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Review

Genomic Mechanisms of Plant Adaptation to Salinity and Drought Stress: Genes, Networks, and Evolutionary Implications

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Abstract

Salinity and drought stresses induced by climate change pose critical threats to global food security, necessitating a comprehensive insight of plant adaptive mechanisms at the genomic level. This review brings together recent advances in identifying genes, regulatory networks, and evolutionary strategies underlying plant responses to osmotic stress. We discuss key transcription factor families (DREB, NAC, MYB, and WRKY), ion transporters (SOS pathway, NHX, and HKT), genes involved in osmolyte biosynthesis, and reactive oxygen species (ROS) scavenging systems. Recent genomic studies have revealed extensive expansions of gene families, neofunctionalization events, and convergent evolution across plant lineages. Multiomics integration has illuminated complex regulatory networks involving microRNAs, long noncoding RNAs (lncRNAs), and epigenetic modifications that fine-tune stress responses. We examine natural variation in stress tolerance, highlighting genomic signatures of selection in halophytes and xerophytes that provide insights for crop improvement. Pangenomic analyses revealed that significant structural variations and presence-absence variations contributed to stress adaptation. Finally, we discuss evolutionary trade-offs, the impact of domestication on stress resistance, and future directions for leveraging genomic knowledge through precision breeding, gene editing, and systems biology approaches to develop climate-resilient crops.

Keywords

Salinity stress; drought tolerance; plant genomics; transcription factors; gene regulatory networks; evolutionary adaptation; climate change; crop improvement; pangenomics; epigenetics

1. Introduction

Global climate change has intensified the frequency and severity of abiotic stresses, particularly salinity and drought, which collectively affect over 50% of agricultural lands worldwide [1]. Soil salinization affects approximately 1 billion hectares of land globally, with an annual extension rate of 1-2 million hectares promoted by irrigation practices, sea-level rise, and altered rainfall patterns [2]. Concomitantly, drought stress reduces crop production in 64% of cultivated areas, causing yield losses exceeding 40% in crucial cereal crops [3]. As the global population moving closer 10 billion by 2050, understanding and enhancing plant stress tolerance has become sovereign for ensuring food security [4].

While distinct environmental challenges, salinity and drought stresses have fundamental physiological impacts on plants through osmotic stress, ion toxicity (particularly in salt stress conditions), and oxidative damage [5]. Overlapping molecular responses, including abscisic acid (ABA) signaling, osmolyte accumulation, activation of antioxidant enzymes, and growth alteration are triggered by both stresses [6]. However, salt stress forces an additional burden of ionic stress, particularly sodium (Na^+) and chloride (Cl^-) toxicity, which requires specialized mechanisms for ion homeostasis [7].

Our understanding of plant stress responses has been modernized by recent advances in genomic technologies, including next-generation sequencing, pangenomics, and multiomic integration [8]. Thousands of genes and regulatory elements involved in stress tolerance have been identified by genome-wide association studies (GWASs), comparative genomics, and evolutionary analyses [9]. Moreover, studies of naturally stress-tolerant plant species (halophytes and xerophytes) have revealed novel adaptive mechanisms that are absent in glycophytic plants [10].

The present review comprehensively examines the genomic basis of plant adaptation to salinity and drought stress, focusing on (1) key genes and gene families that mediate stress tolerance; (2) regulatory networks that orchestrate stress responses; (3) evolutionary mechanisms underlying stress adaptation; (4) natural variation and genomic signatures of selection; (5) epigenetic regulation and transgenerational stress memory; and (6) translational applications for developing climate-resilient crops.

2. Physiological Impacts and Cellular Responses to Osmotic Stress

2.1 Primary Effects of Salinity and Drought

Both salinity and drought lower soil water potential, which reduces the ability of plant roots to take up water and consequently creates an osmotic challenge [11]. In saline environments, this response develops rapidly, often within minutes to hours, and is subsequently accompanied by ion-specific toxicity [12]. Salt stress is therefore commonly described as having two major components: an early osmotic response followed by ionic stress. In contrast, drought is dominated primarily by osmotic effects throughout the stress period [13]. However, this biphasic description should be considered a conceptual framework rather than a rigid sequence of events. When plants are exposed to high salt concentrations over a short period, Na^+ and Cl^- may reach toxic levels before the initial osmotic response has subsided. Consequently, osmotic and ionic effects can occur simultaneously, making the two phases difficult to distinguish experimentally [12, 13]. Extended drought can also produce secondary ionic effects that resemble those associated with salinity. As transpiration declines, the limited water available to plants provides less dilution and redistribution of absorbed ions. This can result in the accumulation of Na^+, Cl^-, and other ions to potentially toxic levels, particularly when drought occurs in saline or sodic soils [12]. The effects of these ions are not identical. Na^+ toxicity is largely associated with competition with K^+ for binding sites on enzymes and transport proteins, which disrupts metabolic processes that depend on K^+. Cl^-, in contrast, can exert toxicity independently by interfering with chlorophyll biosynthesis, photosystem II electron transport, and nitrate uptake and assimilation. Such Cl^--related effects are particularly evident in Cl^--sensitive woody and leguminous crops, including citrus, soybean, and grapevine. Depending on the plant species and tissue, Cl^- toxicity may therefore act together with Na^+ toxicity or occur largely independently of it [12].

Drought stress reduces turgor pressure, closes stomata, decreases photosynthetic rates, and inhibits cell expansion [14]. Prolonged drought induces leaf senescence, alters root architecture, and can lead to cavitation in xylem vessels [15]. When soluble salts, like sodium chloride (NaCl), build up in the soil or irrigation water, it causes salt stress, an abiotic stress state in plants. Both the physiological and metabolic processes of plants are impacted by this excess salinity, which hinders their growth and development. By causing an osmotic imbalance in the substrate and introducing harmful ions such as sodium (Na^+) and chloride (Cl^-), which hinder cellular function, salt stress mainly

interferes with the intake of water. When these factors come together, plants grow less, produce less, and in extreme situations, die (Figure 1) [16-18].

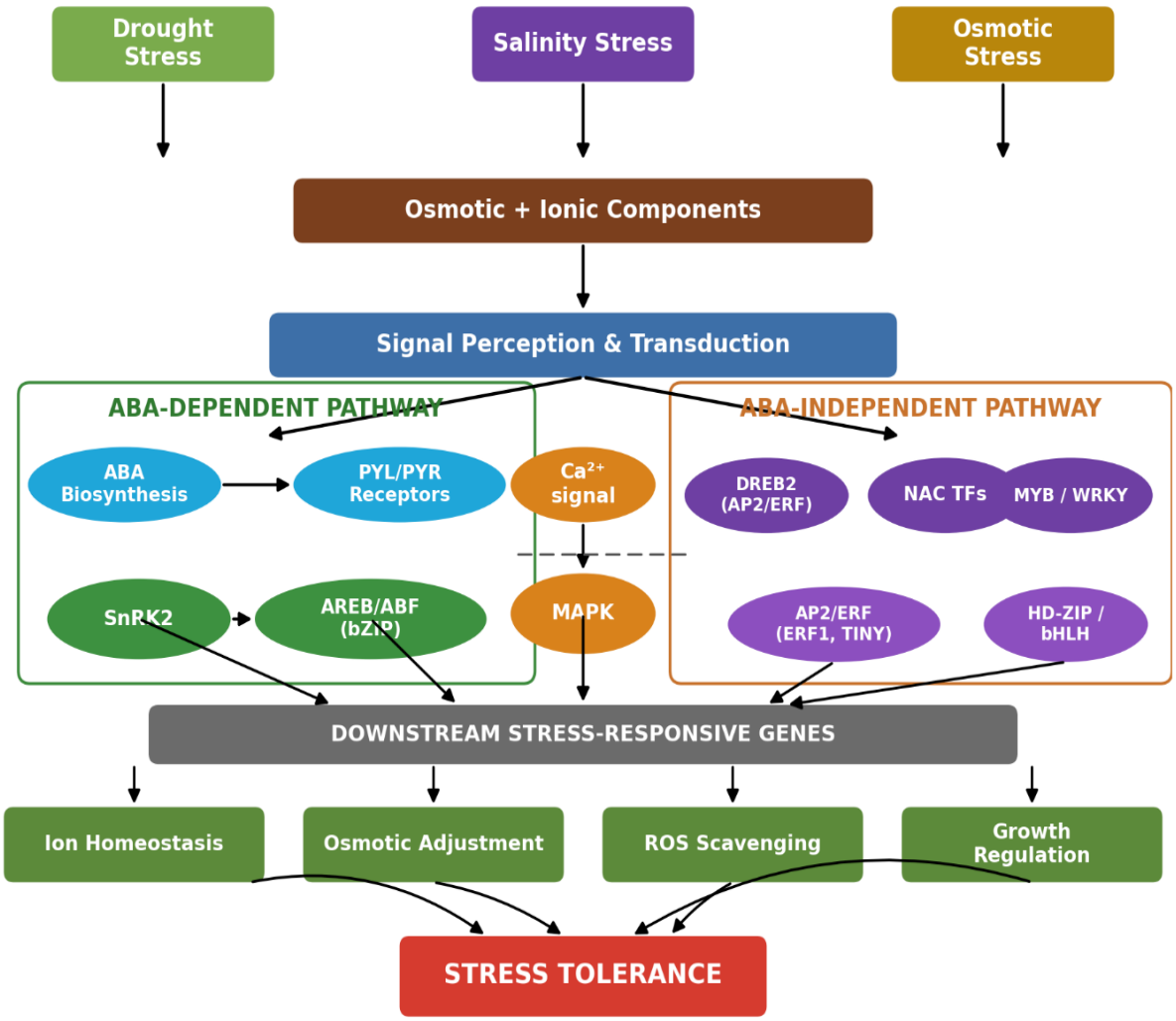

Figure 1 Integrated stress response network in plants under salinity and drought stress. Schematic representation showing the major signaling pathways (ABA-dependent and ABA-independent), key transcription factor families (bZIP/AREB-ABF, AP2/ERF-DREB2, NAC, MYB/WRKY, HD-ZIP/bHLH, and downstream responses, including ion homeostasis, osmotic adjustment, antioxidant defense, and growth regulation. Solid arrows indicate positive regulation, and the dashed line indicates crosstalk between the ABA-dependent and ABA-independent branches. (Abbreviations: ABA - Abscisic Acid; PYL/PYR - Pyrabactin Resistance/Pyrabactin Resistance-Like; SnRK2 - Sucrose Non-Fermenting 1-Related Protein Kinase 2; AREB/ABF - ABA-Responsive Element Binding Protein/ABA-Binding Factor; Ca^{2+} - Calcium ion; MAPK - Mitogen-Activated Protein Kinase; DREB2-Dehydration-Responsive Element Binding Protein 2; NAC TFs - NAM (No Apical Meristem), ATAF1/2, and CUC2 (Cup-Shaped Cotyledon) Transcription Factors; MYB/WRKY - MYB (Myeloblastosis) Transcription Factor/WRKY Transcription Factor).

