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REVIEW ARTICLE

Dynamic interactions between biotic and abiotic stressors in plants: Mechanisms, crosstalk and sustainable mitigation strategies

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Abstract

Abiotic and biotic stresses, whether occurring individually or in combination, have profound effects on plant growth, development and overall productivity. Abiotic stresses such as drought, salinity and extreme temperatures disrupt physiological processes, while biotic stresses from pathogens, pests and herbivores impair plant defenses and nutrient dynamics. When these stressors act simultaneously, they interact in complex ways, often exacerbating damage and creating unique challenges for plants. Research has shown that plants employ sophisticated signalling networks involving hormones such as abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA) and ethylene to coordinate responses to these stress combinations. These signalling pathways can have synergistic or antagonistic effects on stress tolerance, depending on the nature and timing of the stresses. Recent advancements in plant genetics, metabolomics, transcriptomics and genome-editing tools such as CRISPR-Cas (clustered regularly interspaced short palindromic repeats) are providing new insights into how plants adapt to dynamic environments and cope with concurrent stresses. Additionally, microbial inoculations, including arbuscular mycorrhizal fungi(AMF) and plant growth-promoting rhizobacteria (PGPR), are emerging as effective strategies to mitigate stress impacts by enhancing nutrient uptake, regulating hormone levels and improving overall plant resilience. This review emphasizes the need for an integrated approach to understanding the interactions between biotic and abiotic stressors. It highlights innovative strategies such as microbial applications, advanced breeding programs and biotechnological interventions to improve stress tolerance. Addressing these challenges is critical for developing resilient crop varieties capable of withstanding the impacts of climate change and ensuring sustainable agricultural productivity.

Keywords: abiotic stress; biotic stress; genome editing; plant resilience mechanism; stress signalling pathways

Introduction

The term “stress” was first introduced in a biological context by Hans Selye in 1936, who described it as the nonspecific response of the body to any demand for change. While Selye’s work primarily focused on animals, his foundational concept laid the groundwork for understanding stress responses in plants as well. Abiotic stress stemming from physical or chemical variations in the environment is one facet while biotic stress encompasses biological factors such as diseases, insects and other any pests that afflict cultivated plants (1, 2). The likelihood of crops facing biotic and abiotic stresses, either individually or simultaneously is expected to rise eventually making it essential for their survival that they withstand these challenges (3). So far, most research has concentrated on studying individual stressors in highly controlled environments which has certainly advanced our understanding of the essential processes and signalling components involved in plant reaction towards the biotic and abiotic stresses (4). Concurrent presence of environmental stressors like shortage of water and high temperature has been shown to inflict extra severe damage to crop yield than when these stressors occur separately at different stages of crop improvement (5). Abiotic stressors, which include high temperature, low temperature, water scarcity, saltiness, oxidative damage and diet deficiencies, are an initial cause of global yield loss, diminishing both crop production and grade (6, 7).

Plants possess sensors that detect stress stimuli, initiating, signal transduction pathways that involve various signalling components such as secondary messengers, plant hormones and signalling pathways are participating in control stress-inducible genes. These genes generate enzymes and proteins that directly influence how plants react to and adjust to stress, enhancing their ability to cope with specific stressors. This convergence of signals ensures the precise coordination of the plant's adaptive reactions to environmental stressors (8, 9). Plants exhibit diverse responses to stress, leading to changes in expression of gene, cellular metabolism, growth patterns, crop productivity and other physiological processes. Stress-induced plant responses are an outcome of their adaptation to differing ecological factors. Over time, stress-tolerant plant species develop resistance to specific stressors (10). Stress responses vary significantly depending on the plant's growth phase. Seedlings, for instance, may prioritize survival overgrowth, whereas mature plants might reallocate resources to maintain reproductive output (11). External factors such as light intensity, temperature fluctuations, water availability and soil composition further fine-tune stress responses. For example, drought stress combined with high light exacerbates oxidative damage, triggering different defense pathways compared to drought alone (12). Over time, stress-tolerant genotypes are naturally selected or bred for enhanced resilience, demonstrating how genetic potential interacts with environmental pressures to shape adaptive traits (13). Understanding these sources of variability is crucial for developing climate-resilient crops.

When plants face simultaneous biotic and abiotic stressors, they often adopt unique stress-response strategies that can differ from those observed under individual stress conditions. For instance, when *Arabidopsis thaliana* plants experience both heat and drought stress together, they tend to accumulate sucrose instead of proline. This illustrates the effects of interacting stressors on plants is not merely additive; rather, it relies on the complex interaction between these stressors (14).

Certain stresses, like temperature, can be directly sensed by entire cells, while others target specific cellular components; for instance, light primarily impacts chloroplasts. The cell wall together with the cell membrane creates a continuous surface within the apoplastic space, facilitating direct interactions with the external environment (15). As a result, they both act as the primary targets of both stresses, detecting and responding to structural and metabolic disturbances (16). Plants have developed strategies to handle stresses within the apoplastic space by reducing metabolic limitations and lowering the energy costs linked to stress defence.

The concurrent presence of both stresses frequently results in compound interactions that intensify plant stress responses. For instance, drought stress can compromise a plant's immune system, increasing its vulnerability to pathogen attacks (17). Likewise, biotic stressors like insect herbivory can disrupt plant water relations, thereby exacerbating the impacts of drought or salinity stress (18).

Plants have developed advanced systems to manage combined stresses, often through interactions between signalling pathways that coordinate responses to both factors. Crucial hormones like ethylene, salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA) is essential in orchestrating these responses (19). Nevertheless, the interaction among these signalling pathways can be intricate, resulting in either antagonistic or synergistic effects on the plant's stress tolerance.

