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Review Article

Assessment of omics and genome editing approaches for addressing climate challenges: Enhancing stress tolerance in tea (*Camellia sinensis* (L.) O. Kuntze)

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Abstract

Tea (*Camellia sinensis* (L.) O. Kuntze) is a significant global crop that encounters various abiotic stresses, including drought, salinity, extreme temperatures, heavy metals, and UV radiation. These stresses interfere with physiological and biochemical processes, photosynthesis, carbon metabolism, water relations, osmotic balance, oxidative homeostasis, and hormonal regulation. Recent advancements in molecular biology have elucidated the mechanisms underlying stress tolerance in tea plants, emphasizing stress-responsive genes, transcription factors, small RNAs, and epigenetic modifications. Biotechnological strategies, such as genetic engineering, CRISPR/Cas9 genome editing, in vitro selection, and marker-assisted selection, present opportunities to develop stress-resistant tea cultivars. Omics approaches offer insights into stress signaling networks and assist in identifying key biomarkers. The application of growth regulators and antioxidants, along with beneficial microorganisms, such as arbuscular mycorrhizal fungi (VAM), plant growth-promoting rhizobacteria, and endophytes, mitigates the impacts of stress. These methods employ agronomic techniques, such as irrigation management and soil amendments. Integrating these technologies with climate adaptation frameworks is essential for enhancing stress tolerance and sustaining tea productivity under evolving environmental conditions. This review underscores the role of omics and genome editing in advancing research to improve tea cultivation and support its resilience against 21st Century climate changes.

Keywords: Oxidative stress, Transcription factors, CRISPR/Cas9, Marker-assisted selection, Stress tolerance, Climate resilience

Introduction

Camellia sinensis (L.) O. Kuntze, commonly known as tea, is the most widely consumed non-intoxicating beverage globally and serves as a vital plantation crop supporting the economies of tropical and subtropical nations such as India, China, Kenya, and Sri Lanka. The production of tea faces significant challenges from biotic and abiotic stresses that adversely affect growth, yield, and quality (Sahoo *et al.,* 2024). Climate change further intensifies abiotic stresses, including drought, elevated temperatures, cold, soil acidity, salinity, UV radiation, and nutrient imbalances (Chen *et al.,* 2021). These stresses impede the physiological and biochemical functions of tea plants and influence the biosynthesis of essential secondary metabolites, such as catechins, theaflavins, and aroma compounds, which are critical to tea quality (Han *et al.,* 2022). Drought and heat stress particularly impact tea by causing stomatal closure, impaired photosynthesis, oxidative stress, and reduced leaf flush in rain-fed regions. Additionally, cold and frost stress in high-altitude plantations result in leaf damage, diminished cambial activity, and winter dormancy, thereby affecting productivity (Li *et al.,* 2023). Soil-related challenges, including acidity, aluminum toxicity, and nutrient deficiencies (notably nitrogen, potassium and phosphorus), contribute to productivity issues. Additionally, salinity and elevated ozone levels adversely affect root growth, chlorophyll stability, and antioxidant defense systems (Zhang *et al.,* 2020). Tea plants exhibit adaptive responses to stress at both physiological and molecular levels, such as the accumulation of osmolytes like proline and glycine betaine, activation of antioxidant enzymes (superoxide dismutase, peroxidase, and catalase), hormonal signaling (abscisic acid, salicylic acid, and jasmonates), and the expression of stress-responsive genes and transcription factors, including WRKY, NAC, and MYB-p53 groups (Chen *et al.,* 2021; Li *et al.,* 2023). Recent advancements in biotechnology and genomics have elucidated stress-responsive pathways in tea, facilitating the identification of quantitative trait loci (QTLs), single nucleotide polymorphisms (SNPs), and candidate genes associated with drought and temperature tolerance. Approaches, such as transcriptome sequencing, metabolomics, CRISPR/Cas9 editing, and marker-assisted breeding, are being pursued to develop tea cultivars resilient to climatic challenges (Sahoo *et al.,* 2024). Given the economic significance of tea and the impact of abiotic stress due to climate change, a systematic review of research on abiotic stresses affecting tea growth, physiology, biochemistry, and productivity is essential. This synthesis can inform comprehensive strategies, including genetic enhancement, agronomic practices, and biotechnological interventions, to support sustainable tea production amid climate variability (Chen *et al.,* 2021; Sahoo *et al.,* 2024). *C. sinensis* is increasingly vulnerable to abiotic stressors resulting from climate change and soil degradation, which are further intensified by intensive cultivation methods impacting growth, yield, and quality. Despite advancements in understanding stress responses and tolerance mechanisms, the application of this knowledge to enhance agricultural practices remains challenging. This review examines the physiological, biochemical, and molecular regulation mechanisms in tea plants' responses to abiotic stress and explores intervention strategies based on current research. Studies have concentrated on stress factors affecting tea cultivation, their impacts, and adaptive responses, including regulatory networks and omics approaches that reveal stress-responsive cascades in tea bushes. We investigated biotechnological approaches, such as genetic engineering, CRISPR/Cas9 editing, marker-assisted selection, and in vitro screening, to develop stress-tolerant varieties and agronomic interventions to mitigate stresses. The study aimed to identify knowledge gaps and research priorities for incorporating stress tolerance traits into tea improvement programs and to provide guidelines for researchers and agronomists to enhance tea production resilience under various conditions (Figure 1).

Various abiotic stresses impacting tea

Drought stress

In tropical and subtropical regions, particularly in tea plantations dependent on rainfall, drought represents a significant abiotic stressor. As a perennial crop, tea experiences considerable reductions in leaf level, photosynthetic efficiency, and yield during extended dry periods (Sahoo *et al.,* 2024). Climate change projections suggest a substantial increase in drought intensity in key tea-producing areas, including South Asia and East Africa. This development poses a long-term threat to the sustainability of tea plantations, primarily due to climate variability (Han *et al.,* 2022).

Temperature stress

Tea, a perennial crop, thrives in diverse agro-ecological zones and is highly sensitive to temperature fluctuations. The optimal temperature range for growth is 18-30 °C. However, prolonged exposure to temperatures exceeding 35 °C or falling below 10 °C can result in physiological damage, thereby substantially reducing leaf production and quality (Sahoo *et al.,* 2024). Soil temperature significantly affects the growth, physiology, and yield of tea crops, particularly under challenging conditions such as extreme heat or cold (Huang *et al.,* 2024). Temperature stress induced by climate change poses a threat to the sustainability of the tea industry, with forecasts indicating an increase in the frequency and severity of heat waves and frost events in tea-growing regions (Han *et al.,* 2022).

