencing (VIGS) is a temporary induction of RNA interference for plant functional genomics through the use of modified viral vectors. Several crop plant traits were improved through the use of RNAi and VIGS. As an illustration, VIGS of CaWRKY40a in pepper increased resistance to infection by *Xanthomonas campestris* (14).

Most popular genome editing tools were Zinc Finger Nucleases (ZFNs), Transcriptional Activator-like Effector Nucleases (TALENs) and Clustered Regularly Interspaced Short Palindromic Repeat (CRISPR)-Cas9. Using ZFNucleases to reduce anti nutrient content in tomato involved the gene L1L4/NF-YB6 (15). In potato TALEN was used to increase the sugar metabolism (16). A particular HyPRP in tomatoes, known as SlHyPRP1, suppressed a variety of stress reactions. By employing CRISPR-Cas9 to accurately eliminate the negative-response domain(s) SlHyPRP1, tolerance to high salinity was achieved in both germination and vegetative stages (17).

Reduced expression of important genes linked to drought, such as *SlGST, SlDHN* and *Sl-DREB*, was observed in tomatoes as a result of *SlNPR1* mutagenesis mediated by CRISPR-Cas9 (18). Targeting Induced Local Lesions IN Genomes (TILLING) offered a meticulous approach to identify and study specific mutations within an organism's DNA. A mutant in TILLING population was identified in *HSBP1* (heat shock binding protein 1) gene of tomatoes resulting in a partial reduction in protein function. Due to this mutation, mature plants were more resilient to repeated heat stress and young plants had better resistance to high temperatures (19).

Tomato plants consisting of *SlGRAS7* (GAI, RGA and SCR-like protein 7) in upraised level showed good tolerance to salt and drought stress in contrast to the wild-type counterparts (20). Enhanced growth and resistance to environmental challenges like salinity and drought were observed in tomatoes through the excessive expression of Dwarf and Delayed Flowering 2 (*SlDDF2*) in sight of RD29a- stress-responsive promoter (21). In banana, overexpression of *MP-mi397* gene created the tolerance of iron and copper deficiencies, drought and salinity stress (22). Overexpression of *MiMFTs* gene conferred salt and osmatic stress in mango (23). In walnut overexpression of *JrWOX11* gene created the tolerance salt and osmatic stress (24).

Structural genomics aims to define the physical structure of genome. Manipulating genes and controlling DNA segments were essential. Structural genomics involved the development of both physical and genetic maps. These played a pivotal role in crop improvement. Molecular markers were used for identification of QTLs, Marker assisted breeding, germplasm evaluation. The acceleration of the breeding process was facilitated by stress-related Quantitative Trait Loci (QTLs), the selection of stress-tolerant genotypes through marker-assisted methods and advancements in next-generation sequencing (NGS) technologies and techniques for detecting DNA polymorphism.

SOL Genomics Network (SGN) is a database containing taxonomic, genetic and genomic data for the Solanaceae family and other closely linked species. It incorporated molecular indicators (solgenomics.net) (25). Cucurbit Genomics Database (CuGenDB) is database that contains genetic information and cucurbit genomics, including QTLs and molecular markers (http://cucurbitgenomics.org/) (26).

Comparing two or more genomes to identify similarities and distinctions is the process of comparative genomics. Orthologs are genes that share a common ancestry and perform similar functions in species that have evolved from that ancestor (27). This concept helped in examining the expression profiles of under exposed plants during stress conditions, which made it possible to identify genes related to stress and facilitated comparison the expression profiles of different species (28). Tools for visualising a wide variety of genomes are provided by the UCSC Genome Browser, which facilitates the investigation of genomic features and streamlines cross-species comparisons (29). An extensive database of orthologous genes from different species, known as OrthoDB, made it easier to find conserved genes that might play a part in evolutionary processes (30).