This review seeks to improve our understanding of the effect of simultaneous stressors on crops by exploring fundamental concepts, emphasizing their prevalence and assessing their effects on crop development. It offers a comprehensive overview of various stress interactions and their implications for agriculture, with a particular focus on the consequences of combined stresses.

Effects of combined abiotic stresses on plant growth and crop yield

Heat and drought stress: yield and physiological impacts

Abiotic stresses worldwide can decrease grain yield by over 50 % of a crop's potential. In both current and future climates, the cumulative impact of drought and high-temperature stress is expected to significantly affect the global food system (20). However, experiments combining these two stressors are relatively uncommon, despite the profound and interconnected challenges they pose to crop development and yield (21). The anticipated rise in drought events coinciding with heatwaves soon underscores the urgency of studying this combination of stresses to improve the resilience of future crops. Combined heat and drought stress significantly impact crop yields across various species, leading to severe reductions in productivity. In wheat, stress during the reproductive phase typically occurring between March and April in many growing regions can lead to yield depletion of 40-60 %, primarily due to poor grain filling and a decrease in overall grain yield per unit area (22). Maize is particularly sensitive, with potential yield losses of up to 70 % during June to July when flowering coincidence with simultaneous drought and heat leading to poor pollination and reduced biomass (23). Rice experiences up to 50 % yield reduction, especially when coincides with flowering, resulting in poor panicle development and spikelet sterility due to abiotic stress. Soybean yields can decrease by 40-80 % under combined stress during the reproductive phase, particularly affecting pod number and seed size (24). Sorghum, while relatively drought-tolerant, can still suffer yield losses of 30-50 % during critical growth periods due to impaired grain filling and panicle development (25). Cotton yields can decline by 40-60 %, primarily due to reduced boll retention and Fiber quality. These significant losses highlight the need for improved crop management, genetic improvements and climate adaptation strategies to reducing the effects of combined drought and heat stress across various crops.

Physiological and metabolic responses under heat-drought stress : The simultaneous stress of drought and heat causes changes in different physiological responses. Typically, abiotic stresses inhibit photosynthetic activity by destabilizing Rubisco and inflicting damage on photosystem II (PSII) (26). Additionally, these stresses increase levels of ROS and causing harm to proteins, lipids and DNA it leads to ROS stress. To counteract ROS damage, plants increase the generation of different antioxidants. In addition, osmolytes accumulate in reaction to drought and heat stress to aid in stabilizing proteins, membranes and managing H_2O balance (27). Recently, novel retrograde signals, including the metabolite 3′-phosphoadenosine 5′-phosphate, have been discovered. These signals collect under elevated temperatures and dry conditions. These signals are subsequently conveyed from chloroplasts to the nucleus, where they modulate ABA signalling and promote closure of stomata, thereby improving resilience to drought (28). Heat and drought as environmental stressors greatly impact the metabolic profiles of plants. A key mechanism of drought tolerance is the collection of compatible solutes-nontoxic, compounds with low molecular weight that aid in reducing cellular water potential. These solutes consist of sugars (such as glucose, fructose, sucrose and raffinose family oligosaccharides), amino acids (like proline and branched-chain amino acids) and compounds such as glycine betaine. They play a crucial role in stabilizing proteins membranes and reactive oxygen species scavenging. Raffinose family oligosaccharides (RFO) also accumulate under heat stress (29), along with other solutes that help maintain turgor pressure. Elevated temperatures result in a decreasing of polyunsaturated fatty acids in membranes to reduce fluidity, regulated by lipid biosynthetic pathways (30). Polyamines and various secondary metabolites, including flavonoids, also accumulate during drought and heat stress, functioning as antioxidants (31). Metabolite profiles are particular to the type of stress and plant species (32). For instance, *Arabidopsis* accumulates proline under drought conditions, but sucrose replaces proline under combined stress (32).

Interaction of heat and salinity stress

Crops react to heat and saline conditions by triggering a complex array of molecular, metabolic and physiological mechanisms. These processes include intricately connected and precisely regulated to produce clear-cut response that enable plants to adapt to changing abiotic conditions. Key factors such as maintaining the biological membrane potential, enzyme activities and appropriate osmolyte levels for cellular volume regulation rely heavily on ion homeostasis, particularly the balance of sodium and potassium ions (33).

Both types of stress may result in changes to ion transport and distribution (34). Salinity can cause Na^+toxicity, preventing potassium (K^+) absorption by root cells and negatively impacting genes and enzymes, hampering metabolic practices (33). Under high temperatures, nevertheless, changes in membrane fluidity are critical for sensing and modulating gene expression. As a result, heat can affect Ion channels and pumps in the plasma membrane or vacuolar membrane, leading to disturbances in ion balance (35).

Additionally, both forms of stress can impede plant growth and photosynthesis, enhance the buildup of reactive oxygen species (36), suppress essential enzymes, influence the efficiency of enzymatic reactions, modify metabolite profiles and affect the stability of proteins, membranes, ribonucleic acid (RNA) and cytoskeletal structures (37) resulting in metabolic disruptions.