Effect of high temperature

The growth of tea plants is adversely impacted by heat and drought, particularly in regions dependent on rainfall (Jayasinghe & Kumar, 2021). Elevated temperatures disrupt photosynthesis by destabilizing photosystem II, hindering chlorophyll production, and accelerating photorespiration (Li *et al.,* 2023). High temperatures also increase transpiration, leading to rapid water loss and stomatal closure, which restricts carbon assimilation. Extreme heat promotes the generation of reactive oxygen species (ROS), resulting in lipid peroxidation, protein denaturation, and membrane damage (Zhang *et al.,* 2020). Biologically, heat stress affects the biosynthesis of secondary metabolites. Studies have demonstrated decreased levels of catechins and theaflavins, along with reduced volatile aroma compounds, thereby impacting the flavor and commercial value of tea (Han *et al.,* 2022). At the molecular level, heat shock proteins (HSPs), which function as molecular chaperones for protein-folding protection, are activated, and transcription factors governing downstream protective genes, including HSF, WRKY, and bZIP, are upregulated (Chen *et al.,* 2021). Developing heat-resistant cultivars and implementing agronomic practices, such as shade management and mulching, is essential to mitigating the adverse effects of elevated temperatures.

Effects of low temperature

Frosty nights and low temperatures pose a threat to tea plantations situated at high elevations. Exposure to cold temperatures ranging from −10 to 10 °C during winter leads to chlorosis, diminished cambial activity, and dormancy in leaf growth, consequently shortening the productive period (Sahoo *et al.,* 2024). Frost stress results in membrane stiffening and ice crystal formation, thereby damaging cellular components and causing irreversible cell necrosis. Cold stress adversely affects photosynthetic electron transport and reduces Rubisco activity (Li *et al.,* 2023), thereby impeding growth and decreasing plucking efficiency. At the molecular level, the C-repeat binding factor (CBF) transcriptional pathway plays a role in cold

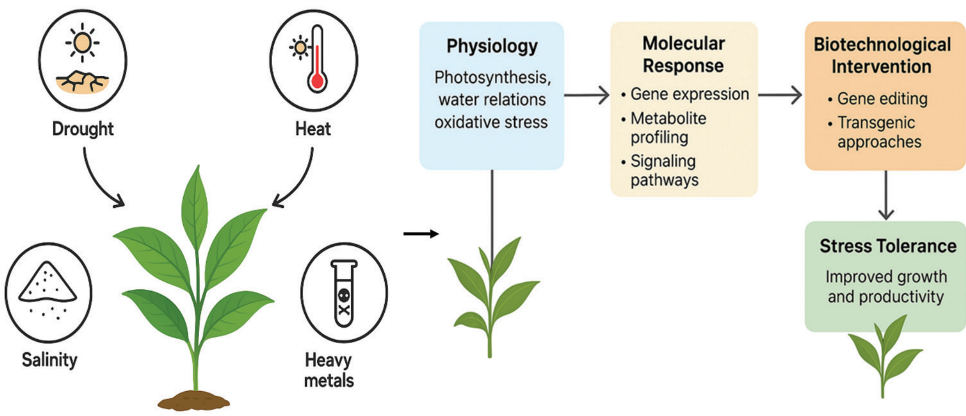

Figure 1: Integrated framework illustrating how diverse abiotic stresses trigger physiological and molecular responses in plants, and how targeted biotechnological interventions translate these responses into enhanced stress tolerance, growth, and productivity

acclimation in tea plants. This pathway regulates the expression of cold-responsive (COR) genes, which are essential for antifreeze proteins, dehydrins, and enzymes necessary for osmolytes. Cold stress also triggers hormonal signaling involving abscisic acid (ABA) and jasmonic acid, thereby orchestrating stomatal regulation and activating antioxidant defenses for adaptation (Chen *et al.,* 2021). Cold-tolerant tea varieties often exhibit elevated antioxidant enzyme expression and accumulate proline and soluble sugars, which serve as cryoprotectants (Zhang *et al.,* 2020).

Salinity effects

Salinity represents a significant abiotic stress challenge for tea plantations located in coastal areas and on irrigated lands, (Hajiboland, 2017; Upadhyaya *et al.,* 2021) where soil and water salinization are exacerbated by climate change, sea-level rise, and intensive agricultural practices. Although tea is traditionally grown in regions with high rainfall, areas in South and Southeast Asia have encountered secondary salinization due to irrigation with suboptimal water quality and soil degradation (Sahoo *et al.,* 2024). Tea plants experience dual stress under saline conditions: osmotic stress resulting from water scarcity and ionic stress due to the accumulation of excessive sodium (Na^+) and chloride (Cl^-) ions in tissues (Zhang *et al.,* 2020). These factors significantly impair plant growth, induce physiological changes in leaves, and cause biochemical variations, ultimately reducing yield and quality.

Heavy metals exposure in tea

Tea plantations located in industrial and mining regions are subject to heightened heavy metals (HM) contamination through water irrigation, atmospheric deposition, and soil accumulation. Elements such as aluminum (Al), cadmium (Cd), lead (Pb), arsenic (As), and mercury (Hg) present significant risks to tea plants, potentially diminishing yield and posing health hazards to humans upon consumption (Li *et al.,* 2021). HM stress disrupts cellular redox balance by inducing the overproduction of reactive oxygen species (ROS), which damage lipids, proteins, and nucleic acids (Chen *et al.,* 2022b). Cadmium stress hinders tea root growth and the uptake of essential nutrients, including calcium (Ca^{2+}), magnesium (Mg^{2+}) and iron (Fe^{2+}), resulting in stunted roots and reduced photosynthesis (Zhang *et al.,* 2023). Similarly, lead exposure alters chloroplast structure and reduces chlorophyll content, thereby decreasing biomass and yield (Wang *et al.,* 2020). In response to HM stress, tea plants activate antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidases (POD), and glutathione reductase (GR) as a defense mechanism (Liu *et al.,* 2024b). Chelating molecules sequester heavy metals within vacuoles, mitigating their effects (Yuan *et al.,* 2020). Research indicates that cadmium exposure alters genes involved in metal transport, including the ZIP, NRAMP, and HMA families, as well as detoxification genes (Huang *et al.,* 2022). Biotechnological strategies, such as the modification of metal-binding protein genes and the use of CRISPR-Cas9 to edit transporter loci, are accelerating the development of heavy metal-resistant tea cultivars (Zhou *et al.,* 2023). Amendments, biochar, and endophytic microbial inoculants demonstrate potential in capturing soil heavy metals and reducing their uptake by tea plants (Kumar *et al.,* 2024).