Transcriptomics

Transcriptome is the collective term for all RNAs, including noncoding and mRNA, that are expressed by a specific cell or cell tissue during a unique functional state. Due to the inherent instability of RNA, it is crucial to freeze plant samples in liquid nitrogen or employ alternative storage methods that safeguard against degradation, as transcriptomics allows for the measurement of gene expression. It is essential to store samples at -80 °C, whether or not RNA isolation is performed. It is important to note that repeated thawing of the RNA sample or melting of the tissue sample can result in inaccurate conclusions due to significant degradation. The second factor, selecting the right control group was crucial because the gene expression profile was greatly influenced by the developmental stage and growth conditions. The plants designated for use as reliable control were grown under similar conditions and subjected to the same treatments, excluding the stress factors and maintaining the vitality and health to solely capture the alterations linked to abiotic stress conditions through comparison of transcriptomes.

The term transcriptomics describes the comprehensive examination of gene transcription and regulatory patterns within cells, encompassing the investigation of new transcriptional regions, transcript structure, noncoding region function and gene transcription level (31). Transcriptomics studies revealed unknown stress tolerance genes in plants and it sped up crop improvement. Northern blotting and PCR techniques are old methods; they analyses only a single transcripts or small groups of transcripts at same times (31).

Real-time RT-PCR, also known as RT-qPCR, became popular for measuring both relative and absolute gene expression because it is a sensitive technique for detecting low-abundance transcripts. In the early stages of transcriptomics research, ESTs (expressed sequence tags) were regarded as a useful tool for efficiently determining an organism's gene content without the need for whole

-genome sequencing (32). SAGE - Serial Analysis of Gene Expression was used for comparing the transcripts with known genes, quantification was accomplished through Sanger sequencing of concatenated random transcript fragments (31). RNA-Seq was a potent method for quantifying and analysing transcripts within an RNA pool that combined computational methods with high-throughput sequencing. Nucleotide sequences, which are usually about 100 base pairs long, were produced during the sequencing process; however, the precise read length could differ based on the particular sequencing technique employed (33).

Third-generation sequencing techniques that can directly sequence RNA molecules generated longer reads. Examples were Oxford Nanopore Technologies (ONT) and Pacific Biosciences (PacBio). This feature made transcriptional profiling much easier because it made it possible to identify full-length transcripts without assembly or the use of complex bioinformatics tools (34). *Rehmannia glutinosa,* a medicinal crop, underwent recent sequencing via ONT. The genome spanned about 2.49 Gb in length with a scaffold N 50 length of 70 Mb. It exhibits heterozygosity up to 2 % which is considered to be high (35).

An investigation of genetic interactions between cucumber (*Cucumis sativus L.*) and the pathogen *Alternaria cucumerina*, causing alternaria leaf spot disease, using RNA-seq analyzed responses of resistant (D1322) and susceptible (Beijing 204) cultivars to infection. Resistant D1322 exhibited 2015 and 162 DEGs at 2 and 6-days post-inoculation, respectively, while susceptible Beijing 204 showed 5276 and 307 DEGs. Upregulated DEGs were linked to defence pathways like phenylpropanoid biosynthesis. However, the susceptible cultivar showed reduced expression of photosynthesis-related genes, including PSI (*PsaD, PsaF, PsaG*) and PSII (*PsbO, PsbP*). This downregulation highlighted compromised photosynthetic processes in susceptible plants, aiding disease progression (36).

Proteomics

Proteomics, a significant field in applied biology, plays a crucial role in studying proteins across diverse parameters and situations. Through proteomic analyses, the entire proteome of the subject organism can be identified, it involves targeted recognition and quantification of particular proteins or peptides (37).

The application of proteomics in tomatoes subjected to extended stress conditions, incorporating aluminum proteomes in their analysis, highlighted alterations in root proteins, which influenced physiological functions, strategies for root development and methods for mineral absorption (38). Furthermore, the biological interactions of proteins encompass aspects such as cellular localization (descriptive proteomics), modifications after translation and transcription (PTMs), as well as protein-nonprotein interactions that determine protein functionality (39). Despite various proteomic studies aimed at understanding tomatoes' resistance to abiotic stress, challenges in data interpretation remained a significant hurdle for more comprehensive proteomics research in crops.

The proteomic profiles of five potato cultivars-Biogold, Fontane, Innovator, Lady Rosetta and Maris Piper-were analyzed using two-dimensional gel electrophoresis (2-DE) and principal component analysis (PCA). Utilizing 13 cm immobilized pH gradient (IPG) strips, each gel revealed between 199 and 320 protein spots, while 24 cm IPG strips displayed 365 to 684 spots per gel. PCA effectively distinguished among the cultivars, demonstrating its utility in proteomic analysis and classification of potato varieties (40).