Cross-tolerance mechanisms in heat and salinity stress : However, in a surprising turn, simultaneous exposure to salt and heat stress, instead of exacerbating the anticipated negative effects on tomato plant performance, elicited a corresponding response that enhanced resistance compared to salt stress alone. Physiological findings indicated several mechanisms contributing to the development of salinity tolerance due to heat stress, including: (i) Improved regulation of potassium (k^+) and sodium ($Na^{+)}$ levels, contrary to expectations. (ii) Enhanced the parameters of water balance. (iii) Strengthened defence against oxidative stress. (iv) Enhanced efficiency in photosynthetic performance. An in-depth and multidisciplinary investigation examined the biochemical, molecular and metabolic responses involved in explaining the underlying protective mechanisms (38). This phenomenon, termed "cross-tolerance", is a well-documented occurrence in crops, where a reaction to one stressor assists in shielding the plant from additional simultaneous or following environmental pressures. The findings from a previous study (38) indicate that plants exhibit increased resilience to saline stress after undergoing a moderate heat stress exposure at 35 °C. This includes physiological changes that boost antioxidant function, preserve chlorophyll and sustain membrane integrity, thus reducing the accumulation of ROS and ion leakage (39). These mechanisms support the resilience strategies outlined (38), suggesting the rapid acquisition of thermos tolerance after the 35 °C treatment is likely a key factor in the observed cross-protection effect.

The responses elicited by the combined heat and salt treatment (38), which provide protection against the negative impacts of salt stress when used alone. Under salt stress, stomatal closure results in a decrease in photosynthesis CO_2 fixation. Consequently, there is an excess electron transfer from photosystem I (PSI) that convert into ROS, impeding the restoration of damaged photosystem II (PSII) (40). However, when heat and salt stress are concurrently applied, stomatal opening occurs. This leads to increased transpiration rates and enhanced CO_2 diffusion into the leaf, which in turn boosts CO_2 uptake rates, enhances photosystem II activity, decreases ROS formation and limits harm to the photosynthetic system. This phenomenon explains why the combination of these stresses decreases the buildup of hydrogen peroxide (H_2O_2), protein oxidation and proteolytic activity. For instance, in wheat (*Triticum aestivum*), the combined effect of drought and heat stress led to reduced H_2O_2 accumulation in drought-tolerant cultivars (e.g., HD 2967) but increased oxidative damage in sensitive genotypes (e.g., PBW 343) (41). Similarly, in soybean (*Glycine max*), a previous study (42) observed that the suppression of proteolytic activity under combined salinity and waterlogging stress was genotype-specific, with the cultivar "Williams 82" showing resilience while "Prima 2000" exhibited significant protein degradation. Another case study in *A. thaliana* revealed that the interaction between light stress and nutrient deficiency altered H_2O_2 scavenging efficiency, but this response varied across ecotypes (43). These findings underscore the necessity of multi-genotype and multi-environment validation to establish universal stress response mechanisms.

Combined effects of heavy metals and radiation stress

Plants can encounter two distinct forms of abiotic stress from heavy metals such as cadmium (Cd), chromium (Cr), lead (pb), mercury (Hg), arsenic (As) and radiation. Under heavy metal stress, plants can face a range of physiological and biochemical changes, such as reduced growth, diminished biomass accumulation, shortened stalk and root lengths and yellowing of younger leaves. With extended exposure, this yellowing may spread to older leaves (44). Conversely, radiation stress in plants can lead to oxidative stress, DNA damage and altered gene expression. While significant studies have been done regarding the impact of radiation stress and metal toxicity stress separately on plants, nothing little is known about the combined effects of these two stresses. Plants have developed various defence strategies against metal toxicity. These include the synthesis of phytochelatins or metallothioneins to chelate metals, followed by their removal from sensitive areas or sequestration in the vacuole with ligands (45).

Abiotic–biotic stress crosstalk in plants

Dominance of abiotic signals in growth and defense regulation

Plants face a dynamic interplay of abiotic and biotic stressors that collectively shape their growth, productivity and stress resilience (Fig. 1). Critically, under combined stress, certain signals dominate, often suppressing or overriding others, which defines the plant's ultimate survival strategy (46). For instance, drought stress can suppress pathogen-responsive pathways via ABA-mediated signalling, prioritizing water conservation over defense (47). The