2.2 Oxidative Stress and Cellular Damage

Both stresses induce excessive production of ROS, including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals ($^{\bullet}OH$), and singlet oxygen ($^1O_2$) [19]. While ROS function as signaling molecules at low concentrations, excessive ROS causes lipid peroxidation, protein oxidation, DNA damage, and ultimately cell death [20]. Plants have evolved sophisticated antioxidant systems, including enzymatic (superoxide dismutase, catalase, peroxidases, ascorbate peroxidase) and nonenzymatic (glutathione, ascorbate, tocopherols, carotenoids) components, to maintain redox homeostasis [19-21].

2.3 Adaptive Responses

Plants employ multiple strategies to cope with osmotic stress: (1) stress avoidance through altered phenology, deep root systems, and reduced transpiration; (2) stress tolerance through osmotic adjustment, ion compartmentalization, and antioxidant defense; and (3) stress escape through accelerated life cycles [22]. At the cellular level, these responses are accompanied by extensive changes in transcription, posttranscriptional regulation, protein modification, and metabolism [23, 24].

3. Key Gene Families and Molecular Players in Stress Tolerance

3.1 Transcription Factors: Master Regulators of Stress Responses

Transcription factors (TFs) occupy central positions in stress-response networks and can control the expression of large sets of downstream genes [25]. Several TF families have been studied in detail for their contributions to salinity and drought tolerance.

3.1.1 DREB/CBF Family

The Dehydration-responsive element-binding (DREB) and C-repeat binding factor (CBF) subfamilies of AP2/ERF transcription factors are among the most-studied groups in stress biology [21, 26]. DREB proteins bind to Dehydration-Responsive Element/C-Repeat (DRE/CRT) cis-elements in the promoters of stress-responsive genes, activating their expression under drought and salinity stress [22, 27]. DREB1/CBF genes are primarily cold-inducible, whereas DREB2 genes respond to drought and salinity in an ABA-independent manner [28].

The overexpression of DREB genes has improved stress tolerance in numerous crop species, including rice, wheat, maize, and soybean [23, 24, 29]. However, constitutive DREB expression often causes growth penalties, necessitating stress-inducible promoters for agricultural applications [30]. Recent structural and functional studies have revealed DNA-binding mechanisms, posttranslational modifications, and protein–protein interactions that modulate DREB activity (Table 1) [25, 31].

Table 1 Major transcription factor families involved in salinity and drought stress responses.

TF Family	Key Members	DNA Binding Domain	Target Genes/ Pathways	Stress Response Function	References
DREB/CBF	DREB1, DREB2, CBF1-3	AP2/ERF	DRE/CRT-containing genes	ABA-independent osmotic stress responses, cold tolerance	[26-31]
NAC	SNAC1, ANAC, ONAC	NAC domain	ABA signaling, ROS scavenging	Stomatal regulation, root development, osmolyte biosynthesis	[32-35]
MYB	MYB2, MYB41, MYB48-1	MYB domain	ABA-responsive genes, secondary metabolism	ROS homeostasis, wax biosynthesis, and osmotic adjustment	[36-38]
WRKY	WRKY18, WRKY40, WRKY63	WRKY domain	W-box containing genes	ABA signaling, defense responses	[39-41]
bZIP	AREB/ABF, TGA	Basic leucine zipper	ABRE-containing genes	ABA-dependent stress signaling	[42-44]
AP2/ERF	ERF1, ERF5, TINY	AP2 domain	GCC-box genes	Ethylene signaling, osmotic stress	[31]
HD-ZIP	ATHB7, ATHB12	Homeodomain + leucine zipper	ABA-responsive genes	Meristem development, drought responses	[45]
bHLH	ICE1, AtMYC2	Basic helix-loop-helix	CBF genes, JA-responsive genes	Cold acclimation, JA-ABA crosstalk	[46]

3.1.2 NAC Family

NAC (No Apical Meristem-NAM, *Arabidopsis thaliana* Activating Factor-ATAF, and Cup-shaped Cotyledon-CUC) transcription factors form a major plant-specific TF family involved in development as well as responses to environmental stress [32]. Stress-responsive NAC members, including SNAC, ANAC, and ONAC proteins, participate in ABA signaling, osmolyte production, antioxidant defense, and senescence-related pathways [33].

Key NAC genes such as *Stress-Responsive NAC 1* (SNAC1), *Stress-Responsive NAC 2* (SNAC2), and *Oryza sative NAC gene 10* (OsNAC10) increase drought and salinity tolerance in rice by maintaining root growth, improving photosynthesis, and increasing osmolyte accumulation [34]. Comparative genomic analyses also suggest that NAC genes have undergone lineage-specific expansion, and some stress-responsive members bear signatures consistent with positive selection [35].

3.1.3 MYB Family

MYB transcription factors contain conserved DNA-binding domains and are involved in stress responses, secondary metabolism, and development [36].

R2R3-MYB proteins are particularly important in osmotic stress tolerance, regulating ABA signaling, ROS scavenging, and osmolyte biosynthesis [37]. Genes such as AtMYB2, AtMYB41, OsMYB48-1, and TaMYB33 increase stress tolerance through multiple mechanisms [38].

3.1.4 WRKY Family

WRKY transcription factors contain conserved WRKY domains that recognize W-box elements and participate in stress responses, defense, and senescence [39]. Members of the family may act either positively or negatively, resulting in complex regulatory interactions [40].

WRKY genes modulate ABA sensitivity, osmotic adjustment, and ROS homeostasis [41].

3.1.5 bZIP Family

Basic leucine zipper (bZIP) transcription factors, especially members of the AREB/ABF group, are important components of ABA-dependent stress signaling [42]. They regulate genes containing ABA-responsive elements (ABREs) and thereby contribute to stomatal closure, osmolyte production, and stress-protein accumulation [43]. Phosphorylation by SnRK2 kinases activates AREB/ABF proteins during stress, enabling them to regulate ABRE-containing genes involved in stomatal closure, osmolyte biosynthesis, and stress-protein production [43, 44].

3.2 Ion Transporters and the SOS Pathway

3.2.1 Salt Overly Sensitive (SOS) Pathway

The Salt Overly Sensitive (SOS) pathway is a major route for removing Na^+ from the cytosol and maintaining ionic balance during salinity stress [47]. It consists of three principal components: SOS3, a Ca^{2+}-binding protein; SOS2, a serine/threonine protein kinase; and SOS1, a plasma-membrane Na^+/H^+ antiporter [48]. When salt stress raises cytosolic Ca^{2+}, SOS3 detects the signal and activates SOS2. The resulting SOS3-SOS2 complex phosphorylates SOS1, promoting Na^+ efflux from the cell (Figure 2) [49].

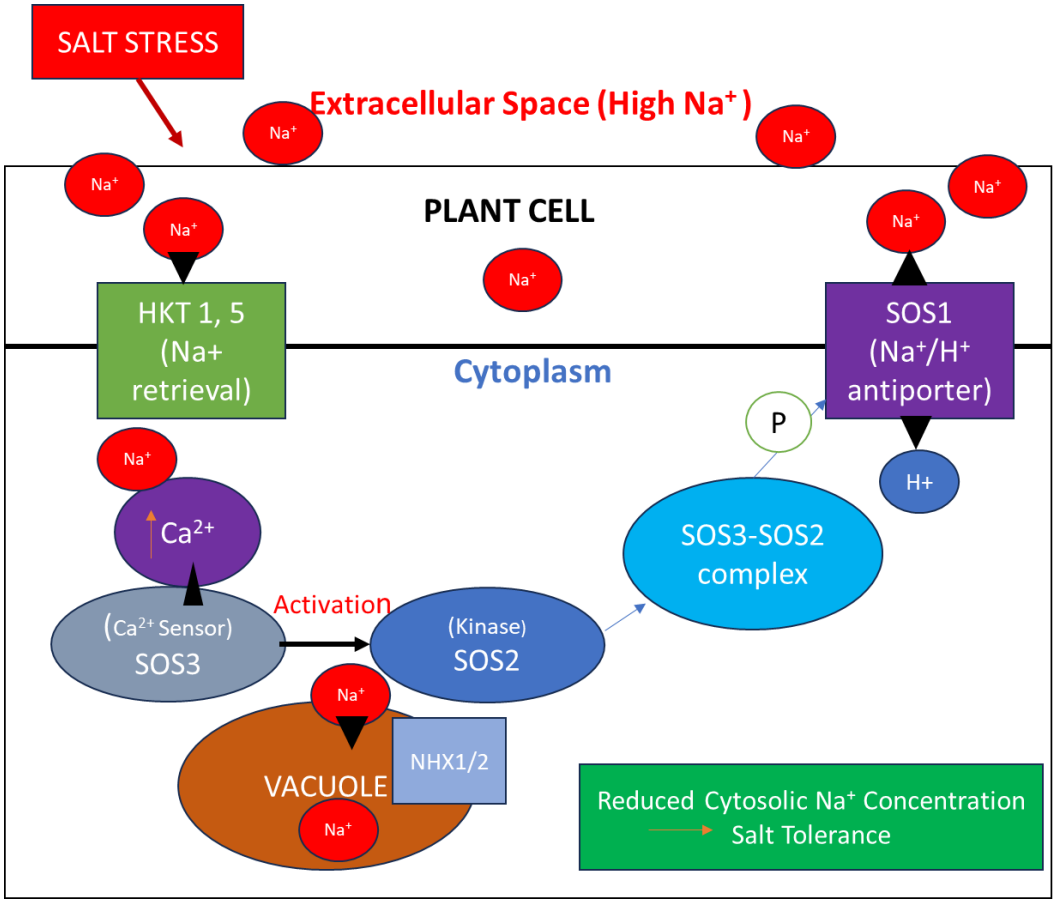

Figure 2 The SOS pathway is involved in Na^+ homeostasis. The molecular mechanism of the Salt Overly Sensitive (SOS) pathway involves Ca^{2+} signal perception by SOS3, activation of SOS2 kinase, and phosphorylation of the SOS1 Na^+/H^+ antiporter, leading to Na^+ efflux. Integration with other Na^+ transport systems (HKT, NHX) is shown.