UV stress

Increased ultraviolet (UV) exposure poses a significant challenge to tea plantations due to the thinning of the ozone layer and climate change (Yuan *et al.,* 2020). Tea plants cultivated in high-altitude regions with thinner atmospheres are particularly susceptible to UV radiation (Wang *et al.,* 2021a). UV-B radiation disrupts photosynthesis by damaging the D1 protein in photosystem II, thereby impairing electron transport and reducing chlorophyll fluorescence (Li *et al.,* 2022). The impact of UV on leaf area, biomass, and yield adversely affects economic returns (Khan *et al.,* 2021). A response to UV stress is the overproduction of reactive oxygen species (ROS), which leads to oxidative damage (Zhou *et al.,* 2023). Tea plants activate antioxidant defenses, including enzymatic components such as SOD, CAT, ascorbate peroxidase (APX), and GR, as well as non-enzymatic antioxidants such as flavonoids and catechins (Tang *et al.,* 2020). These substances provide photoprotection and enhance the nutraceutical value of tea. UV-B induces the production of UV-absorbing compounds, such as flavanols, phenolic acids, and anthocyanins, which protect tissues (Zhang *et al.,* 2021). Transcriptomic studies in *C. sinensis* have demonstrated that genes such as UV resistance locus 8 (UVR8), elongated hypocotyl 5 (HY5), and chalcone synthase (CHS) are upregulated (Chen *et al.,* 2022a). Strategies such as CRISPR-Cas9 editing of UVR8 and HY5 pathways and developing lines with enhanced flavonoid biosynthesis can be employed to cultivate UV-resistant growth (Liu *et al.,* 2024a). Research on crops, including tea, has concentrated on utilizing shade structures, intercropping, and biostimulant sprays with antioxidants to mitigate UV stress (Ghosh *et al.,* 2023).

Effects of stresses on tea production

Salinity stress adversely affects shoot development and leaf area, while inducing significant alterations in the chemical composition of tea, particularly phytochemicals. This results in a reduction of flavor, aroma, and polyphenolic compounds, thereby directly impacting the market value and export potential of tea. With the increasing global issue of soil salinization, particularly in Asia and Africa, it is imperative to understand salinity tolerance mechanisms in tea cultivation and to integrate physiological, molecular, and agronomic approaches to sustain tea productivity and quality in saline environments (Sahoo *et al.,* 2024). Drought stress modifies the biochemical composition of tea leaves, influencing shoot development and plucking intervals. The reduction of catechins, theaflavins, and volatile/aromatic compounds under drought conditions adversely affects tea quality and market value (Han *et al.,* 2022). Although mild drought stress may stimulate specific phenolic compounds as a protective response, prolonged or intense stress generally diminishes both yield and quality (Chen *et al.,* 2021) (Figure 2 & Table 1).

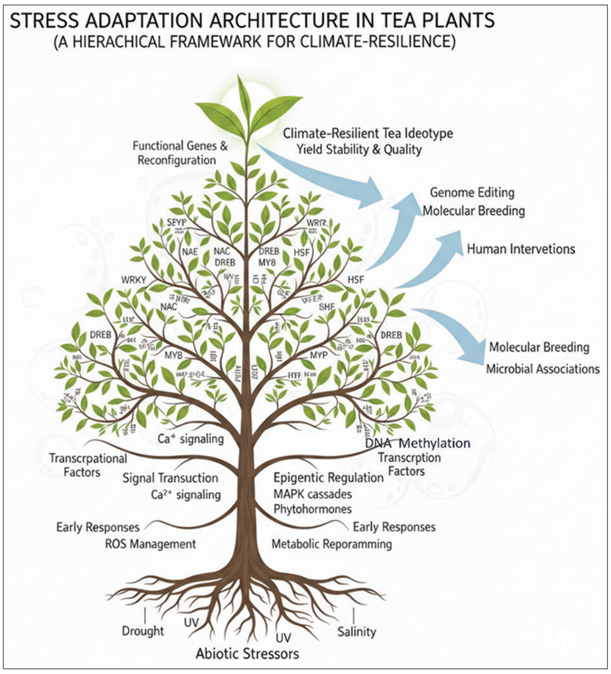

Figure 2: Abiotic stress signalling in *Camellia sinensis*. Environmental cues activate MAPK cascades and WRKY transcription factors, driving transcriptional reprogramming and associated physiological responses that support stress adaptation and growth maintenance

Physiological and biochemical changes

Physiological responses

Photosynthesis in *C. sinensis* is susceptible to abiotic stresses, which diminish its efficiency. Drought, salinity, and elevated temperatures result in stomatal closure, thereby limiting CO_2 assimilation and reducing the net photosynthetic rate (Pn) (Han *et al.,* 2022). Cold stress leads to a decrease in chlorophyll levels and causes damage to thylakoid membranes (Li *et al.,* 2023). Salinity and heavy metal toxicity disrupt water potential and ion balance, while UV radiation adversely affects the D1 protein of photosystem II, impairing electron transport (Li *et al.,* 2022). These stress-induced alterations impact the structure and growth of leaves and roots. Drought restricts leaf expansion and shoots plucking, whereas salinity and aluminum toxicity impede root growth and nutrient absorption (Sahoo *et al.,* 2024). Extreme temperatures and UV radiation reduce cambial activity, consequently shortening productive growth periods and diminishing yield (Khan *et al.,* 2021).

Biochemical responses

ROS including hydrogen peroxide (H_2O_2), superoxide radicals (O_2), and singlet oxygen are generated under abiotic stress conditions. Excessive production of ROS leads to oxidative stress, impacting lipids, proteins, and nucleic acids (Zhou *et al.,* 2023). Enzyme-based antioxidants, such as SOD, CAT, POD, APX, and GR, play a crucial role in maintaining redox balance and eliminating ROS in plants (Tang *et al.,* 2020). Tea plants utilize compatible solutes or osmolytes, including proline, glycine betaine, soluble sugars, and polyols, to stabilize proteins, membranes, and osmotic balance under drought and salinity conditions (Wang *et al.,* 2021b). Stress also induces the production of secondary metabolites, such as catechins, theaflavins, flavanols, and phenolic acids, which function as antioxidants and photoprotectants. Zhang *et al.* (2021) demonstrated that UV-B radiation enhances the levels of flavonoids and phenolics, thereby improving stress tolerance and tea quality. Hormonal regulation is essential, with ABA, salicylic acid (SA), JA, and ethylene (ET) orchestrating stress response signaling. ABA is pivotal for stomatal regulation under drought and salinity, while JA and SA modulate antioxidant defenses and secondary metabolism (Chen *et al.,* 2021). Recent research on *C. sinensis* has revealed that increased transcription factors from the WRKY, NAC, MYB, and bZIP families are critical for osmo-protection, ROS detoxification, and metabolic reprogramming (Liu *et al.,* 2024a).