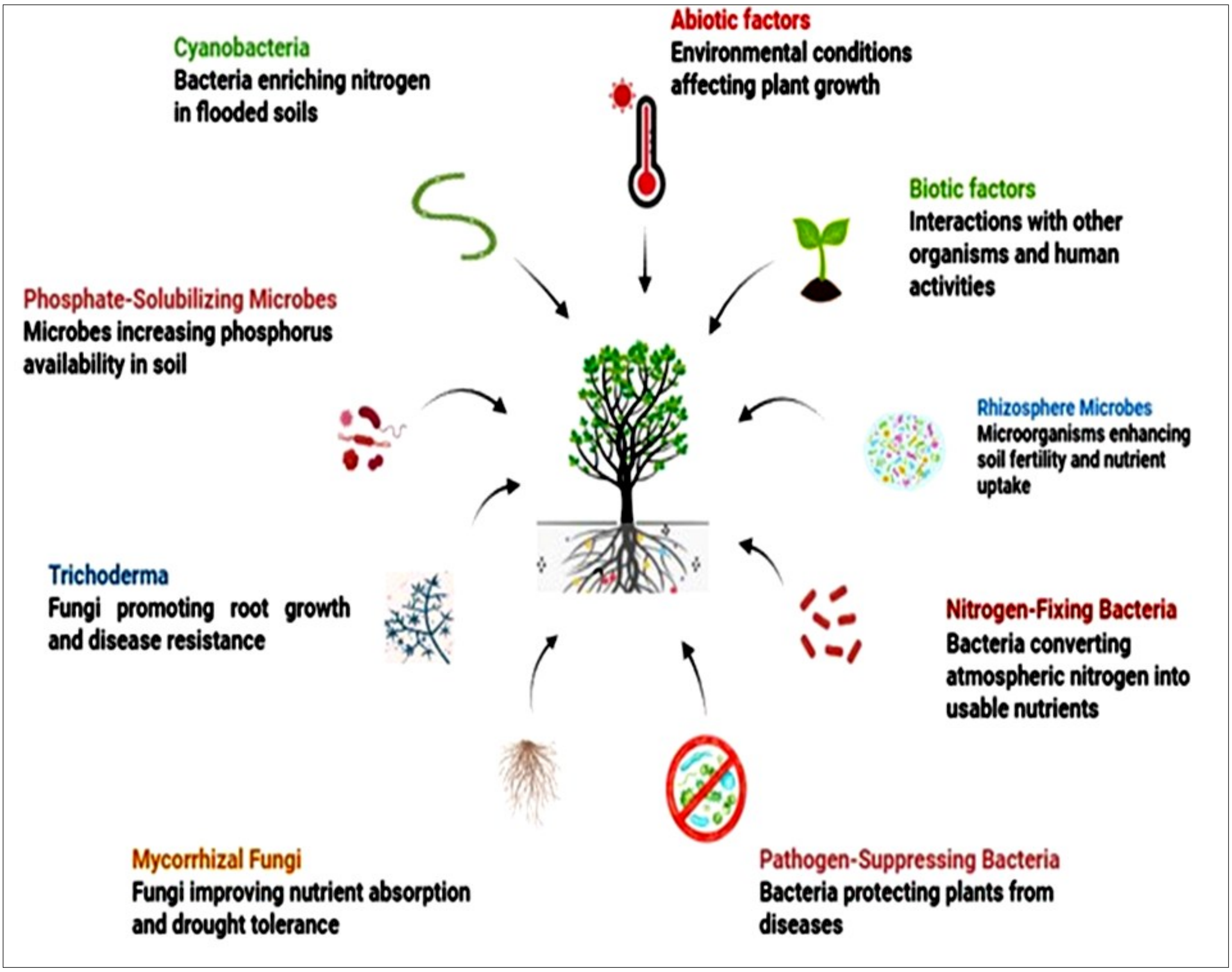

Fig. 1. Integrated roles of rhizospheric microorganisms and environmental factors in supporting plant vitality.

rhizosphere microbiome exemplifies this interaction: microbes enhance soil fertility and nutrient uptake (e.g., phosphate solubilisation by *Pseudomonas* spp.) (48) while root exudates mediate stress resistance by recruiting beneficial bacteria for biocontrol (e.g., *Bacillus* induced systemic resistance) (49). However, the dominance of specific signals such as ROS bursts under combined heat-pathogen stress-can determine whether plants prioritize growth arrest or defense activation (50). In maize, ABA accumulation under drought suppresses salicylic acid (SA)-dependent pathogen defenses, increasing susceptibility to Fusarium wilt (51). Arsenic stress in rice shifts root exudate profiles, favouring *Enterobacter* mediated arsenic detoxification over nutrient-acquisition symbioses (52).

Drought stress and pathogen interactions

The relationship between drought stress and pathogen infection can result in both beneficial and detrimental effects. Given the prevalence of drought stress and its influence on diseases and this combination is among the most significant stress factors universally impacting crop yields (53). The outcome of this interaction largely depends on variations in the H_2O pressure within plants. Alterations in hydraulic potentiality caused by a single stressor may either heighten a plant's vulnerability to subsequent stresses or enhance its ability to withstand them. For instance, when drought reduces a plant's hydration status, it can make the plant more vulnerable to root pathogens, as observed in *Phaseolus vulgaris*, where reduced water potential caused by drought increased vulnerability to *Macrophomina phaseolina* the pathogen responsible for charcoal rot infection (54). Indeed, there is evidence that *Nicotiana benthamiana* plants experience significant cell death when infected with *Sclerotinia sclerotiorum*, the pathogen that causes white mold in beans. However, cell death in drought-adapted plants is significantly less extensive (55).

Hormonal signalling pathways in abiotic–biotic stress crosstalk

The ABA hormone is a hormone identified mainly based on its responses to abiotic stress; a similar antagonistic relationship between the signalling pathways of SA and JA/ethylene exists in reaction to distinct biotic attackers. Recent studies support contrasting logics: ABA interacts with biotic stress signalling through both opposing and synergistic interactions, forming a detailed network of pathways with varying degrees of interaction (56). ABA can benefit pathogen defence mechanisms as well discovered that plants used ABA-induced stomatal closure, which also needed intact SA signalling, as a defence tactic to stop microbes entering their plant through open stomata. Additionally, ABA is required for the deposition. The induction of callose by β-aminobutyric acid (BABA) during the defence response against fungal pathogens despite the intriguing fact that ABA can also prevent the synthesis of callose generated by bacteria (57).

Abscisic acid likely plays a major role in modulating responses to both stresses. *Arabidopsis* plants treated with ABA exhibit increased susceptibility to a non-pathogenic variant of *Pseudomonas syringae* (58). As a result, a deficiency of ABA may cause increased pathogen resistance. For instance, the *Arabidopsis* mutants abi1-1 and abi2-1 demonstrated tolerance to the fungal disease *Fusarium oxysporum* and the oomycete *Peronospora parasitica*. In contrast, the tomato sitiens mutant, which has lowered ABA levels, demonstrated increased resistance to *B. cinerea* and increased levels of SA-dependent defence genes such as pathogenesis-related protein 1 (59).