Recent structural studies have elucidated the molecular mechanisms of SOS1 activation and Na^+ transport [50]. Cryo-electron microscopy structures of plant SOS1 show that it assembles as a homodimer with an NhaA-fold transmembrane domain and a large cytosolic regulatory region, and that the resting, autoinhibited state is converted to the active, transporting state through an elevator-type conformational transition centered on a conserved proline in transmembrane helix 5; in the autoinhibited structure, the C-terminal cytosolic domain folds back to occlude the transport pathway, and phosphorylation by the SOS3-SOS2 complex (or, in shoot tissue, by an SOS2-SCaBP8 complex) releases this autoinhibition rather than directly gating ion flux, explaining at a structural level why loss of SOS2 kinase activity—but not loss of SOS1 itself—can be partially bypassed by C-terminal truncation of SOS1. Regarding the SOS3-SOS2 interaction, SOS3 is an EF-hand Ca^{2+}-binding protein that is N-terminally myristoylated for plasma-membrane targeting; Ca^{2+} binding triggers a conformational change that allows SOS3 to engage the autoinhibitory FISL/NAF motif of SOS2, displacing it from the kinase domain and thereby relieving SOS2 autoinhibition, after which the activated SOS2-SOS3 complex docks onto and phosphorylates specific serine residues in the SOS1 C-terminal autoinhibitory domain. This activation is not rigidly root-specific: in shoots, an SOS3-like calcium-binding protein (SCaBP8/CBL10) substitutes for SOS3 in complex with SOS2 to trigger SOS1, and SOS2 additionally phosphorylates the ethylene-pathway repressor CTR1 and stabilizes the ABA-

signaling regulator AFP2, linking the center ion-transport module to hormonal crosstalk beyond Na^+ efflux itself [51]. Concerning regulatory timing, SOS2 kinase activity is normally kept low by intramolecular FISL-domain autoinhibition and by association with clade A PP2Cs (e.g., ABI2), which compete with SOS3 for SOS2 binding; salt-induced Ca^{2+} elevation shifts this equilibrium toward the activating SOS3-SOS2 complex, providing a fast-onset, reversible switch that is separate from, but can integrate with, the slower transcriptional reprogramming driven by ABA-dependent and ABA-independent pathways (Section 4). Natural variation in SOS genes contributes to intraspecific differences in salt tolerance, with allelic variants showing differential salt sensitivity [52]. Manipulation of components of the SOS pathway has improved salt tolerance in various crop species (Table 2) [53].

Table 2 Key ion transporter and osmolyte biosynthesis genes involved in stress tolerance.

Gene/Protein	Function	Subcellular Location	Stress Response	Crop Applications	References
Ion Transporters					
SOS1	Na^+/H^+ antiporter	Plasma membrane	Na^+ efflux, long-distance Na^+ transport	Overexpression improves salt tolerance	[45-53]
NHX1/2	Na^+/H^+ exchanger	Tonoplast	Vacuolar Na^+ sequestration	Enhanced salt tolerance in multiple crops	[53-57]
HKT1;5	Na^+ transporter	Plasma membrane	Xylem Na^+ retrieval	Natural variation linked to salt tolerance	[58-62]
AKT1	K^+ channel	Plasma membrane	K^+ uptake	Maintains K^+/Na^+ homeostasis	[63-65]
Osmolyte Biosynthesis					
P5CS	Δ^1-pyrroline-5-carboxylate synthetase	Cytosol	Proline biosynthesis	Overexpression enhances drought tolerance	[66-70]
BADH	Betaine aldehyde dehydrogenase	Chloroplast	Glycine betaine biosynthesis	Improved stress tolerance in transformants	[71-73]
TPS/TPP	Trehalose-6-phosphate synthase/phosphatase	Cytosol	Trehalose metabolism	Drought tolerance, yield improvement	[74-76]
Water Channels					
PIP1/PIP2	Plasma membrane aquaporins	Plasma membrane	Water transport, hydraulic conductivity	Differential regulation under stress	[77-81]
TIP1/TIP2	Tonoplast aquaporins	Tonoplast	Vacuolar water movement	Osmotic adjustment	[78, 79]
Stress Proteins					
LEA	Late embryogenesis abundant proteins	Various compartments	Protein/membrane stabilization	Desiccation tolerance	[82-84]
Dehydrins	LEA D-11 family	Cytosol, nucleus	Cryoprotection, ion sequestration	Cold and drought protection	[84]

3.2.2 NHX Exchangers

Na^+/H^+ exchangers (NHXs) located on vacuolar and endosomal membranes help sequester Na^+ in vacuoles, thereby lowering cytosolic Na^+ and contributing to osmotic adjustment [54]. Plant genomes typically contain 6–8 NHX genes, which differ in their cellular locations and functions. Among them, the vacuolar isoforms NHX1 and NHX2 have important roles in Na^+ compartmentalization [55].

Higher NHX expression can promote Na^+ sequestration and thereby improve salt tolerance, although the outcome varies with genetic background and expression level. In contrast, endosomal NHX5 and NHX6 function mainly in protein trafficking and vesicular pH regulation and influence salt tolerance indirectly [56]. The NHX family is therefore not a functionally uniform group of Na^+/H^+ exchangers. Vacuolar NHXs (NHX1–NHX4 in Arabidopsis) exchange Na^+ or K^+ for H^+ across the tonoplast using the proton gradient generated by V-ATPase and V-PPase. NHX1 and NHX2 show overlapping but distinct expression patterns and substrate preferences: NHX1 contributes more strongly to vacuolar Na^+ sequestration during acute salt stress, whereas NHX2 has a greater role in K^+ homeostasis and turgor-related processes such as stomatal movement. Consistent with this partial redundancy, nhx1 nhx2 double mutants show stronger salt-sensitivity and stomatal phenotypes than either single mutant. Endosomal NHX5 and NHX6 are found mainly in the trans-Golgi network and prevacuolar compartments, where they regulate luminal pH, vesicle trafficking, protein sorting, and cell expansion rather than directly removing Na^+ from the cytosol. Their effect on salt tolerance is therefore largely indirect, through proper trafficking of plasma-membrane transporters such as SOS1. Thus, the functions of NHX proteins depend strongly on the specific paralog and its subcellular location, and overexpression results should be interpreted accordingly [57].

3.2.3 HKT Transporters

High-affinity K^+ transporters (HKT proteins) help maintain ionic balance by regulating the distribution of Na^+ and K^+ [58]. HKT1-type transporters primarily mediate Na^+ transport, whereas HKT2-type proteins can function as Na^+-K^+ cotransporters [59]. In rice and wheat, HKT1;5 retrieves Na^+ from root xylem sap, thereby limiting its transport to the shoots [60].

Natural variation in HKT genes contributes substantially to differences in salt tolerance within species, with particular alleles being associated with stronger Na^+ exclusion [61]. Favorable HKT alleles from wild relatives have therefore been introduced into cultivated wheat and rice to improve salt tolerance [62].

3.2.4 AKT/KAT Potassium Channels

Adequate K^+ supply is particularly important for plants exposed to salinity [63]. The AKT (Arabidopsis K^+ transporter) and KAT (K^+ channel in Arabidopsis thaliana) families contribute to K^+ uptake and distribution [64], while high-affinity HAK/KUP/KT transporters also support K^+ acquisition under stress [65].

3.3 Osmolyte Biosynthesis Genes

Osmolyte accumulation is a common stress response because these compatible solutes help stabilize cellular structures and preserve osmotic balance [66]. Major osmolytes include proline, glycine betaine, polyamines, trehalose, and soluble sugars [67].

3.3.1 Proline Metabolism

During stress, proline can accumulate to high concentrations and perform several roles, including osmotic adjustment, ROS scavenging, and molecular chaperoning [68]. Its synthesis and degradation are regulated mainly by Δ^1-pyrroline-5-carboxylate synthetase (P5CS) and proline dehydrogenase (ProDH), respectively [69]. Increased P5CS expression has been associated with improved osmotic stress tolerance in several plant species [70].

3.3.2 Glycine Betaine

Glycine betaine (GB) accumulates in many plant species and helps protect proteins and membranes during stress [71]. Its biosynthesis involves betaine aldehyde dehydrogenase (BADH) and choline monooxygenase (CMO) [72]. Enhancing or introducing GB biosynthetic pathways in species that normally accumulate little GB can improve stress tolerance, although species that naturally accumulate GB are generally more tolerant [73].

3.3.3 Trehalose and Other Sugars

Although trehalose is usually present at low concentrations in plants, it can contribute to both stress protection and signaling [74]. Trehalose metabolism is controlled by trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP) [75]. Other soluble sugars, such as glucose, fructose, and sucrose, also accumulate under stress and support osmotic adjustment and carbon storage [76].

3.4 Aquaporins: Water Channel Proteins

Aquaporins (AQPs) facilitate water transport across membranes and therefore contribute to the maintenance of plant water balance during drought [77]. Plant AQPs comprise several subfamilies, including plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin26-like intrinsic proteins (NIPs), and small basic intrinsic proteins (SIPs) [78].