Pollen grains, upon desiccation and release from anther locules, facilitate the delivery of sperm cells to the female gametophyte, culminating in seed development (41). 2-DE was used to analyze the proteome of mature tomato pollen, identifying 158 protein spots corresponding to 133 unique proteins (42). These proteins were predominantly associated with functions such as energy production (19 %), defence mechanisms (18 %), protein synthesis and processing (18 %), cytoskeletal organization (7 %), transport processes (6 %), calcium signalling pathways (5 %) and allergenic responses (2 %). Further investigation into the membrane proteome of mature tomato pollen revealed proteins involved in energy-related pathways, including glycolysis and the Krebs cycle. The major techniques applied in proteomics are presented in Table 2 (43–48).

Sub cellular proteomics

Subcellular proteomics focuses on studying the proteome of specific subcellular compartments or organelles within a cell. The aim of subcellular proteomics is to analyze, characterize and quantify proteins found in specific cellular organelles or substructures. It held subcellular constituents during abiotic stressors in plant growth. (49). CropPAL created voting consensus with species-specific for a dozen individuals based on the annotated location database of crop proteins (50). The major bioinformatics tools and databases supporting crop subcellular proteomics are summarized in Table 3 (51-56).

Table 2. Different techniques of proteomics

Technique	Tool for detection	Advantages and disadvantages
DIGE (Cy3, Cy5)/ MALDI-TOF/MS	TOF	Efficient in terms of both time and cost/ Inappropriate for proteins with hydrophobic characteristics (43)
MudPIT	Conversion dynode/electron multiplier	Time consumption is less/ The detection of PTMs is not possible (43)
LC-MS/MS	ESI	Faster with more concise extraction methods and high clarity/ Extracts more time (44)
MALDI-TOF/MS	TOF	Quick, accuracy and cost effective/reduced analytical sensitivity Second (45)
GeLC-MS/MS	ESI-MS/MS	Rapid speed combined with excellent quantification characteristics/Reduced sensitivity for large proteins (45)
LC-MS/MS	SRM/MRM	Necessary for validating biomarkers/Distinct ionization of each peptide modifications (46)
iTRAQ-LC-MS/MS	Multiplex stable isotope	Reagent specific to amino acids with the ability to conduct High-throughput multiplexing/Extracts time, more work demanding and cost risky (47)
SWATH-MS	DIA	Comprehensive quantitative analysis/sophisticated software tools are necessary for analysis of hard data sets (48)

Table 3. Bioinformatics tool and database for crop subcellular proteomics

Tool or database	Uses
pLocbal-mPlant	Identifying the subcellular localization of plant proteins (51)
STRING	Protein-protein interactions (52)
ARAMEMNON	Assemble a range of computational forecasts for the membrane proteins of plants (53)
Plant-mSubP	To depict the protein, it employed a number of hybrid features, including quasi-sequence-order descriptors and autocorrelation (54)
MU-LOC	To predict mitochondrial proteins (55)
VacPred	To predict vacuole protein (56)

Post-translational modifications

Chemical alterations known as post-transitional modifications (PTMs) occur on proteins following their synthesis through the process of translation. These modifications can alter the chemical structure, properties, interactions, localization and functions of proteins within a cell.

Abiotic stress mitigation is facilitated by certain proteins present in cells, which improve cellular functions that help plants survive under abiotic stress conditions (Table 4). But proteins that exist within plant cells may undergo various PTMs, allowing for a quick and effective reaction. Further support for stress responses may be provided by these activated proteins. Abiotic stresses induced different PTMs to function in different ways (57).

Metabolomics

Metabolomics is a cutting-edge scientific discipline that involves the comprehensive study of small molecules, known as metabolites, within cells, tissues or organism. Metabolomics enables the assessment of biological processes under complex environments. Metabolomics can provide valuable insights of plant metabolism through growth stages and in response to diverse stresses by identifying a range of substances, including molecules involved in the plant's acclimatisation response, stress signal transduction molecules and derivatives of stress metabolism. The collective count of metabolites across the entire plant kingdom encompassing polar to nonpolar and volatile to non-volatile is estimated to surpass 200000 (58).