Photosynthesis and carbon metabolism

Changes in photosynthetic efficiency

Photosynthesis is a critical physiological process in tea plants, and it is vulnerable to abiotic stressors. Disruptions in carbon assimilation can directly impede growth, leaf expansion, and the production of essential metabolites that determine quality. Various environmental factors, such as drought, salinity, temperature fluctuations, heavy metals, and ultraviolet radiation, significantly affect light absorption, electron transport, and carbon fixation, thereby inducing complex metabolic changes (Han *et al.,* 2022; Li *et al.,* 2023).

Impact on photosynthetic machinery

Abiotic stress adversely affects the net photosynthetic rate (Pn), stomatal conductance (gs), and transpiration rate (E). Drought and salinity impede diffusion into the mesophyll, while elevated temperatures enhance photorespiration (Wang *et al.,* 2021b), thereby diminishing Rubisco carboxylation efficiency. Cold stress negatively impacts thylakoid membranes, resulting in a decrease in PSII's maximum quantum yield (Fv/Fm) and chlorophyll fluorescence. Zhou *et al.* (2003) established that heavy metal toxicity and UV-B radiation inflict damage on PSII reaction centers, leading to the degradation of the D1 protein and obstructing electron transport. Tea plants mitigate oxidative damage to photosystems by modifying the chlorophyll a/b ratio, augmenting carotenoids, and activating non-photochemical quenching (NPQ). The ultrastructure of chloroplasts facilitates stress adaptation; for example, in olive trees, extracellular adventitious roots under sub-water-saturated conditions are associated with thylakoid swelling and grana disorganization (Khan *et al.,* 2021).

Amendments in carbon metabolism

The effectiveness of photosynthesis in tea plants is associated with carbon metabolism. Under stress conditions, tea plants accumulate soluble sugars, such as sucrose, glucose, and fructose, as well as polyols like mannitol

Table 1: Biotechnological strategies for enhancing abiotic stress tolerance in *C. sinensis*

Category	Strategy/Approach	Key Targets/ Components	Mechanism of Action	Outcome in Tea Plants	Key References
Genetic Engineering	Antioxidant gene overexpression	SOD, CAT, APX	ROS scavenging, membrane stabilization	Improved oxidative stress tolerance and photosynthesis	Kumar *et al.,* 2021; Roy *et al.,* 2022
	LEA proteins & dehydrins	LEA, Dehydrins	Protein and membrane stabilization under dehydration	Enhanced drought and cold tolerance	Upadhyaya *et al.,* 2021
	Heat shock proteins	CsHSP70, CsHSFA2	Protein folding and stress protection	Increased thermotolerance	Liu *et al.,* 2021
	Osmoprotectant biosynthesis	P5CS, BADH	Proline and glycine betaine accumulation	Improved osmotic balance and drought resistance	Li *et al.,* 2021
	Hormonal pathway engineering	NCED, ABA-related genes	Stomatal closure, stress signaling	Enhanced drought and salinity tolerance	Zhang *et al.,* 2022
	Stress-inducible promoters	RD29A, HVA22	Stress-specific gene activation	Reduced growth penalty, improved adaptation	Sun *et al.,* 2021
Transformation Systems	Agrobacterium-mediated transformation	Agrobacterium tumefaciens, A. rhizogenes	Gene transfer and expression	Functional validation, stress-tolerant lines	Roy *et al.,* 2022
	Hairy root cultures	P5CS, BADH	Enhanced metabolite synthesis	Improved osmotic adjustment	Li *et al.,* 2021
Genome Editing	CRISPR/Cas9 editing	DREB, WRKY, NAC, NHX, HKT	Targeted gene modification	Improved drought, salinity, and cold tolerance	Li *et al.,* 2021; Zhang *et al.,* 2022
	Multiplex editing	Multiple stress genes	Simultaneous pathway regulation	Accelerated development of resilient cultivars	Zhang *et al.,* 2022
Molecular Breeding	QTL mapping	RWC, proline, antioxidant traits	Trait–marker association	Identification of stress-resilient loci	Li *et al.,* 2021; Roy *et al.,* 2022
	Marker-assisted selection (MAS)	SNPs, SSRs	Early genotype screening	Reduced breeding cycle	Roy *et al.,* 2022
	Genomic selection (GS)	Genome-wide markers	Breeding value prediction	Efficient polygenic trait selection	Zhang *et al.,* 2022
In Vitro Strategies	*In vitro* stress selection	PEG, NaCl, heavy metals	Selection under controlled stress	Identification of tolerant lines	Upadhyaya *et al.,* 2021; Roy *et al.,* 2022
	Somaclonal variation	Genetic/epigenetic variation	Novel trait generation	Enhanced stress tolerance	Roy *et al.,* 2022
	Molecular screening	qRT-PCR, RNA-seq, SSR/SNP	Gene validation	Reliable elite line selection	Li *et al.,* 2021
Omics Approaches	Genomics & transcriptomics	WRKY, NAC, MYB, ABA genes	Gene discovery and expression profiling	Identification of stress pathways	Li *et al.,* 2021; Zhang *et al.,* 2022
	Proteomics	HSPs, SOD, CAT, APX	Protein-level regulation	Functional stress adaptation	Roy *et al.,* 2022
	Metabolomics	Proline, catechins, flavonoids	Metabolic adjustment	Improved osmoprotection and antioxidation	Sun *et al.,* 2021
	Multi-omics integration	Gene–protein–metabolite networks	Systems biology analysis	Identification of regulatory hubs	Zhou *et al.,* 2021
Microbial Interventions	AMF	Root symbiosis	Nutrient uptake, ROS detoxification	Enhanced drought and salinity tolerance	Roy *et al.,* 2022
	PGPR	Bacillus, Pseudomonas	Hormone production, ACC deaminase	Improved growth under stress	Sun *et al.,* 2021
	Endophytes	Bacteria, fungi	Hormonal and metabolic modulation	Enhanced multi-stress tolerance	Li *et al.,* 2021
Chemical Interventions	Osmoprotectants & antioxidants	Proline, glycine betaine, ascorbate	Osmotic balance, ROS detoxification	Improved physiological stability	Li *et al.,* 2021; Roy *et al.,* 2022
	Plant growth regulators	ABA, SA, JA, BRs	Stress signaling and regulation	Improved stress tolerance and yield	Li *et al.,* 2021; Sun *et al.,* 2021
	Signaling molecules	NO, H_2S	Stress signal transduction	Enhanced adaptive responses	Roy *et al.,* 2022

and sorbitol, which function as osmoprotectants and ROS scavengers (Tang *et al.,* 2020). Prolonged stress results in a shift of carbon allocation from growth to protective secondary metabolism. Drought and salinity stress enhance the phenylpropanoid and flavonoid pathways, leading to an increase in catechins, flavonols, and anthocyanins, which serve as antioxidants or UV filters (Zhang *et al.,* 2021). Heat stress and elevated CO_2 levels reprogram tricarboxylic acid (TCA) cycle intermediates to sustain energy for stress adaptation (Han *et al.,* 2022). Transcriptomic analyses indicate a reduction in Calvin cycle enzymes, such as Rubisco activase and fructose-1,6-bisphosphatase, under drought and heat conditions (Chen *et al.,* 2021; Liu *et al.,* 2024a), while sucrose synthase, invertase, and trehalose-6-phosphate synthase (TPS), which aid in osmotic adjustment, are upregulated. Exposure to UV-B radiation activates the shikimate and phenylpropanoid pathways, redirecting carbon towards phenolic compounds (Chen *et al.,* 2022a).