AQP abundance and activity can change substantially during stress through transcriptional regulation, posttranslational modifications such as phosphorylation and methylation, and protein turnover [79]. Specific AQP isoforms may enhance drought tolerance by supporting root water uptake, cell-to-cell water movement, and the regulation of transpiration [80]. Under severe stress, however, some AQPs are downregulated, which can help limit further water loss [81].

3.5 Late Embryogenesis Abundant (LEA) Proteins

LEA proteins accumulate during seed desiccation and in vegetative tissues exposed to osmotic stress [82]. These intrinsically disordered proteins help protect cellular components from dehydration by sequestering ions, stabilizing membranes, and providing molecular shielding [83]. Different LEA groups, including LEA1-6 dehydrins, have distinct structural characteristics and protective roles [84].

4. Gene Regulatory Networks and Signaling Pathways

4.1 ABA-Dependent Signaling

Abscisic acid (ABA) is a central phytohormone in plant responses to osmotic stress [85]. Stress increases ABA biosynthesis through enzymes such as zeaxanthin epoxidase (ZEP), 9-cis-epoxycarotenoid dioxygenase (NCED), and abscisic aldehyde oxidase (AAO) [86]. NCED is the rate-limiting step in this pathway and is rapidly induced by drought and salinity [87].

ABA is perceived by PYR/PYL/RCAR receptors, which bind ABA and inhibit clade A protein phosphatases 2Cs (PP2Cs) [88]. This inhibition permits SnRK2 kinases to become active and phosphorylate downstream targets, including AREB/ABF transcription factors, ion channels, and NADPH oxidases [89]. The PYR-PP2C-SnRK2 module is broadly conserved across land plants [90]. However, its components are not functionally interchangeable. The 14-member *Arabidopsis* PYR/PYL/RCAR family differs in ABA affinity, dimerization, and PP2C partner preference, allowing individual receptors to establish distinct sensitivity thresholds and tissue-specific responses. Clade A PP2Cs such as ABI1, ABI2, HAB1, and PP2CA also differ in their interactions with SnRK2s and downstream targets, helping regulate the strength and timing of ABA signaling. SnRK2 activation additionally involves ABA-independent basal autophosphorylation of subclass III SnRK2s (SnRK2.2/2.3/2.6), which is normally restrained by PP2C-mediated dephosphorylation. When ABA-bound receptors sequester PP2Cs, this phosphorylation can persist and kinase activity increases. Upstream MAPKKK-like and Raf-like kinases may provide another route to SnRK2 activation during osmotic stress, partly bypassing the canonical receptor-PP2C pathway [81].

ABA-responsive genes contain ABA-responsive elements (ABREs) in their promoters, which are recognized by AREB/ABF and other bZIP transcription factors [91]. ABA signaling regulates stomatal closure, root hydraulic conductivity, seed dormancy, and stress-responsive gene expression [92].

4.2 ABA-Independent Pathways

While ABA plays a central role, significant ABA-independent stress responses exist [93]. DREB2-type transcription factors activate stress genes independently of ABA, responding directly to osmotic stress [45]. Other ABA-independent pathways involve the NAC, MYB, and WRKY transcription factors, which respond to stress through distinct signaling cascades [94].

4.3 Calcium Signaling

Calcium (Ca^{2+}) functions as a universal second messenger in stress signaling [95]. Stress-induced Ca^{2+} signatures—spatial and temporal patterns of cytosolic Ca^{2+} elevation—are decoded by Ca^{2+}

sensors, including calmodulins (CaMs), calmodulin-like proteins (CMLs), calcineurin B-like proteins (CBLs), and Ca^{2+}-dependent protein kinases (CDPKs/CPKs) [96].

CBL-CIPK modules participate in several stress responses, including the SOS pathway, ABA signaling, and ion transport [97]. CDPK/CPK kinases also phosphorylate transcription factors, metabolic enzymes, and ion channels, thereby adjusting stress responses [90]. Different stresses generate distinct Ca^{2+} signatures that are decoded by Ca^{2+} sensors and translated into specific downstream responses [98]. Although CBLs and CDPKs/CPKs both act downstream of Ca^{2+}, their modes of action differ. CBLs are Ca^{2+}-sensing adaptors without catalytic activity and recruit specific CIPKs at the plasma membrane or tonoplast. Pairs such as CBL4-CIPK24/SOS2 and CBL10-CIPK24 preferentially regulate ion transporters and channels, including SOS1, NHX, and AKT1, giving this system an important role in ion homeostasis during salinity [94]. CDPKs/CPKs are single-chain kinases that contain their own calmodulin-like Ca^{2+}-binding domain. Ca^{2+} binding therefore directly relieves autoinhibition, allowing these proteins to act on a broader range of targets, including RBOHs, aquaporins, and stress-responsive transcription factors [45]. CBL-CIPK modules appear particularly well suited to decoding sustained or oscillatory Ca^{2+} signals, whereas some CDPK isoforms respond to rapid Ca^{2+} spikes immediately after stress begins. This distinction allows the two sensor systems to generate partly separate spatial and temporal outputs from related Ca^{2+} signals [93].

4.4 MAPK Cascades

Mitogen-activated protein kinase (MAPK) cascades transduce stress signals through sequential phosphorylation of the MAPKKK-MAPKK-MAPK modules [99]. Multiple MAPK cascades are activated by osmotic stress, regulating transcription factors, enzyme activities, and cytoskeletal reorganization [100]. The MPK3/MPK6 pathways are particularly important in drought and salinity responses, phosphorylating transcription factors and modulating ROS production [101].

4.5 ROS Signaling Networks

While excessive ROS causes cellular damage, controlled ROS production functions in signal transduction [102]. NADPH oxidases (respiratory burst oxidase homologs, RBOHs) generate ROS in response to stress stimuli, with ROS functioning as signaling molecules that activate stress-responsive genes, modulate ion channel activity, and trigger stomatal closure [103].

ROS signaling interacts extensively with the Ca^{2+}, ABA, and MAPK pathways, creating an integrated stress response network [104]. Redox-sensitive transcription factors and kinases respond to ROS levels, adjusting cellular responses based on the degree of oxidative stress [105].

4.6 Hormonal Crosstalk

In higher plants, phytohormones coordinate signaling pathways that integrate osmotic, ionic, and oxidative cues. ABA has a major role in stomatal and transcriptional responses to osmotic stress (Section 4.1), whereas ethylene (ET), jasmonate (JA), and salicylic acid (SA) have distinct and context-dependent functions. Ethylene production increases transiently through stress-induced ACC synthase and ACC oxidase activity, and EIN3/EIL1 can activate ERF genes such as ERF1, ERF5, and TINY (Table 1), supporting ion homeostasis and antioxidant defense at moderate levels. However, prolonged or excessive ethylene signaling can promote senescence and inhibit growth. JA

is synthesized through the LOX-AOS-AOC-OPR3 pathway and perceived through the COI1-JAZ-MYC2 module. It intersects with ABA signaling at several points; for example, ABA can stimulate JA biosynthesis, while MYC2 can activate ABA-responsive genes and promote stomatal closure independently of ABA [106]. SA, produced mainly through the isochorismate pathway, can enhance abiotic stress tolerance by priming antioxidant defenses, supporting photosynthetic stability, and influencing proline and glycine betaine accumulation. Excess SA, however, may interfere with growth-promoting hormone pathways and JA signaling. Under combined salinity and drought, ABA and ethylene can also act antagonistically, so their relative balance may influence the final effects on stomatal behavior and growth [106]. Auxin, cytokinin, and gibberellin signaling generally decline during osmotic stress and interact with ABA, SA, ET, and JA as resources are redirected from growth toward defense. Brassinosteroids, strigolactones, and polyamines can further modify the magnitude of these responses. Overall, this context-dependent hormonal crosstalk helps explain why altering a single hormone pathway can produce different, and sometimes unfavorable, effects on salinity and drought tolerance [107, 108].

5. Posttranscriptional and Epigenetic 5. Posttranscriptional and Epigenetic Regulation

5.1 MicroRNAs in Stress Responses

MicroRNAs (miRNAs) are small noncoding RNAs (20-24 nucleotides) that regulate gene expression post-transcriptionally through mRNA cleavage or translational repression [109]. Numerous miRNAs respond to drought and salinity stress, fine-tuning stress responses by targeting transcription factors, signaling components, and metabolic enzymes [110].

Conserved miRNA families (miR156, miR159, miR169, miR319, miR393, miR396, and miR397) regulate stress responses across plant species [111]. For example, miR169s target the NFYA5 transcription factor, modulating drought tolerance by affecting stomatal aperture and root development [112]. Species-specific miRNAs also contribute to lineage-specific stress adaptations [113].

5.2 Long Non-Coding RNAs

Long noncoding RNAs (lncRNAs) provide an additional layer of regulation in plant stress responses [114]. Generally, longer than 200 nucleotides, these transcripts do not encode proteins but can affect gene expression through processes such as chromatin modification and transcriptional interference. Some lncRNAs also serve as miRNA precursors or function as competing endogenous RNAs (ceRNAs) [115].

Stress-responsive lncRNAs linked to drought and salinity tolerance have been identified in several plant species [116]. Their relatively limited conservation across species suggests that lineage-specific regulatory changes may make an important contribution to stress adaptation [117].

5.3 Alternative Splicing

Alternative splicing (AS) enables a single gene to generate multiple mRNA isoforms, thereby increasing proteomic diversity [118]. Drought and salinity can markedly alter splicing patterns, with many genes displaying stress-dependent changes in AS [119]. Stress conditions can also affect the

abundance or activity of splicing factors, creating feedback that further modifies stress-response pathways [120].

SR proteins (serine/arginine-rich proteins) and heterogeneous nuclear ribonucleoproteins (hnRNPs) contribute to the control of alternative splicing during stress [121]. Stress-induced changes in splicing can affect transcription factors, signaling proteins, and RNA-binding proteins, thereby refining the broader stress-response network [122].

5.4 DNA Methylation and Chromatin Modifications

Epigenetic processes, particularly DNA methylation and histone modification, help regulate the expression of stress-responsive genes [123]. Stress can change DNA methylation patterns, and some of these alterations persist after the stress has ended, indicating a possible role in stress memory [124].