Abiotic stress response is not made possible without the involvement of metabolites. Analytical methods like nuclear magnetic resonance (NMR), gas chromatography mass spectrometry (GCMS), liquid chromatography mass spectrometry (LCMS) and Fourier Transform Ion Resonance (FTIR) have facilitated the quantification of metabolites, employing both specific and non-specific target approaches (58). A new technique called pseudo targeted metabolomics combines the benefits of both targeted as well as non-targeted metabolomics approaches. This method eliminates the need for reference values by automatically defining metabolite ion pairs for Multi Reaction Monitoring (MRM) through the utilization of MM-Ion Pair Finder software for TQMS (59).

Plants generate primary metabolites, which are necessary for their growth and development. Secondary metabolites and the factors that control them respond to environmental changes, such as extremes in salinity, UV light, temperature, light, water availability, heavy metals, oxidative stress and nutritional requirements not met (60). Some plant metabolites function as osmolytes and osmoprotectants, which can help to mitigate the negative effects of harsh stressors like salt, drought and water deficiency (61). Such metabolites include, for example, glycine betaine and dimethyl sulfonio propionate (DMSP); sugars like fructan, trehalose and sucrose along with amino acids such as proline and ectoine; and certain metabolites of polyols, sorbitol and mannitol. (62).

Targeted metabolomics faces challenges due to a lack of available reference standards, whereas untargeted metabolomics encounters issues such as a low identification rate for metabolites with known structures, inconsistent results and complex data analysis. A semi targeted approach, often referred to as suspect screening analysis, detects metabolites by utilizing compound-specific information instead of relying on reference standards (63, 64). Additionally, pseudo targeted metabolomics merges the advantages of both targeted and untargeted methods, leading to the development of a novel technology. This approach employs the MM-Ion Pair Finder tool to pinpoint ion pairs of metabolites for multi reaction monitoring (MRM) (59). Several metabolites play critical roles in enhancing tolerance to abiotic stresses in plants (65 - 71) (Table 5).

QTL for tolerance against abiotic stresses

Regulating gene expression is an intricate process controlled not only by a specific promoter but also by various trans - acting factors and epigenetic mechanisms, contributing to the ultimate gene expression outcome. Hence, recognised gene with molecular marker alone does not guarantee genotypic expression under certain conditions. Nearly every cultural trait is centralised by a complex network that included an unspecified number of genes resulting in altered phenotypic expression within natural populations as a quantitative trait. Thus, in crossing programmes aimed at enhancing stress tolerance, it is essential to employ strategies involving quantitative trait mapping analysis. This approach statistically associates genetic markers with variation in

Table 4. PTM proteomics in Tomato

PTMs	Organ	PTM detection methods	MS	Major findings
Phosphorylation	Leaf	PolyMAC-Ti kit	LC-MS/MS	Tomatoes were able to endure prolonged cold stress with the help of the activation of SnRK2s and their direct substrates (54)
Ubiquitination	Leaf	Anti-ubiquitin monoclonal antibody	LC-MS/MS	The crucial involvement of tomato carboxyl terminus of hs70-interacting proteins in heat stress response is primarily associated with their role in detection of misfolded proteins debasement evolvedat the moment of heat stress (54)

Table 5. Abiotic stress tolerance-related metabolites

Metabolites	Function	Result
Lipids	Scavenge the ROS production	Heavy metals stress (65)
Nitrogen-containing metabolites	Enhance tolerance level and protection against herbivore assault	Drought, herbivores (66)
Alkaloids		
Glucosinolates	Osmoprotectants increased phytochemical contents	Drought, waterlogging (67)
Non-protein amino acids		
Solyc04g014600	Known as Universal Stress Protein. It is a profiling protein in the phloem.	Tolerance to water stress (68)
C2H2-Type Zinc	The overall expansion and maturation of plant tissues are influenced by Finger Protein	Repones to abiotic stress factors (69)
SlMAPK3	Reported good germination and seedlings development. Furthermore, the genetically modified crops show improved food production due to high chlorophyll accumulation and promotes higher root dry weight under cadmium stress	Heavy metals (Cd2+) and drought tolerance (70)
Melatonin	Protects proteins and membranes from damage	abiotic stress tolerance (71)

phenotype, thereby defining quantitative trait loci (QTLs) (72). Using such approaches, several QTLs linked to crop yield and stress tolerance have been identified, as summarized in Table 6 (73-88).