In agriculturally important crops like tobacco and *Arabidopsis*, ABA treatment inhibits the systemic acquired resistance (SAR) pathway both before and after salicylic acid (SA) induction, highlighting its potential impact on crop immunity under stress. It also inhibits the production of key defense molecules, including lignins and phenylpropanoids (60). Additionally, ABA suppresses the activation of defence genes like plant defensin 1.2, which are normally induced by JA and ethylene and this suppression continues even after JA or ethylene are applied. Ethylene treatment subsequently triggers ABI1 and ABI2, which are negative regulators of ABA signalling (56). Critically, ABA also disrupts the synthesis of lignin and phenylpropanoids (61), which are essential for physical defense barriers in crops like wheat (*Triticum aestivum*) and rice (*Oryza sativa*) against fungal pathogens (62).

Biotic interactions under combined stresses

Nematode–insect interactions

The interaction between nematodes and insects creates compounded stress on plants, leading to more severe damage than either pest alone. Nematodes, such as root-knot nematodes, cause physical damage to plant roots, which can increase the plant's susceptibility to insect pests like aphids and beetles, potentially leading to enhanced damage and impaired nutrient dynamics (63). This combined stress also raises the risk of secondary pathogen infections due to weakened plant defences. Plants deploy various defence mechanisms, including mechanical barriers, chemical defences and hormonal signalling, to manage stress from both nematodes and insects. Mechanical defences include thickened cell walls and trichomes, while chemical defences involve secondary metabolites like phenolics and glucosinolates. Hormonal signalling pathways, particularly those involving JA and SA, play crucial roles in coordinating these defences (64). Transcriptomic studies reveal that plants exhibit distinct gene expression profiles under simultaneous nematode and insect stress with some genes specifically upregulated in reaction to combined stress example, the G-box binding factor 3 (GBF3) gene shown under various stress conditions, indicating its involvement in general stress responses. The combined stress of nematodes and insects can lead to significant reductions in plant growth and yield, posing considerable economic challenges (65). Additionally, research has identified specific genes and pathways that are responsive to both nematode and insect stress, highlighting the complex interactions between these pests and the plant's defensive strategies (66).

Plant–microbe interactions

Abiotic factors, including light, temperature, water availability and soil nutrient content, significantly affect the mode and consequence of plant-microbe interactions and the development of plant disease epidemics (67). Other elements influencing these biotic-abiotic interactions include plant genotype, age and developmental stage; the type and method of infection of the pathogen; the kind, intensity and timing of abiotic stress and the effect of stress on plant metabolic activities (67).

A. thaliana leaves of varying ages differentially prioritize both stress responses to sustain development and reproduction under combined stress. Environmental stresses like high salinity and drought were found to suppress host defense mechanisms in senescent rosette leaves via ABA signalling. However, this antagonistic effect was counteracted in new rosette leaves by Gretchen Hagen 3.12 (GH3.12), a signalling component of the defence phytohormone salicylic acid (SA) (68). In general, environmental stresses tend to enhance vulnerability to partially biotrophic and necrotropic pathogens, including facultative pathogens with low virulence while decreasing vulnerability to living tissue dependent pathogens (67). Various environmental stress conditions have been demonstrated to modify the transcriptomic response of plants to biotic pathogens, thereby increasing their vulnerability to infection. For instance, a transcriptomic analysis of *A. thaliana* exposed to a combination of heat, drought and virus infection showed that this stress combination suppressed the expression of transcripts related to R-mediated disease responses while increasing the expression of those associated with heat stress responses. These findings indicate that environmental stress elemental stress elements can modify pathogen-related signalling networks, potentially suppressing defence responses (69). For example, the combined effects of water stress and insect herbivory were found to decrease yields by enhancing herbivore performance on water-stressed faba beans. Moreover, elevated temperatures have been shown to enhance the toxicity of the pathogens in various plants (70). In *Oryza* plants are infected by the fungus *Magnaporthe oryzae*, the causative agent of rice blast, higher temperatures were associated with quicker pathogen multiplication and more severe disease indicators (71). In *Arabidopsis*, elevated temperatures reduced the expression of the immune receptor flagellin sensing 2 (FLS2), thereby suppressing immunity to the pathogen *Pseudomonas syringae* pv. *tomato*. Furthermore, it has been reported that simultaneous exposure to pathogens and high temperatures can impact not only pathogen resistance but also heat resistant. For instance, tomato plants showed increased susceptibility to tomato yellow leaf curl virus (TYLCV) under heat stress, while heat responses in tomato plants infected with TYLCV were compromised (72). In addition to high temperatures, some studies have suggested that drought conditions may increase plant vulnerability to pathogen attacks (70). A recent meta-analysis revealed that higher temperatures, increased CO_2 concentrations, drought stress and nutrient deficiencies resulted in greater herbivore consumption, particularly in agricultural systems (73).

Mitigation strategies for biotic–abiotic combined stresses

Enhancing crop resilience to different stresses involves complex regulatory pathways that govern gene expression, protein stability and physiological adaptations. These pathways help plants respond to drought, salinity, extreme temperatures and oxidative stress, improving their survival and productivity. Fig. 2 illustrates these regulatory mechanisms and their role in strengthening crop stress tolerance.