DNA methyltransferases (MET1, CMT3, DRM2) and demethylases (ROS1, DME, DML2, DML3) dynamically regulate methylation patterns [125]. Chromatin remodeling complexes and histone-modifying enzymes (histone acetyltransferases, deacetylases, methyltransferases, and demethylases) alter chromatin accessibility, controlling stress gene expression [126].

5.5 Stress Memory and Priming

Plants can retain a form of "memory" of earlier stress exposure, which can enhance tolerance to a later stress episode (stress priming) [127]. For osmotic stress, mild, sub-lethal exposure to salinity or drought during early growth can prime plants for subsequent, more severe episodes of the same or a related stress, improving ion homeostasis, ROS scavenging, and stomatal regulation during the second exposure [128]. This memory can be maintained for days to weeks (somatic memory) or transmitted across generations (transgenerational memory) [129]. Epigenetic modifications, particularly DNA methylation, histone modifications, and small-RNA-directed chromatin states, underlie stress memory phenomena [130].

Primed plants show faster and stronger transcriptional responses to recurring stress, involving transcriptional memory genes that remain in accessible chromatin states [115]. Some stress-induced epigenetic changes are heritable, potentially facilitating rapid adaptation to changing environments. However, the proportion of priming responses that are truly transgenerational rather than somatic or intergenerational—remains an active area of investigation [131].

6. Pangenomics and Structural Variation in Stress Tolerance

6.1 Pangenomic Approaches

Pangenomics analyzes genetic diversity across multiple individuals or accessions, revealing structural variations, presence–absence variations (PAVs), and copy number variations (CNVs) not captured by single reference genomes [132]. Pangenome studies in rice, wheat, soybean, and other crops have identified thousands of dispensable genes—genes present in some but not all accessions [133].

Many stress-responsive genes are associated with PAV, and stress-tolerant accessions possess unique genes absent in sensitive varieties [134]. For example, rice pangenome analyses revealed that salinity tolerance-associated genes are present only in salt-tolerant cultivars [135], a conclusion

corroborated by a combined eQTL-GWAS analysis of a 251-accession rice super pan-genome, which identified expression-associated structural variants at multiple salt-tolerance loci that were not resolvable using a single linear reference genome [136]. Wheat pangenomics identified drought tolerance-associated genes whose CNV patterns correlated with environmental adaptation (Figure 3) [137].

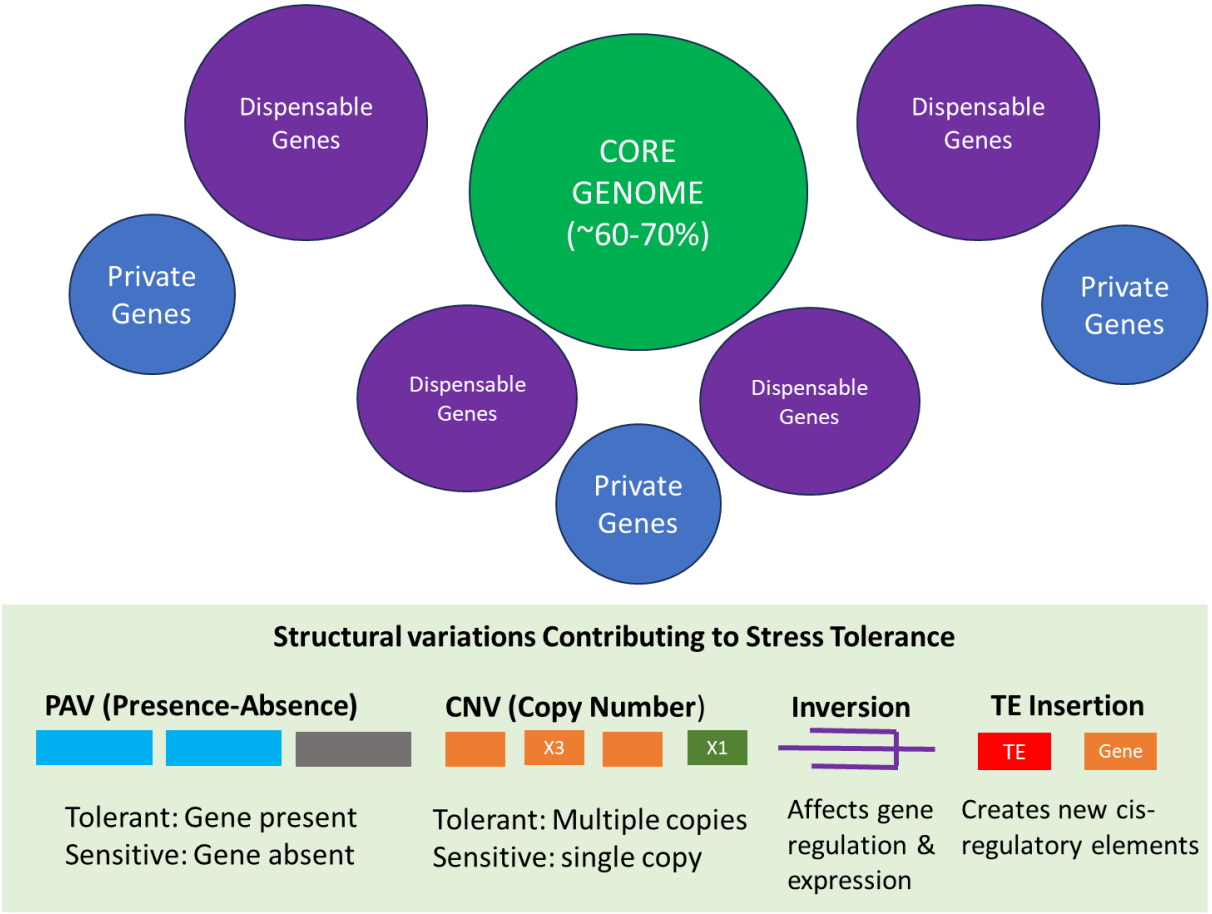

Figure 3 Pangenomic landscape of stress-tolerance genes: Conceptual diagram illustrating core genes (present in all accessions), dispensable genes (present in some accessions), and private genes (accession-specific) related to stress tolerance. Examples of structural variations (PAVs, CNVs, inversions) affecting stress gene expression are highlighted.

6.2 Structural Variations and Stress Adaptation

Large structural variations (SVs), including insertions, deletions, inversions, and translocations, significantly contribute to phenotypic diversity and stress adaptation [138]. SVs can affect gene expression through altering regulatory elements, creating new gene fusions, or disrupting gene function [139].

Specific structural variants (SVs) have been linked to stress-related traits. Examples include HKT1;5 translocations associated with Na^+ exclusion in wheat, inversions near flowering-time genes that affect drought escape in barley, and NHX duplications associated with salt tolerance in wild tomato [140]. Detecting these variants requires advanced sequencing and analytical methods, and long-read sequencing has substantially improved their identification [136].

6.3 Transposable Elements in Stress Responses

Transposable elements (TEs) constitute a substantial fraction of many plant genomes and contribute to genetic diversity as well as stress adaptation [141]. Their movement can create new regulatory elements, modify gene-expression patterns, and generate genomic novelty [142]. Some stress-responsive genes have also arisen through TE-mediated duplications or insertions that introduce stress-responsive regulatory sequences [143].

Stress can increase TE activity, potentially generating new genetic variation that may contribute to adaptation [144]. Such mobilization is not always beneficial, however, and plants use mechanisms such as DNA methylation and small interfering RNAs (siRNAs) to keep TEs under control [145].

7. Evolutionary Perspectives on Stress Adaptation

7.1 Gene Family Evolution and Neofunctionalization

Many stress-responsive genes occur in large families that have expanded through tandem or segmental duplication [146]. After duplication, individual paralogs may acquire new functions through neofunctionalization, divide the ancestral functions through subfunctionalization, or become pseudogenes [147].

Compared with housekeeping genes, stress-responsive gene families have accelerated evolution rates, with positive selection acting on specific functional domains [148]. For example, the DREB, NAC, and NHX gene families have expanded independently in different plant lineages, with lineage-specific paralogs acquiring specialized stress-responsive functions [149].

Whole-genome duplications (WGDs) have been major drivers of gene family expansion in angiosperms [150]. Ancient polyploidy events in cereal genomes, legumes, and Brassicaceae contributed to stress gene repertoire expansion [151]. However, most duplicated genes have been lost over evolutionary time, with retention biased toward genes involved in stress responses, transcriptional regulation, and signal transduction [152].

7.2 Convergence Evolution in Stress Tolerance

Comparative genomics reveals convergent evolution of stress tolerance mechanisms across distantly related lineages [153]. Halophytes from different families independently evolved enhanced Na^+ transport capacity, vacuolar sequestration, and compatible solute accumulation [154]. Similarly, desert plants convergently evolved CAM photosynthesis, succulent structures, and specialized root systems [155].

At the molecular level, distantly related stress-tolerant plants often rely on similar transcription-factor networks and signaling pathways even when their underlying gene sequences differ [156]. This convergence points to functional constraints on stress adaptation and emphasizes a set of core pathways that are repeatedly used to tolerate environmental stress (Figure 4) [157].