Water relations and osmotic adjustment

Water dynamics play a critical role in enabling tea plants to endure abiotic stresses, including drought, salinity, and extreme temperatures. Such stresses disrupt water balance, leading to reduced leaf turgor and stomatal activity. Drought notably diminishes the relative water content (RWC), leaf water potential, and stomatal conductance, thereby hindering gas exchange and photosynthesis (Upadhyaya *et al.,* 2021). To adapt osmotically and maintain cell turgor during dehydration, tea plants accumulate solutes such as proline, glycine betaine, and soluble sugars (Paul & Jeyaraman, 2020). Salinity stress induces osmotic imbalance and ion toxicity. To mitigate these adverse effects, tea plants employ vacuolar sequestration to regulate Na^+ and Cl^- ions and produce osmoprotectants, such as polyols and sugar alcohols, to manage osmotic potential (Sharma *et al.,* 2021).

Oxidative stress and antioxidant defense system

Abiotic stressors, such as drought, salinity, extreme temperatures, and heavy metals, lead to the overproduction of ROS, including superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (·OH), and singlet oxygen ($^1O_2$). In *C. sinensis*, the accumulation of ROS results in oxidative stress, which damages proteins, lipids, nucleic acids, and pigments, thereby disrupting cellular functions and reducing productivity (Kumari *et al.,* 2021). Tea plants mitigate ROS effects by activating an antioxidant defense mechanism that involves both enzymatic and non-enzymatic pathways. Key antioxidant enzymes include SOD, CAT, POD, APX, GR, and monodehydroascorbate reductase (MDHAR). SOD converts superoxide into H_2O_2, which is subsequently decomposed by CAT or APX (Upadhyaya *et al.,* 2021). Enhanced activities of SOD and APX in drought-resistant tea clones suggest their role in stress resilience (Goswami *et al.,* 2020). In addition to enzymatic antioxidants, tea contains non-enzymatic antioxidants, such as ascorbic acid (AsA), glutathione (GSH), carotenoids, phenolics, and flavonoids, which are essential for ROS scavenging. Tea leaves are rich in polyphenols, including catechins and theaflavins, which function as antioxidants and signaling molecules, aiding in stress adaptation (Wang *et al.,* 2022). Flavonoids accumulate in outer tissues under UV-B exposure, contributing to protection by regulating ROS generation (Shen *et al.,* 2021). Furthermore, oxidative stress activates the ascorbate–glutathione (AsA–GSH) pathway, a cellular redox center that maintains balance. Increasing levels of AsA and enzymes such as APX and GR facilitates the regeneration of AsA and GSH, thereby enhancing stress tolerance (Liu *et al.,* 2023). Molecular studies have demonstrated that transcription factors, such as WRKY and NAC, regulate the expression of antioxidant genes (Table 2) under abiotic stress conditions (Zhang *et al.,* 2022).

The hormonal regulations and pathways

Phytohormones play a pivotal role in enabling tea plants to respond to abiotic stress by influencing gene expression, regulating physiological processes, and initiating stress-responsive pathways to enhance resilience. ABA serves as the primary stress hormone, particularly during conditions of drought, high salinity, or extreme temperatures, by inducing stomatal closure, promoting osmolyte production, and activating antioxidant defenses

Table 2: Transcription factors and regulatory networks in tea stress tolerance

TF Family	Key Genes (Tea)	Primary Function	Regulated Pathways	Stress Response Outcome	Key References
WRKY	CsWRKY2, CsWRKY45	Regulation of ROS-scavenging genes	ABA signaling, antioxidant defense	Enhanced drought and salinity tolerance	Li *et al.,* 2021; Zhang *et al.,* 2022
NAC	CsNAC7	Stress-induced senescence and detoxification	ABA, JA pathways	Improved cold tolerance and ROS balance	Upadhyaya *et al.,* 2021
DREB/CBF	CsDREB1A, CsCBF1	ABA-independent stress signaling	RD29, COR genes	Enhanced drought, salinity, and cold tolerance	Ghosh *et al.,* 2022
MYB	CsMYB59	Secondary metabolism regulation	Phenylpropanoid, lignin biosynthesis	Improved drought tolerance and cell wall strength	Roy *et al.,* 2022
bZIP	CsbZIP18, CsbZIP42	ABA-responsive transcription	ABA signaling, osmolyte genes	Improved osmotic adjustment and stress tolerance	Kumar *et al.,* 2021
HSF	CsHSFA2	Regulation of heat shock proteins	HSP expression	Enhanced thermotolerance	Liu *et al.,* 2021
bHLH	(emerging)	Growth and stress signaling	Hormonal and developmental pathways	Adaptive stress responses	Zhang *et al.,* 2022
ERF/AP2	(emerging)	Ethylene-mediated stress signaling	Ethylene pathway	Improved tolerance to abiotic stress	Zhang *et al.,* 2022
HD-ZIP	(emerging)	Developmental regulation	Leaf morphology, drought adaptation	Improved water-use efficiency	Zhang *et al.,* 2022

(Upadhyaya *et al.,* 2021). Transcriptomic analyses indicate the upregulation of ABA biosynthesis genes and drought-responsive transcription factors, such as AREB/ABF, in stressed tea leaves (Ghosh *et al.,* 2022). SA is essential for tolerance to both biotic and abiotic stresses by regulating ROS, inducing pathogenesis-related (PR) proteins, and influencing phenolic metabolism. The external application of SA enhances antioxidant enzyme activity, thereby improving cold stress tolerance in tea plants (Kumar *et al.,* 2020). JA is involved in regulating defense mechanisms against physical damage and abiotic stresses. Tea plants treated with JA exhibit increased production of antioxidants, such as catechins and flavonoids, which provide protection against UV radiation (Wang *et al.,* 2022). JA collaborates with ABA in drought signaling and counteracts SA in stress-response trade-offs. ET is associated with growth responses under conditions such as flooding, salinity, and heavy metal stress. In cadmium-exposed tea roots, ET biosynthetic genes are activated, suggesting a role in root architecture remodeling and detoxification (Liu *et al.,* 2021). Indole-3-acetic acid (IAA) and cytokinins (CKs) are critical for root growth and leaf function under stress. The interaction between ABA and auxin affects root growth during water scarcity, while CKs, which are less active, support survival over growth when water is limited (Basu *et al.,* 2023). Molecular analyses reveal that hormones operate through complex signaling pathways involving receptors, protein kinases, and transcription factors. MAPK cascades, CDPKs, and transcription factors such as NAC, WRKY, MYB, and bZIP are key regulators of hormone signaling in tea (Zhang *et al.,* 2022). Interactions among ABA–SA, ABA–JA, and JA–ET fine-tune stress responses, optimizing plant adaptation without causing metabolic overload.