Integration of stress signalling pathways

Crops use various mechanisms to sense and integrate multiple stress signals, including specific sensors, calcium channels, ROS producers and kinases, which work together to create distinct stress responses. Stress signaling proteins often co-localize in “signalosomes”, which may be stress specific. Organelles communicate with the nucleus via anterograde and retrograde

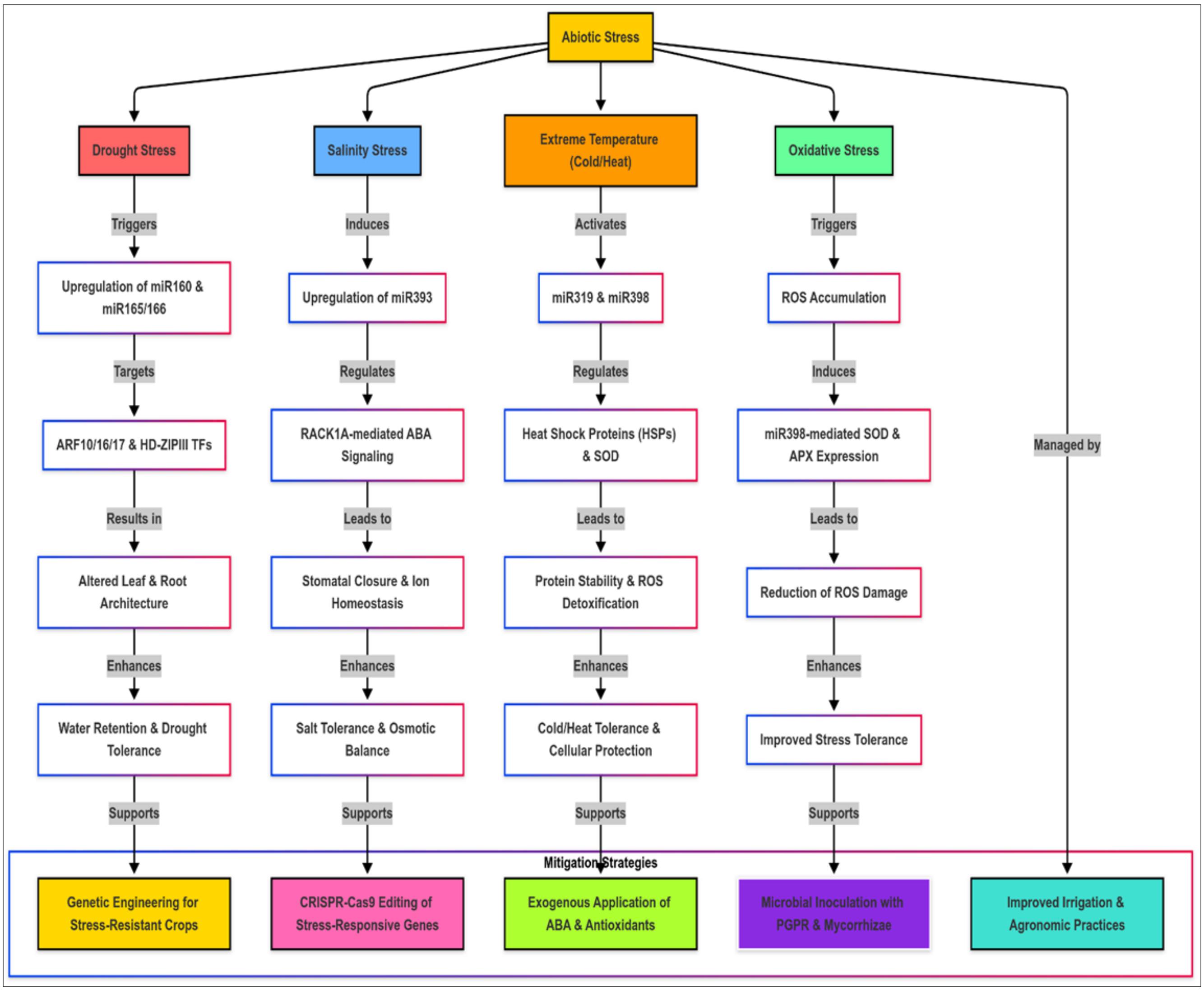

Fig. 2. Regulatory pathways and mitigation strategies for enhancing crop stress tolerance.

signalling to coordinate responses, utilizing processes such as ubiquitination and S-nitrosylation (74). Transcription factors (TFs) like MYB (myeloblastosis), WRKY (conserved amino acid sequence at the N-terminus of the DNA binding domain) and AP2/ERF (APETALA2/ethylene responsive factor) are crucial in integrating stress signals. For example, in *Arabidopsis*, MYB7 (myeloblastosis 7) and MYB32 (myeloblastosis 32) are upregulated during heat and salt stress, while WRKY DNA-binding protein 40 (WRKY40) modulates responses to salt and osmotic stress through ABA signalling. MYB7 and MYB32 are distinct members of the large MYB transcription factor family in *Arabidopsis*. Each gene has a unique function and their numbering reflects their individual roles in regulating stress responses like heat, salt and hormone signaling. The presence of multiple MYB proteins such as MYB7 and MYB32 reflects the large and diverse MYB transcription factor family in plants, where each member has evolved distinct roles. The numbering indicates different genes with unique sequences and functions, allowing *Arabidopsis* to finely regulate gene expression in response to various environmental stresses (75). Additionally, dehydration-responsive element binding transcription factor (DREB TFs) regulate responses to combined stresses like heat and drought by activating specific stress-responsive genes (76). Recent studies highlight molecular regulators like receptor-like kinases (RLKs) and MAPK cascades that mediate the integration of both stress signalling. For instance, THESEUS1 (THE1) links cell wall integrity to defence responses and root elongation under salt stress (62). Lysin-motif receptor like kinase is involved in both defense against pathogens and salinity responses (77). Additionally, NADPH oxidase proteins (RBOHs) are central in producing ROS signatures, crucial for stress responses. TFs like ERF1 integrate abiotic and biotic signals by regulating both pathogen defense and environmental stress tolerance. Calmodulin-binding transcription activators (CAMTA) TFs are key regulators of SA-mediated immunity and integrate cold stress responses with pathogen defense, demonstrating the complex crosstalk between abiotic and biotic stress pathways (78).