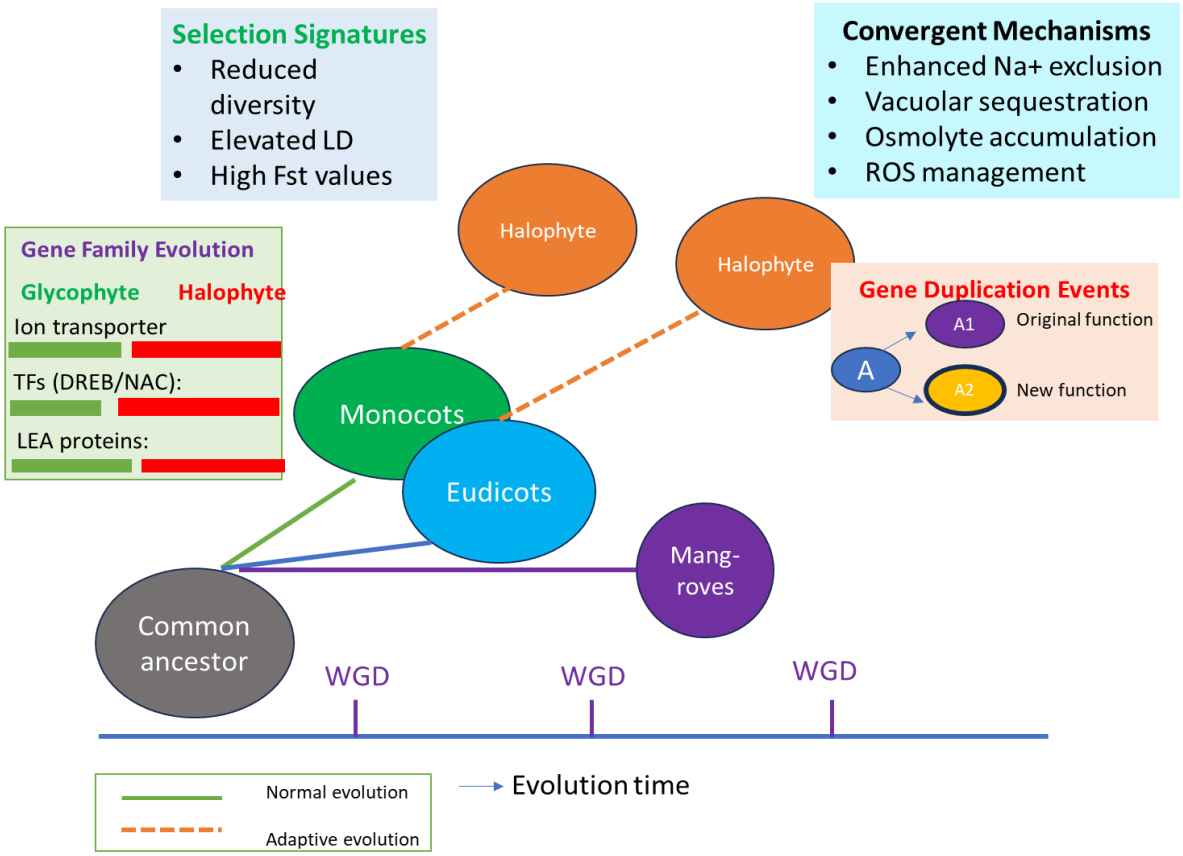

Figure 4 Evolutionary trajectories of stress tolerance mechanisms: Phylogenetic tree showing convergent evolution of salt tolerance across different plant lineages (monocots, dicots, halophytes) with gene family expansions, neofunctionalization events, and highlighted lineage-specific innovations.

7.3 Natural Selection Signatures in Stress Genes

Population genomic studies can identify genes that have undergone positive selection in stress-adapted populations [158]. Signatures of selective sweeps, such as reduced nucleotide diversity, increased linkage disequilibrium, and skewed allele-frequency distributions, provide evidence for recent strong selection [159].

Several important stress-tolerance genes, including HKT1;5, BADH, DREB, and NAC, show signatures of selection in locally adapted populations [160]. Environmental association analyses can connect particular alleles with climatic variables, helping to reveal the genomic basis of local adaptation [161]. These naturally selected variants are potentially useful sources for crop improvement [162].

7.4 Trade-Offs and Evolutionary Constraints

Adaptation to stress can involve trade-offs among growth, reproduction, and defense [163]. Constitutive activation of stress-protection mechanisms can reduce fitness when conditions are favorable, which favors regulatory systems that induce these responses only when needed [164]. Such growth-defense antagonism contributes to trade-offs between growth-promoting processes and stress-response pathways [165].

Other trade-offs arise when plants allocate limited resources among different forms of stress tolerance, such as drought versus salinity or biotic versus abiotic stress, as well as between water-use efficiency and carbon assimilation or between early and late reproduction [166]. Recognizing these constraints is important for breeding because improving one trait can sometimes reduce performance in another [167].

8. Comparative Genomics: Lessons from Halophytes and Xerophytes

8.1 Halophyte Model Systems

Halophytes are naturally adapted to saline environments and therefore provide useful models for studying salt tolerance [168]. Representative systems include Thellungiella salsuginea (Eutrema salsugineum), Salicornia and Suaeda species, and mangroves [169]. Comparative genomic studies of halophytes and related glycophytic plants have revealed genetic and regulatory features associated with extreme salt tolerance [170].

Halophyte genomes often show expansion of ion-transporter families such as HKT, NHX, and AKT, together with relatively high expression of protective genes even under nonstress conditions [171]. Compared with Arabidopsis, Lllungiella has been reported to maintain higher constitutive expression of stress-responsive genes, which may allow a more rapid response when stress develops [172].

Genomic studies of mangroves have identified distinctive adaptations, including genes associated with vivipary, enhanced lignin biosynthesis for structural support, and specialized pathways involved in salt-gland development [173]. These features broaden the range of salt-tolerance mechanisms that could potentially inform crop improvement [174].

8.2 Xerophyte Adaptations

Xerophytes are adapted to dry environments and use a range of strategies, including CAM photosynthesis, succulence, deep rooting, and mechanisms that allow tissues to tolerate severe dehydration [175]. Comparative genomic studies of plants such as Opuntia (cactus), Welwitschia mirabilis, and resurrection plants have uncovered a variety of specialized adaptations to water limitation [176].

Resurrection plants such as Craterostigma, Boea, and Sporobolus can survive extreme dehydration through mechanisms that include constitutive LEA protein expression, trehalose accumulation, and production of protective metabolites [177]. Their genomes contain expanded LEA gene families and distinctive regulatory elements associated with desiccation responses [178]. These mechanisms are being explored as potential strategies for improving desiccation tolerance in crops [179].

8.3 Translating Extremophile Knowledge to Crops

Using stress-tolerance mechanisms from extremophile plants in crops is challenging because of genetic complexity, potential yield penalties, and metabolic costs [180]. Even so, examples such as introgression of favorable wild-relative alleles, expression of halophyte ion transporters in crops, and transfer of resurrection-plant mechanisms into desiccation-sensitive species illustrate the potential of this strategy [181].

Synthetic biology strategies that combine several stress-tolerance genes from extremophile plants may offer new routes toward climate-resilient crops [182]. For successful transfer, however, it is important to understand not only the stress-response genes themselves but also the regulatory features that control their activity in extremophile species [183].

9. Multi-Omics Integration and Systems Biology

9.1 Transcriptomics and Co-Expression Networks

RNA sequencing has produced large transcriptome datasets covering many stress conditions and genotypes [184]. Co-expression analyses use these datasets to identify groups of genes that change together, providing clues about functional relationships and regulatory hierarchies [185]. Highly connected hub genes often encode important transcription factors or signaling components [186].

Weighted gene co-expression network analysis (WGCNA) has identified stress-responsive modules that are conserved among species as well as modules that are specific to particular stress conditions [187]. Combining these networks with metabolomic and proteomic data can connect changes in gene expression with downstream metabolic and phenotypic responses (Figure 5) [188].

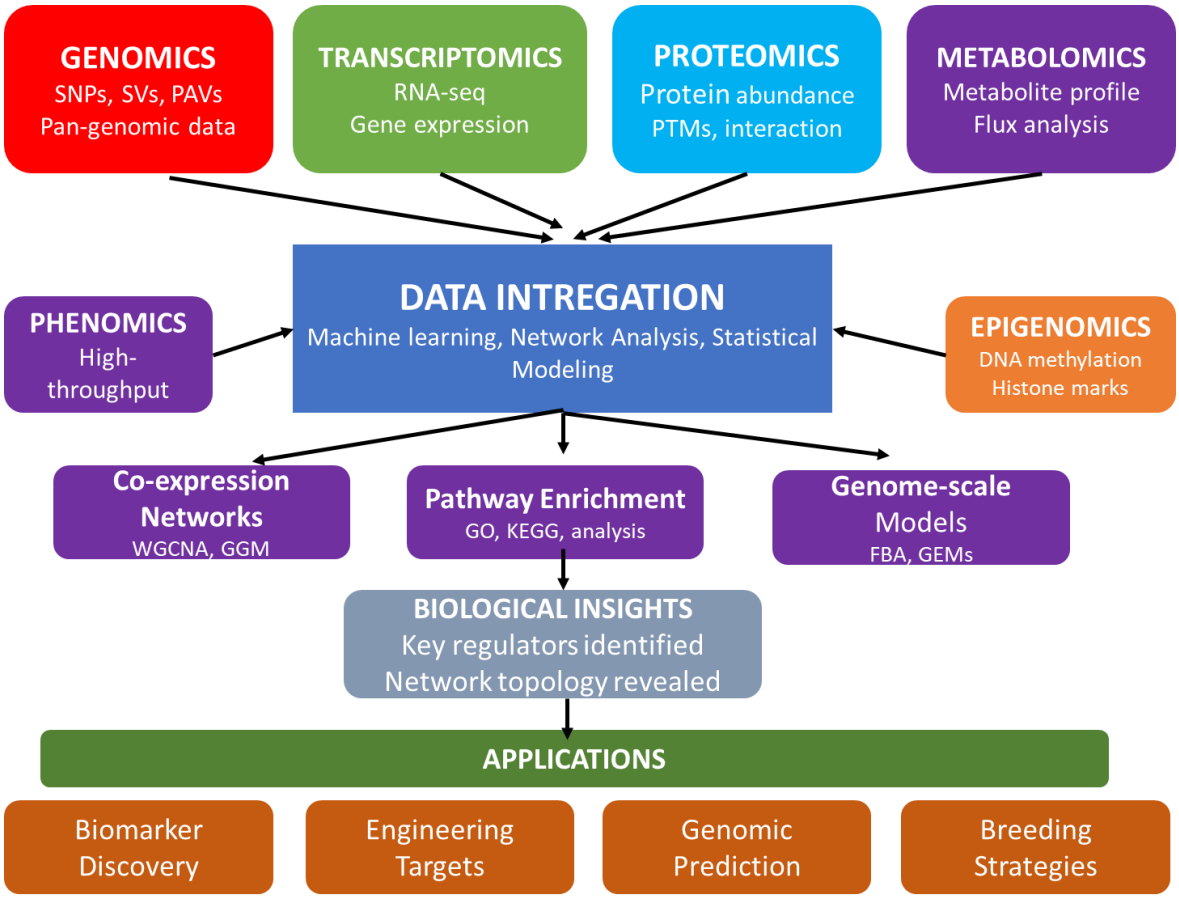

Figure 5 Multiomics integration for understanding stress responses: Framework showing the integration of genomics, transcriptomics, proteomics, metabolomics, and phenomics data through systems biology approaches to identify key regulators and predict stress tolerance phenotypes.