Mitigation of abiotic stresses through agronomic practices

Agronomic strategies are instrumental in mitigating abiotic stress in tea plants caused by factors such as drought, salinity, temperature fluctuations, and soil nutrient deficiencies. Traditional practices, including optimized irrigation, mulching, soil amendments, and shade management, effectively reduce water stress by conserving soil moisture, decreasing evapotranspiration, and stabilizing the root zone. The application of organic manures, biofertilizers, and balanced fertilization improves soil structure, nutrient availability, and microbial activity, thereby alleviating plant stress. Techniques such as contour planting, intercropping, and cover cropping help to minimize erosion, reduce heat, and enhance the local microclimate. These strategies, when combined with the selection of stress-adaptive cultivars, pruning, and canopy management, improve water-use efficiency, photosynthesis, and overall plant health under abiotic stress conditions (Upadhyaya *et al.,* 2021; Roy *et al.,* 2022).

Irrigation management

Drought and heat stress pose significant challenges to crops such as tea (*C. sinensis*), particularly in the context of clone adaptation. Effective irrigation management is essential to mitigate these stresses. Irrigation protocols are tailored based on soil moisture levels, evapotranspiration rates, and plant hydration to maintain leaf turgor, stomatal conductance, and photosynthesis. Techniques such as drip irrigation and micro-sprinklers enhance water use efficiency, minimize evaporation, and ensure uniform water distribution. The integration of mulching with irrigation practices conserves soil moisture and moderates temperature. Implementing appropriate irrigation during critical growth phases, such as flush development and bud emergence, can enhance yield and quality under conditions of water scarcity. Furthermore, the use of soil moisture sensors and automated irrigation systems facilitates precise water management, promoting sustainable tea cultivation in regions experiencing drought conditions (Upadhyaya *et al.,* 2021; Roy *et al.,* 2022).

Soil amendments

Enhancing soil quality is essential for enabling tea plants to withstand abiotic stressors, such as drought, salinity, and nutrient deficiencies. The application of organic amendments, including compost, vermicompost, and manure, can improve soil structure. This leads to increased water retention, nutrient availability, and the proliferation of beneficial microbial communities, thereby enhancing plant resilience. Biochar contributes to improved soil porosity, moisture retention, and cation exchange capacity, which mitigates salinity and heavy metal stress. Inorganic amendments, such as gypsum and lime, are utilized to adjust soil pH and nutritional balance in acidic and sodic soils. Tea cultivation often involves the use of both inorganic and organic amendments, along with microbial inoculation, to enhance nutrient cycling, root growth, and the production of stress-reducing antioxidants (Li *et al.,* 2021; Upadhyaya *et al.,* 2021). These soil management practices are cost-effective and sustainable, supporting the maintenance of tea production and quality under challenging weather conditions.

Shade management

Effective shade management significantly mitigates abiotic stress, including heat and light stress, in tea plantations. The implementation of shading trees regulates excessive sunlight, leaf temperature, and water loss through evaporation and transpiration. This approach sustains leaf water potential, photosynthetic efficiency, and chlorophyll levels, even under elevated temperatures. Shade trees and artificial structures alter microclimatic conditions, enhance soil moisture retention, and diminish heat-induced oxidative damage to tea leaves. Furthermore, shade management augments secondary metabolites, such as catechins and flavonoids, which are essential for stress resistance and tea quality. Integrating shading with conventional tea cultivation practices, such as irrigation and soil enhancement, facilitates improved plant growth and productivity under high-temperature conditions (Upadhyaya *et al.,* 2021; Roy *et al.,* 2022).

Cross-cutting mitigation and management approaches

Incorporating organic amendments, such as biochar, manure, and vermicompost, alongside silicon supplementation, effectively reduces sodium ion accumulation and enhances soil structure, thereby improving salt tolerance in perennial crops. The external application of osmoprotective compounds (proline and glycine betaine) and plant growth regulators (salicylic acid and brassinosteroids) mitigates salinity damage and modulates antioxidant systems while maintaining ion equilibrium (Han *et al.,* 2022). Molecular techniques, including marker-assisted selection and transgenic approaches, have identified genes responsible for salt exclusion and compartmentalization, although their application in disease-free environments remains limited (Table 3). Advances in CRISPR/Cas9-based gene editing present opportunities to modify critical ion transporter genes and transcription factors, potentially leading to the development of salt-tolerant tea varieties (Li *et al.,* 2023).

CRISPR/Cas9-Mediated genome editing

The advent of clustered regularly interspaced short palindromic repeats (CRISPR)-associated protein 9 (Cas9) genome-editing technology has revolutionised plant biotechnology by enabling precise and multiplex genome editing. In tea, a long-lived perennial with extended breeding cycles and complex genomes, CRISPR/Cas9 is a promising tool for enhancing abiotic stress tolerance. It can precisely modulate genes governing stress-response pathways in tea. Editing transcription factors such as DREB/CBF, WRKY, and NAC can improve tolerance to drought, cold, and salinity. Upregulating genes encoding ROS-scavenging enzymes, including SOD, CAT, and APX, can strengthen antioxidant systems and mitigate oxidative damage under stress (Li *et al.,* 2021). In this research, a protocol for protoplast editing using CRISPR/Cas9 has been developed for the tea cultivar Kolkhida, successfully inducing targeted mutations in three specific genes. The co-transfection screening system provides a consistent method to expedite precision breeding in this perennial crop, which typically improves at a slow pace (Egorova *et al.,* 2025). Manipulating biosynthesis genes such as P5CS and BADH can stimulate proline accumulation and glycine betaine synthesis, facilitating osmotic adjustment during drought and salinity. Targeting PYR/PYL/RCAR receptors or ABA-responsive elements to modify ABA signalling pathways is a viable strategy for improving stomatal regulation and water-use efficiency (Zhang *et al.,* 2022). Additionally, transporters such as NHX, HKT, and water channel aquaporins can be modified to enhance ion homeostasis and water transport, contributing to stress adaptation. Collectively, these targeted efforts highlight CRISPR's potential to accelerate the development of climate-resilient tea cultivars. CRISPR/Cas9 also offers advantages for CsHB1 gene regulate of caffeine biosynthesis of tea cultivation through precise genome editing, including target knockouts, knock-ins, base editing, and promoter modification, with minimal off-target risk (Ma *et al.,* 2021). Its multiplexing ability allows simultaneous editing of multiple stress-related genes, which is essential for addressing complex polygenic traits such as drought and temperature tolerance. Importantly, not all gene edits require foreign DNA integration; therefore, some modifications may be classified as non-GMO under certain