Role of microorganisms in stress mitigation

Extreme climate events resulting from climate change have adverse effects on soil properties, encompassing physical aspects such as texture, structure, bulk density and porosity, as well as chemical factors like pH and nutrient distribution. These alterations significantly influence the biological processes within the soil, exacerbating the negative effects that climate change has on the rhizosphere and ultimately impacting soil fertility and crop yields. Treating soil with bio-stimulants has proven to have the ability to reduce climate change effect on agriculture and the environment (79). The application of microbes and organic compounds are among the bio-stimulants used to counteract the damaging effects of adverse environmental stresses. Microorganisms help plant performance through various mechanisms, some of these promote plant growth and aid in nitrogen fixation, while others contribute to enhanced disease resistance and provide protection against abiotic stresses such as heat and drought (80). Microbial bio-stimulants are categorized into two broad groups: mycorrhizal fungi and plant growth promoting rhizobacteria Mycorrhizal fungi include different groups based on the mechanism used for colonizing plant tissues. The most relevant group from an agronomic perspective is constituted by endomycorrhizas also known as arbuscular mycorrhizal fungi (AMF) which occupy plants by piercing their tissues until the root cortex zone and extending their hyphae outside the root. Other important groups include vesicular arbuscular mycorrhizas and ectomycorrhizal, living only outside the root surface and surrounding the root cortex (81). The AMF can form a mutualistic symbiosis with most terrestrial plants providing multiple benefits to its host plant under various biotic or abiotic stress conditions. This kind of fungi improves the uptake of almost all essential nutrients, both macro and micronutrients like zinc and copper, meanwhile decreasing the absorption of Na and Cl, leading to growth stimulation (82). Inoculation with the AMF *Rhizophagus irregularis* or *Glomus proliferous* increases photosynthetic activities and stimulates the uptake of N, P and C, which move toward roots and support the growth of tubers in potato plants (83).

AMF reduces drought stress in crops like wheat, barley, maize, soybean, strawberry and onion by enhancing the volume of soil explored by roots (84), by controlling ABA metabolism and in consequence, stomatal regulation and enhancing proline and glutathione levels (85). In salt-affected soils, AMF inoculation enhances physiological parameters like photosynthetic rate, stomatal conductance and leaf water relations, mitigating the unfavourable effects of salinity on photosynthetic and gas exchange traits. Meanwhile, PGPRs are soil bacteria that play a key role in promoting plant growth and development. Some are associated with the roots, living in the rhizosphere and others live within the plant endosphere. PGPRs primarily belong to the genera *Agrobacterium*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Serratia* and *Streptomyces* (81). The use of these microorganisms has proven effective in promoting plant growth and development while enhancing plant stress tolerance through various mechanisms. The most important mechanisms are (i) the improvements in enzymatic antioxidant capacity in inoculated plants under diverse stressful conditions, such as salinity (86) or drought (87) resulting in a reduction of oxidative damage caused by stress situations. (ii) Nitrogen fixation transforming the atmospheric N_2 into ammonia (88). (iii) The solubilisation of inorganic phosphate (89). (iv) The production of indole-3-acetic acid (IAA) which induces root elongation improving the mineral absorption from soil, favouring plant growth (90). (v) 1-Aminocyclopropane-1-carboxilate deaminase (ACCD) production which is an enzyme produced by PGPR that can decrease ACC and ethylene accumulation making inoculated plants more resistant to ethylene induced stresses and (vi), the accumulation of osmolytes, under high temperatures or cadmium stress (91). Table 1 provides a comprehensive overview of the mechanisms by which microorganisms mitigate various environmental stresses in plants, including drought, salinity, heavy metals and temperature extremes.

Future challenges and strategies for enhancing crop resilience

Current efforts in plant genetics aim to explore genetic variability at the single nucleotide level through approaches such as genome-wide association study, genetic mapping and genome sequencing, integrated with sophisticated phenotyping methods. The study of the spatial and temporal regulation of gene expression and metabolic pathways has greatly advanced using large-scale sequencing, metabolomics, machine learning and CRISPR-Cas technologies. However, the success of these innovations relies on identifying the strategies that controls plant productivity, growth and yield under field conditions, especially when facing combinations of stress factors. Understanding the metabolic, cellular and developmental pathways that crops utilize to respond to their dynamic environments, including interactions with pathogens and pollinators, is essential. Developing new and improved crop

Table 1. Role of microorganism for mitigating effects of environmental stress conditions.

Micro-organism species	Crop	Stress condition	Improvement	References
Glomus sp.	Cucumber (*Cucumis sativus*)	Water stress	Increase in water use efficiency	(92)
Funneliformis mosseae + methyl jasmonate	Saffron (*Crocus sativus*)	Salt stress	Increase in SOD and CAT activities, chlorophyll content, reduction of damage	(93)
Funneliformis mosseae, *Rhizophagus irregularis*	Tomato (*Solanum lycopersicum*)	Water stress	Plant height, stomatal conductance, WUE and reduction of ROS and ABA	(94)
Pseudomonas aeruginosa, *Burkholderia gladioli*	Tomato (*Lycopersicum esculentum*)	Metal stress (Cd)	Increment in phenolic compound levels and osmoprotectants	(91)
Rhizoglomus fasciculatum, *Gigaspora* sp.	Pea (*Pisum sativum*)	Salt stress	Enhancement of biomass, chlorophyll content, accumulation of compatible osmolytes	(95)
Rhizophagus irregularis	Tomato (*Solanum lycopersicum*)	Salt stress	Growth of root and shoot biomass and improvement in leaf structure	(96)
Bacillus safensis	Wheat (*Triticum aestivum*)	Heat stress	Reduction of photosynthetic damage, increased osmoregulation and reduced ROS	(87)
Rhizoglomus irregularis, *Funneliformis mosseae*	Grapevine (*Vitis vinifera*)	Heat stress	Improved substrate carbon conversion efficiency and stomatal conductance, better plant growth	(97)
Bacillus sp.	Pea (*Pisum sativum*)	Salt stress	Increase in IAA, phosphate solubilization, siderophore production and antioxidant enzyme production	(86)
Rhizophagus intraradices	Eucalyptus (*Eucalyptus tereticornis*)	Mn toxicity	Induction of vascuolar sequestration and transport of complex Mn	(98)