9.2 Proteomics and Posttranslational Modifications

Proteomic analyses often show that changes in protein abundance do not closely mirror transcript-level changes, emphasizing the importance of posttranscriptional and posttranslational regulation [189]. Stress can rapidly alter proteins through phosphorylation, ubiquitination, SUMOylation, and other modifications, thereby changing their activity, localization, or stability [190].

Phosphoproteomic studies have identified thousands of stress-regulated phosphorylation sites on signaling proteins, transcription factors, and metabolic enzymes [191]. These modifications can produce rapid changes in protein activity without requiring new transcription [192]. Redox proteomics has also revealed oxidative modifications of proteins under stress, some of which appear to have regulatory roles [193].

9.3 Metabolomics and Flux Analysis

Metabolomic profiling can quantify hundreds or even thousands of metabolites and reveal the metabolic reprogramming associated with stress [194]. Compatible solutes, amino acids, organic acids, and secondary metabolites can change markedly during osmotic stress [195]. Metabolite-QTL (mQTL) analysis further connects genetic variation with differences in metabolic phenotypes [196].

Metabolic flux analysis based on isotope labeling follows carbon and nitrogen movement through metabolic pathways and can reveal stress-induced changes in pathway activity [197]. Integrating these measurements with transcriptomic and proteomic data provides a more complete systems-level view of stress responses [198].

9.4 Integrated Multiomics Models

Systems biology combines multiple omics layers to build integrated models of plant stress-response networks [199]. Such models can help predict gene functions, reveal regulatory interactions, and guide engineering strategies [200]. Machine-learning and network-based approaches can also identify candidate regulators and predict stress phenotypes from molecular profiles [201].

Genome-scale metabolic models (GEMs) simulate cellular metabolism under different conditions, allowing researchers to estimate metabolic fluxes and identify possible points for optimization [202]. Linking GEMs with transcriptional regulatory networks can produce dynamic models that represent several layers of metabolic and regulatory control [203].

10. Natural Variation and Quantitative Trait Loci

10.1 QTL Mapping for Stress Tolerance

Quantitative trait locus (QTL) mapping in biparental populations has identified hundreds of genomic regions associated with stress-tolerance traits [204]. Major QTLs affecting Na^+ exclusion, osmotic adjustment, and root architecture have been mapped and, in some cases, cloned. Because many stress-tolerance traits are influenced by numerous small-effect QTLs, however, their genetic architecture can make breeding more difficult [205].

10.2 Genome-Wide Association Studies

Genome-wide association studies (GWASs) use historical recombination in diverse germplasm to achieve finer mapping resolution than many biparental QTL studies [206]. These analyses have identified numerous loci associated with stress tolerance, including known candidates such as HKT1;5, DREB, and NAC as well as previously unrecognized genes [207].

Multi-environment GWAS can account for genotype-environment interactions and distinguish broadly expressed stress-tolerance loci from loci whose effects depend strongly on the environment [208]. Combining GWAS with transcriptomic data through eQTL analysis can further identify regulatory variants that influence stress-gene expression [209].

10.3 Genomic Selection and Prediction

Genomic selection uses genome-wide marker information to estimate breeding values, allowing selection decisions to be made before phenotyping [210]. For complex stress-tolerance traits, genomic prediction can outperform marker-assisted selection based on a small number of major QTLs [211]. Its accuracy depends on factors such as training-population design, statistical modeling, and marker density [212].

Multi-trait and multi-environment genomic prediction models leverage genetic correlations between traits and environments, improving prediction accuracy [213]. The integration of high-throughput phenotyping with genomic prediction accelerates breeding cycles [214].

11. Crop Improvement Strategies: From Discovery to Application

11.1 Conventional Breeding and Wild Relative Introgression

Conventional breeding continues to be important for crop improvement, while genomic tools can make selection more efficient [215]. Wild relatives contain substantial genetic diversity for stress tolerance that has accumulated through long-term natural selection [216]. Wide crosses and related introgression strategies have already transferred useful wild alleles into wheat, rice, tomato, and other crops [217].

Pre-breeding programs use the diversity present in wild relatives to develop introgression lines and advance backcross populations [218]. Genomic tools help track these wild genomic segments and can reduce linkage drag between desirable stress-tolerance traits and unfavorable agronomic characteristics (Figure 6) [219].

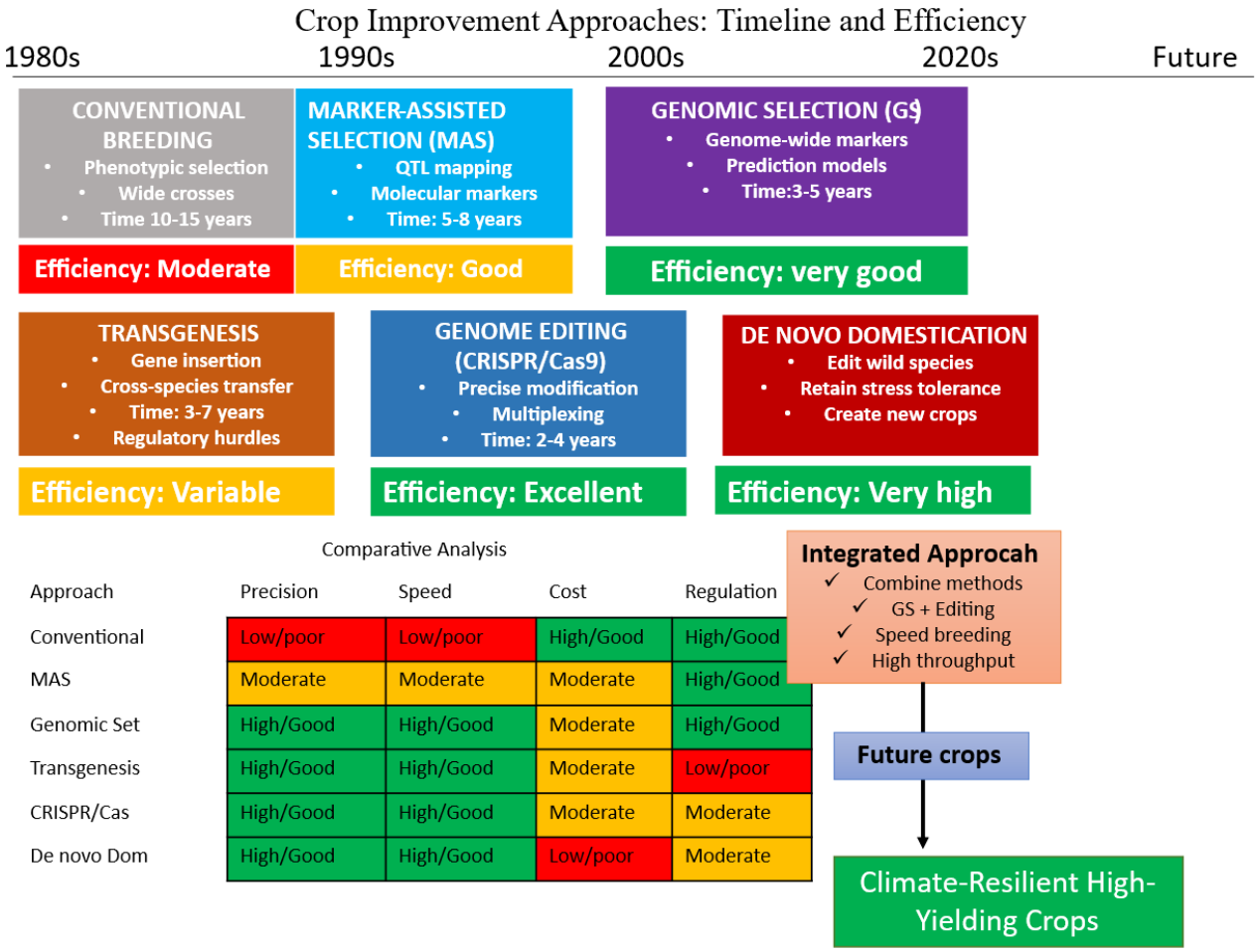

Figure 6 Breeding strategies for climate-resilient crops: Comparison of conventional breeding, marker-assisted selection, genomic selection, transgenesis, genome editing, and *de novo* domestication approaches for developing stress-tolerant crops. Timeline and efficiency considerations are indicated.

11.2 Transgenesis and Biotechnology

Genetic transformation can introduce stress-tolerance genes from different organisms, thereby overcoming barriers imposed by sexual incompatibility [220]. Early transgenic approaches often focused on overexpressing individual genes, such as DREB, LEA, or ion transporters, and generally produced measurable but modest improvements [221]. Because constitutive expression can also restrict growth, stress-inducible promoters are often favored [222].

Second-generation transgenic approaches combine multiple genes within a metabolic pathway, such as proline biosynthesis, or within a regulatory cascade, with the aim of producing stronger tolerance than single-gene strategies [29]. Transgenic crops with improved drought or salinity tolerance have been developed in several species, although only a limited number have progressed to commercialization [223].

11.3 Genome Editing for Precision Breeding

CRISPR/Cas9 and other genome-editing systems allow targeted changes to plant genomes, including gene knockouts, base editing, and prime editing [224]. Unlike conventional transgenesis,

genome editing can generate alleles that are indistinguishable from naturally occurring mutations, which may simplify some regulatory considerations [225].

Examples include the disruption of negative regulators such as OsBADH2 to increase proline accumulation and OsDST to alter stomatal regulation, as well as editing cis-regulatory elements to modify gene expression and generating HKT or NHX alleles with improved activity [226, 227]. Multiplex genome editing can modify several genes at once, making it possible to assemble favorable allele combinations [228].