Introgressiomics

Introgressiomics is the term used to describe the large-scale production of plant materials and populations that have genome fragments introgressed into the genetic background of crops, primarily from wild crop relatives. This process enables the development of new cultivar generations with enhanced traits (89). Embryo rescue technique, advanced backcross QTL analysis, backcross inbred lines (BIL), introgression lines (ILs), chromosome segments substitution lines (CSSLs) support successful breeding with crop wild relatives (90). Crossing and backcrossing of crop wild relatives (CWRs) traditionally requires a long time for crop improvement, the Introgressiomics approach helps eliminate time - consuming steps ad accelerate progress.

As water shortage worsen, incorporating drought-tolerant genes from wild species into crops has becomes critical. For example, nine eggplant (*Solanum melongena*) ILs containing 71.6 % of the wild relative *S. incanum,* were evaluated under water stress (91). After 14 days at 30 % field capacity, growth slowed and stress signs such as proline increased. While most ILs had lower biomass than the cultivated parent, several wild alleles improved features such as stem and root dry weight, leaf water content, water use efficiency and chlorophyll content during drought circumstances. Fine mapping these locations is critical for improving eggplant drought tolerance through breeding.

Table 6. List of QTLs and traits associated

Crop	Stress	Traits	Markers	Chromosome /LG
Potato	Heat tolerance	Yield of tuber	SNP	LG1, 4 and 9 (73)
		Number and viability of pollen, anther and style length, style protrusion, female fertility and number of inflorescences	SNP	1, 2, 3, 7, 8 and 11 (74)(75)
Tomato		chlorophyll content, maximum photochemical quantum efficiency relative electrical conductivity,	SSR	1 and 2 (76)
		Number and viability of pollen and flower protrusion, length of style	SNP	1, 2, 3, 9, 11 and 12 (77)
		Stigma exertion, Flower and fruit number per truss and pollen viability	SNP	2, 4, 6, 7 and 11 (78)
Broccoli		head size and uniformity, size and color and head maturity, head shape and smoothness,	SNP	6, 9 (79)
Cucumber		Seed germination and early heat stress	Indel markers	1(80)
Lettuce		Seed germination	SNP	9(81)
Pea		Internode, pod number and reproductive stem length, chlorophyll content	SNP	3, 4, 5, 6, 7 (82)
Cucumber	Cold tolerance	Germination rate and radicle	SSR and SNP	length 1, 2 and 4 (83)
		Low-temperature injury index	SSR	5 and 6 (84)
Pumpkin		Chilling index	SSR	LG1, 4 and 10 (74)(75)
Apple	Drought tolerance	Carbon isotope composition	SNP	LG8, LG15 and LG16 (85) (86)
Grape		Chlorophyll content	SSR	4, 13 and 17 (87)
Cucumber	Salinity tolerance	NaCl tolerance	SSR	3 (88)

Conclusion

Advancements in omics technologies have deepened our understanding of plant responses to abiotic stresses at the molecular level. High-throughput analyses have identified key genes, proteins, metabolites and regulatory networks involved in stress tolerance, paving the way for targeted breeding and biotechnological interventions. Genomic techniques like genome editing and quantitative trait locus mapping have accelerated the development of resilient crop varieties. Transcriptomics has uncovered novel stress-responsive genes, proteomics has detailed protein activation via post-translational modifications and metabolomics has identified metabolites acting as osmoprotectants and signaling molecules. Integrating multi-omics data through systems biology is elucidating complex molecular pathways, while advancements in analytical tools are enhancing phenotypic characterization at the molecular level. Leveraging these insights can strategically enhance horticultural crops to withstand climate change challenges, thereby contributing to global nutritional security.

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Authors' contributions

AB, JK and RP were involved in the conceptualization of the review, provided critical insights and finalizing the manuscript for submission. PA and KSVS conducted the literature search, drafted the initial manuscript and prepared the tables and figures. AB and JK also contributed by writing and summarizing sections on specific subtopics, while RP assisted in writing and revising various sections of the manuscript. KSV performed the final revision. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

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