Table 3: Molecular mechanisms of abiotic stress tolerance in *Camellia sinensis*

Regulatory Level	Key Components	Mechanism	Physiological/Cellular Outcome	Key References
Stress perception & signaling	Ca^{2+}, ROS, inositol phosphates, CDPKs, MAPKs	Signal sensing and amplification via kinase cascades	Activation of stress-responsive gene networks	Upadhyaya *et al.,* 2021
Transcriptional regulation	WRKY, NAC, MYB, bZIP, DREB/CBF	Regulation of stress-inducible genes	Enhanced osmolyte synthesis, ROS detoxification, hormone signaling	Ghosh *et al.,* 2022; Li *et al.,* 2021
Post-transcriptional regulation	miR156, miR159, miR166, miR398, miR393	mRNA cleavage or translational repression	Fine-tuning of antioxidant enzymes and hormone signaling	Deng *et al.,* 2020; Sun *et al.,* 2021; Zhang *et al.,* 2022
siRNA-mediated regulation	siRNAs, RdDM pathway	DNA methylation and gene silencing	Regulation of ABA-responsive and stress genes	Ghosh *et al.,* 2022
DNA methylation	Promoter methylation (ABA, osmolyte genes)	Epigenetic modification and stress memory	Faster response to recurring stress	Wang *et al.,* 2021b
Histone modifications	H3K4me3, H3K27me3, HDACs	Chromatin remodeling	Rapid activation/repression of stress genes	Zhou *et al.,* 2021
Epigenetic memory	DNA methylation, histone marks	Stress priming	Enhanced tolerance to repeated stress	Roy *et al.,* 2022
Stress-responsive proteins	HSPs, LEA, dehydrins, aquaporins, MTs	Protein stabilization, detoxification, water transport	Improved cellular protection and homeostasis	Kumar *et al.,* 2021; Li *et al.,* 2021; Roy *et al.,* 2022
Antioxidant system	SOD, CAT, APX, GR	ROS detoxification	Reduced oxidative damage	Upadhyaya *et al.,* 2021
Transport & ion homeostasis	NHX, ABC transporters, V-PPase	Ion transport and compartmentalization	Salinity and drought tolerance	Zhang *et al.,* 2022
Metabolite reprogramming	Proline, glycine betaine, sugars, catechins	Osmoprotection and antioxidation	Maintenance of cellular integrity	Roy *et al.,* 2022
Pathway crosstalk	ABA, SA, JA, ET+ROS+TFs	Integrated signaling networks	Coordinated stress adaptation	Zhang *et al.,* 2022

regulatory frameworks, easing approval and adoption. Faster than traditional breeding, CRISPR is transformative for developing resilient, high-performance tea cultivars despite tea's prolonged juvenile phase and long timelines for cultivar development in breeding programs.

Perspectives and challenges

The increasing frequency and intensity of abiotic stresses, such as drought, salinity, temperature extremes, and heavy metal contamination, threaten tea crop productivity and quality. Future research should integrate genomics, transcriptomics, proteomics, metabolomics, and epigenomics to unravel stress-response networks. Genome editing technologies like CRISPR/Cas9 offer precise tools for developing stress-resilient cultivars, while marker-assisted and genomic selections can accelerate breeding cycles. High-throughput phenotyping platforms incorporating imaging, spectral analysis, and environmental sensors allow accurate assessment of stress responses under field and controlled conditions. Integrating multi-omics approaches provides a comprehensive understanding of stress response networks, enabling identification of key regulatory genes and metabolic pathways for targeted interventions. Artificial intelligent (AI) and machine learning (ML) tools are increasingly applied to predict stress tolerance traits, optimize breeding strategies, and analyze large-scale multi-omics and environmental data sets. Additionally, nanotechnology-based approaches, including nanoparticle-mediated delivery of nutrients, growth regulators, and stress-mitigating compounds, have shown promise in enhancing stress tolerance by improving nutrient uptake, antioxidant defense, and cellular homeostasis. Combining beneficial microorganisms, biostimulants, and precision agronomy with these technologies offers a holistic strategy for sustainable improvement of tea productivity and quality under adverse conditions (Li *et al.,* 2021; Zhang *et al.,* 2022). Beneficial microorganisms, exogenous stress-mitigating compounds, and optimized agronomic practices provide sustainable solutions for field-level stress management. Challenges include the polygenic nature of stress tolerance, the long juvenile period of tea, limited regeneration efficiency in tissue culture, and complex interactions between environmental factors and plant responses, complicating breeding and biotechnological interventions. Translating laboratory and greenhouse findings to field conditions requires long-term trials in diverse agroclimatic zones. Integrating multi-omics data with phenotyping platforms and advanced computational modeling is crucial for predicting stress responses and identifying robust candidate genes. Addressing these challenges while leveraging biotechnological and agronomic tools will enable the development of climate-resilient, high-quality tea cultivars, ensuring sustainable production under changing conditions (Roy *et al.,* 2022).

Adaptation strategies should integrate genetic, biotechnological, microbial, and agronomic interventions. Developing stress-resilient cultivars through marker-assisted selection, genomic selection, and genome editing enhances tolerance to extreme temperatures and water deficits. Beneficial microorganisms, exogenous stress-mitigating compounds, and soil amendments improve plant resilience. Precision irrigation, shade management, mulching, and optimized fertilization conserve soil moisture and maintain microclimatic stability. Climate-smart practices like contour planting, intercropping, and real-time monitoring using remote sensing and sensor technologies support adaptive cultivation (Zhang *et al.,* 2022).

At the molecular level, cross-talk among signalling pathways mediated by ABA, SA, JA, and ET coordinates multi-stress responses. Shared regulatory hubs, such as HSPs, ROS, scavenging enzymes, and late embryogenesis abundant (LEA) proteins, provide broad-spectrum tolerance. Advanced breeding and biotechnological tools, including marker-assisted selection, genomic selection, and CRISPR/Cas9-mediated genome editing, enable stacking multiple tolerance traits into elite cultivars. Integrating multi-omics data helps identify key genetic networks for combined stress resilience. Agronomic strategies like shade management, precision irrigation, soil amendments, and beneficial microorganisms enhance multiple tolerance-related traits. Balancing trade-offs is challenging, as traits improving tolerance to one stress (e.g., stomatal closure for drought) may increase sensitivity to another (e.g., heat). Addressing these complexities requires systems biology approaches and predictive modeling, supported by AI and ML, to design tea cultivars and management practices for diverse stress scenarios (Li *et al.,* 2021; Zhang *et al.,* 2022; Roy *et al.,* 2023).