Base editing and prime editing enable precise nucleotide changes without introducing conventional double-strand breaks, extending genome-editing applications to both promoter and coding regions [229]. Emerging methods for editing organellar genomes may also provide new opportunities to improve photosynthetic performance under stress [230].

11.4 De Novo Domestication

De novo domestication of stress-tolerant wild species through genome editing represents a paradigm shift in crop development [231]. By editing key domestication genes in extremophiles, researchers have aimed to create crops that combine wild stress tolerance with domesticated productivity and quality [232].

Proof-of-concept studies have edited flowering, seed shattering, and plant architecture genes in wild tomato relatives, quinoa, and groundcherry [233]. This approach could rapidly develop crops adapted to marginal lands unsuitable for conventional agriculture [234].

11.5 Synthetic Biology and Systems Approaches

Synthetic biology enables the rational design of stress tolerance circuits that combine promoters, transcription factors, and downstream effectors [235]. Approaches include synthetic stress-responsive promoters with improved dynamics, protein scaffolds that organize metabolic enzymes for increased flux, and synthetic oscillators that prevent growth penalties from constitutive stress responses [236].

Systems biology-guided engineering uses computational models to identify optimal modification strategies for predicting the effects of multiple genetic changes [237]. Digital twins—computational models of specific genotypes—could guide personalized breeding strategies [238].

11.6 Comparative Effectiveness of Breeding and Engineering Strategies: Case Evidence

The strategies described above (Sections 11.1-11.5) differ substantially in terms of development timelines, regulatory burden, and field-validated effectiveness, and these trade-offs are best illustrated with specific cases rather than treated as broadly interchangeable options. Marker-assisted backcrossing of the Saltol QTL (encompassing OsHKT1;5) from the landrace Pokkali into high-yielding rice mega-varieties (e.g., BRRI dhan, IR29 backgrounds) has produced seedling-stage salt-tolerant derivatives within 3-5 backcross generations, illustrating the speed advantage of marker-assisted introgression when a major QTL of known effect is already characterized. However, gains are typically limited to the specific stress component (here, Na^+ exclusion) controlled by the introgressed locus. Pre-breeding from crop wild relatives has delivered a comparable example in wheat: introgression of the Nax1 and Nax2 loci from Triticum monococcum into durum wheat

reduced leaf blade Na^+ concentration by roughly half and increased grain yield by approximately 25% under saline field conditions, demonstrating that wild-relative introgression can achieve field-level yield protection, albeit over a longer pre-breeding timeline needed to break linkage drag from the wild donor. Single-gene transgenic approaches, such as vacuolar AtNHX1 overexpression in tomato, improved salt tolerance and maintained fruit yield under high salinity in controlled trials, showing strong proof-of-concept effectiveness, but, consistent with the broader pattern noted in Section 11.2, most such single-gene transgenics have not reached commercial cultivation, reflecting regulatory, cost, and multigenic-trait-complexity barriers rather than a lack of biological efficacy. Genome editing offers a faster, often non-transgenic alternative: CRISPR/Cas9 knockout of the negative regulator OsRR22 in rice conferred heritable salt tolerance without introducing foreign DNA, illustrating how targeted disruption of a single negative regulator can phenocopy the effect of multigene engineering while simplifying the regulatory pathway in jurisdictions that exempt edited-but-transgene-free lines. Overall, the case evidence indicates that marker-assisted and genome-editing approaches currently offer the most favorable balance of speed, precision, and (for editing) regulatory tractability for single, well-characterized loci, whereas pre-breeding remains the more effective route for capturing polygenic, field-relevant tolerance from wild germplasm, and transgenic overexpression—despite strong experimental efficacy—faces the steepest path to deployment [103].

12. Climate Change Implications and Future Challenges

12.1 Projected Climate Scenarios

Climate projections indicate rising temperatures, changes in precipitation, more frequent extreme weather events, and increasing atmospheric CO_2 concentrations by the end of this century [103]. Together, these changes are expected to intensify drought and salinity in many agricultural regions and increase risks to food security [239].

Sea-level rise is increasing the risk of saltwater intrusion in coastal regions, while inland areas may face greater evapotranspiration and soil salinization associated with irrigation [240]. Heat stress can also interact with drought and salinity, producing combined stress conditions that are often more damaging than individual stresses [241].

12.2 Adapting Agriculture to Climate Change

Meeting future food demands under climate change will require a combination of approaches, including stress-resilient crops, more efficient water use, adapted crop-management practices, and productive use of marginal lands [242]. Genomic approaches can contribute by enabling precision breeding for specific environments, developing varieties with tolerance to multiple stresses, and targeting crops to increasingly extreme conditions [243].

Climate-smart agriculture can bring together stress-tolerant varieties, conservation practices, precision irrigation, and agroecological management [244]. Diversifying cropping systems with underused stress-tolerant crops, including quinoa, pearl millet, and Bambara groundnut, can further strengthen resilience [245].

12.3 Ethical and Regulatory Considerations

The development of stress-tolerant crops, particularly transgenic and genome-edited varieties, raises important ethical and regulatory questions [246]. Meeting food-security needs while accounting for environmental risks, farmer rights, and public acceptance will require transparent governance [247]. Because regulatory frameworks for genome-edited crops differ among countries, these differences can affect how readily such technologies are adopted [248].

Equitable access to improved varieties is also an important concern, particularly regarding intellectual property and the distribution of benefits to vulnerable smallholder farmers [249]. Participatory breeding, which involves farmers in variety development, can improve adoption while helping ensure that new cultivars respond to local needs [250].

13. Conclusions and Future Directions

Over the past two decades, genomic research has greatly expanded our understanding of how plants adapt to salinity and drought. High-throughput sequencing, genome editing, and systems biology have helped link individual stress-response genes with broader regulatory networks and genome-wide patterns of tolerance. Several major themes have emerged from this progress:

Complex genetic architecture: Stress tolerance is governed by hundreds or thousands of interacting genes, with substantial redundancy and compensation among pathways.

Multilayered regulation: Transcriptional, posttranscriptional, translational, and epigenetic processes act together to control stress responses, allowing plants to adjust rapidly while also supporting longer-term adaptation.

Evolutionary innovations: Gene-family expansion, neofunctionalization, and changes in regulatory systems have generated diverse mechanisms of stress tolerance across plant lineages.

Natural variation: Crop germplasms and wild relatives contain extensive allelic diversity in stress-related genes, providing a substantial but still underused resource for crop improvement.

Pangenomic diversity: Structural variation, presence-absence variation, and copy-number variation can make important contributions to stress tolerance in addition to conventional SNP variation.

Despite these advances, important gaps remain. Mechanistic understanding: The functions of many stress-responsive genes are still unknown, and interactions between combined stresses such as heat-drought or salinity-pathogen stress remain poorly characterized.

Long-distance signaling that coordinates stress responses across the whole plant is another area that requires further investigation.

Genotype-to-phenotype prediction: Predicting stress tolerance from genomic information remains difficult because of genetic complexity, environmental interactions, and developmental effects. More accurate models that integrate multiomic information with environmental variables are needed.

Translation to crops: Many discoveries made in model plants have not yet translated effectively into crop improvement. A better understanding of regulatory context and more effective gene-deployment strategies should help close this gap.

Field performance: Stress tolerance demonstrated under laboratory conditions does not always translate into higher field yields because stress timing is unpredictable, multiple stresses occur

together, and growth-defense trade-offs can limit performance. Breeding programs therefore need to evaluate plants under realistic field stress conditions.

Climate adaptation: Developing crops for future climates requires anticipation of new combinations of stresses and environmental conditions. Speed breeding and genomic selection can help shorten the time needed to develop varieties suited to these changing conditions.

Sustainable intensification: Increasing stress tolerance while maintaining yield potential, resource-use efficiency, and environmental sustainability will require systems-level approaches that bring genomics together with agronomy and ecology.

Future research directions include the integration of emerging technologies such as long-read sequencing for improved structural-variation detection, spatial transcriptomics for tissue-specific analysis, single-cell omics for cell-type resolution, and proteogenomics for more accurate gene annotation, which could substantially deepen our understanding of stress adaptation.

Integration of emerging technologies: Long-read sequencing can provide more comprehensive structural-variation detection, while spatial transcriptomics can resolve tissue-specific responses; single-cell omics can provide cell-type resolution, and proteogenomics can improve gene annotation.

Artificial intelligence applications: Machine-learning approaches could assist genotype-to-phenotype prediction, image-based phenotyping, and the optimization of breeding strategies.

Microbiome engineering: Manipulating plant-associated microbiomes may improve stress tolerance by enhancing nutrient acquisition, hormone production, and stress priming.

Synthetic biology: Synthetic approaches could be used to design compact stress-response circuits, engineer new tolerance mechanisms, and develop stress-adaptive crops through rational biological design.

Evolutionary-guided engineering: Evolutionary principles can help identify feasible engineering strategies while reducing the risk of introducing changes that are maladaptive under realistic environmental conditions.

As climate change intensifies, genomic approaches to understanding and enhancing plant stress tolerance are increasingly critical. Continued investment in fundamental research, technology development, and translation to agriculture will be essential for ensuring global food security in a changing climate.

Author Contributions

Md Arif Sakil: conceptualization, investigation, supervision, writing - original draft, writing - review & editing; Shagata Islam Shorna, Maisha Rahman, Tahmina Akter, Prodipto Bishnu Angan, Arpita Rani Roy, and Mohammed Arif Sadik Polash: writing - original draft, writing - review & editing. All the authors critically revised and approved the final version of the manuscript.

Competing Interests

The authors declare no competing interests related to this research.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

AI-Assisted Technologies Statement

Artificial intelligence (AI) tools were used solely for basic grammar correction and language refinement in the preparation of this manuscript. Specifically, OpenAI's ChatGPT was employed to improve the readability and linguistic clarity of the English text. All scientific content, data interpretation, and conclusions were developed independently by the author. The authors have thoroughly reviewed and edited the AI-assisted text to ensure its accuracy and accept full responsibility for the content of the manuscript.

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