Although omics technologies have generated extensive datasets, their integration into system-level stress-response networks is nascent. Functional validation of candidate stress-responsive genes is constrained by inefficient transformation and long generation cycles, slowing translation from gene discovery to trait development. Most studies focus on single stress factors under controlled conditions, leaving combined and field-relevant stress responses underexplored. Emerging approaches, such as genome editing, microbial-assisted stress mitigation, and predictive climate–productivity modeling, hold promise but require optimization and field validation. Addressing these challenges through integrated molecular, physiological, and agronomic research pipelines will bridge laboratory discoveries with field applications, ensuring sustainable tea production under changing environmental conditions (Figure 3).

Conclusions

Current research has advanced our understanding of abiotic stress responses in tea plants, revealing complex adjustments at physiological, biochemical, molecular, and genetic levels. Major stresses like drought, temperature extremes, salinity, heavy metals, and UV radiation disrupt photosynthesis, water relations, carbon metabolism, and cellular redox balance, affecting tea yield and quality. Tea plants respond through osmotic adjustment, antioxidant defense activation, hormonal signalling,

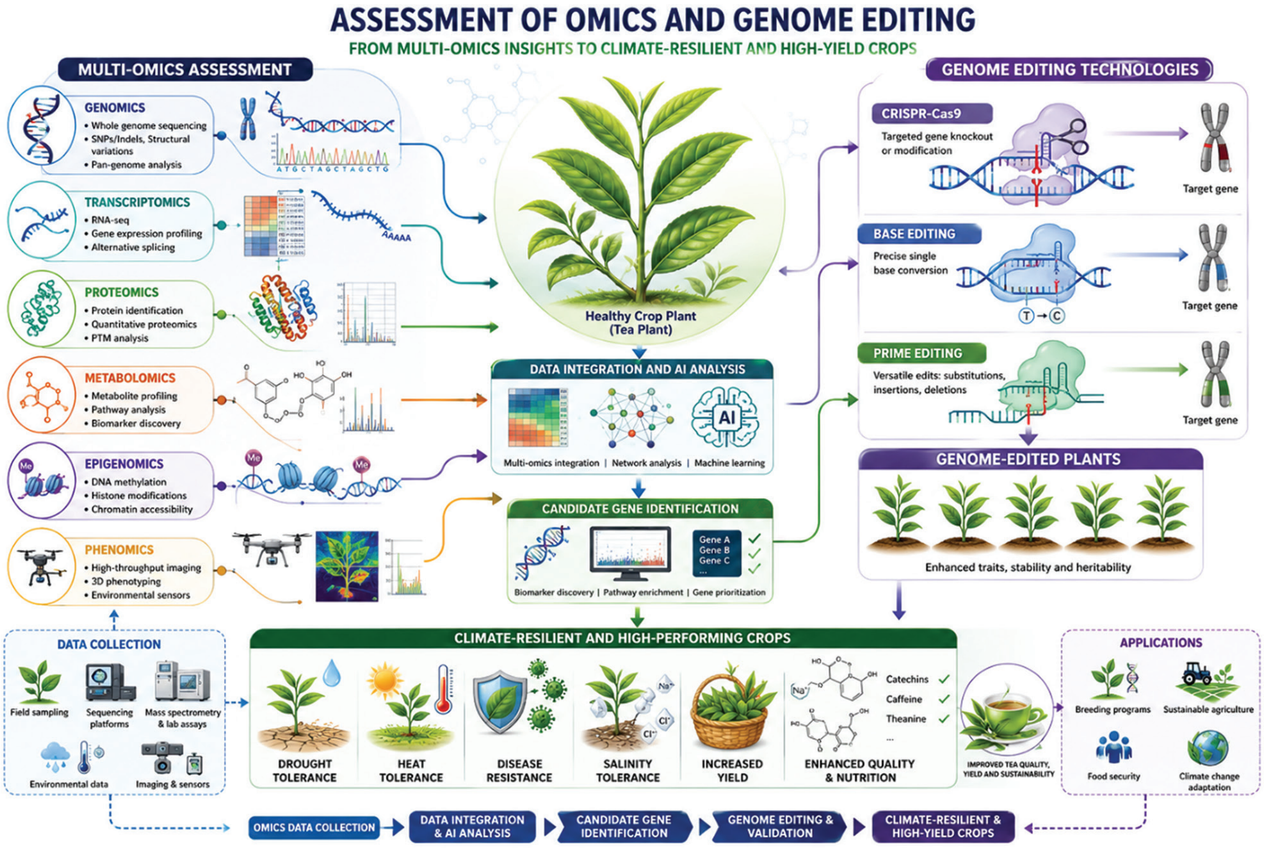

Figure 3: Schematic overview of the stress-response architecture showing how abiotic stress perception is resolved through multi-omics integration to drive the development of a climate-resilient phenotype

and metabolic reprogramming. At the molecular level, stress perception triggers signal transduction cascades regulating transcription factors, stress-responsive genes, protective proteins, transporters, and metabolic pathways. Recent transcriptomic and metabolomic studies have identified regulatory networks, highlighting small RNAs and epigenetic modifications in stress response fine-tuning. Progress in genetic engineering, genome editing, and marker-assisted breeding offers new possibilities for improving stress tolerance, complemented by agronomic and microbial interventions under field conditions. These findings establish a foundation for developing climate-resilient tea varieties and emphasize integrated multi-level approaches to translate molecular insights into sustainable tea production systems. Growing knowledge on abiotic stress tolerance in tea plants offers translational potential for developing climate-resilient cultivation systems. Advances in genomics, transcriptomics, and metabolomics have identified regulatory genes, stress-responsive pathways, and molecular markers for breeding and selection programs. Emerging genome-editing technologies offer opportunities to modify stress tolerance master regulators without compromising tea quality traits. Simultaneously, improved in vitro screening methods, microbial-assisted stress mitigation, and targeted agronomic interventions offer tools for enhancing stress resilience under plantation conditions. The convergence of molecular breeding, biotechnology, and field-level management practices creates a pathway for translating laboratory discoveries into high-performance tea cultivars adapted to future climate scenarios. However, successful implementation depends on coordinated efforts linking fundamental research, breeding pipelines, large-scale field validation, and stakeholder adoption to ensure sustainable and economically viable tea production in a changing environment.

Author contributions

Sasidharan Perumal was involved in the research and preparation of the original manuscript. He has conceived the theme and critically reviewed the manuscript and Mepully Thomas Antony Mathew collected the relevant references, reviewed and revised the manuscript. TT. Raj Kumar and A. Babu reviewed and revised the manuscript. All authors have contributed to the article and have approved the submitted version.

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