varieties with a "balanced" genetic makeup is crucial for reducing losses caused by abiotic stresses, pests and instantly changing conditions. Key objectives involve enhancing photosynthetic efficiency, optimizing the regulation of stomata, ensuring stable and resourceful nutrient and water utilize and fostering beneficial plant-microorganism interactions.

Conclusion

Understanding the interplay between biotic and abiotic stress factors is essential for improving crop resilience and productivity. This review highlights the multifaceted effects of stress combinations, emphasizing how their simultaneous occurrence exacerbates plant vulnerabilities. Advances in genetic, molecular and physiological research have illuminated key mechanisms, such as hormone signaling, metabolic adjustments and beneficial plant-microbe interactions, that enable plants to mitigate these stresses. However, addressing the global challenges posed by climate change necessitates a holistic approach that integrates innovative crop management practices, microbial inoculations and biotechnological interventions. Developing stress-tolerant crop varieties and optimizing resource use efficiency are crucial for sustainable agriculture. Future efforts must prioritize understanding field-level stress dynamics and enhancing adaptive strategies to ensure food security in an increasingly unpredictable environment.

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Authors' contributions

All authors made equal contributions to its writing, data verification and interpretation. Each author reviewed and approved the final version of the manuscript.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used QuillBot, an AI-assisted writing tool, to reframe certain sentences to enhance the use of research-specific terminology. After utilizing this tool, the authors thoroughly reviewed and edited the content as necessary and take full responsibility for the accuracy and integrity of the final publication.

References

1. Gimenez E, Salinas M, Manzano-Agugliaro F. Worldwide research on plant defense against biotic stresses as improvement for sustainable agriculture. Sustainability. 2018;10(2):391. https://doi.org/10.3390/su10020391
2. Fich EA, Segerson NA, Rose JK. The plant polyester cutin: biosynthesis, structure and biological roles. Annu Rev Plant Biol. 2016;67(1):207-33. https://doi.org/10.1146/annurev-arplant-043015-111929
3. Mittler R. Abiotic stress, the field environment and stress combination. Trends Plant Sci. 2006;11(1):15-9. https://doi.org/10.1016/j.tplants.2005.11.002
4. Zhu JK. Abiotic stress signaling and responses in plants. Cell. 2016;167(2):313-24. https://doi.org/10.1016/j.cell.2016.08.029
5. Prasad PV, Pisipati SR, Momčilović I, Ristic Z. Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. J Agron Crop Sci. 2011;197(6):430-41. https://doi.org/10.1111/j.1439-037X.2011.00477.x
6. Carmo-Silva AE, Gore MA, Andrade-Sanchez P, French AN, Hunsaker DJ, Salvucci ME. Decreased CO_2 availability and inactivation of Rubisco limit photosynthesis in cotton plants under heat and drought stress in the field. Environ Exp Bot. 2012;83:1-11. https://doi.org/10.1016/j.envexpbot.2012.04.001
7. Awasthi R, Kaushal N, Vadez V, Turner NC, Berger J, Siddique KH, et al. Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. Funct Plant Biol. 2014;41(11):1148-67. https://doi.org/10.1071/FP13340
8. Cvikrová M, Gemperlová L, Martincová O, Vanková R. Effect of drought and combined drought and heat stress on polyamine metabolism in proline-over-producing tobacco plants. Plant Physiol Biochem. 2013;73:7-15. https://doi.org/10.1016/j.plaphy.2013.08.005
9. Casaretto JA, El-Kereamy A, Zeng B, Stiegelmeyer SM, Chen X, Bi YM, et al. Expression of *OsMYB55* in maize activates stress-responsive genes and enhances heat and drought tolerance. BMC Genomics. 2016;17:1-5. https://doi.org/10.1186/s12864-016-2659-5
10. Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, et al. Crop production under drought and heat stress: plant responses and management options. Front Plant Sci. 2017;8:1147. https://doi.org/10.3389/fpls.2017.01147
11. Huot B, Yao J, Montgomery BL, He SY. Growth-defense tradeoffs in plants: a balancing act to optimize fitness. Mol Plant. 2014;7(8):1267-87. https://doi.org/10.1093/mp/ssu049
12. Choudhury FK, Rivero RM, Blumwald E, Mittler R. Reactive oxygen species, abiotic stress and stress combination. Plant J. 2017;90(5):856-67. https://doi.org/10.1111/tpj.13299
13. Varshney RK, Sinha P, Singh VK, Kumar A, Zhang Q, Bennetzen JL. 5Gs for crop genetic improvement. Trends Plant Sci. 2020;25(3):226-38. https://doi.org/10.1016/j.pbi.2019.12.004
14. Ramu VS, Paramanantham A, Ramegowda V, Mohan-Raju B, Udayakumar M, Senthil-Kumar M. Transcriptome analysis of sunflower genotypes with contrasting oxidative stress tolerance reveals individual- and combined- biotic and abiotic stress tolerance mechanisms. PLoS One. 2016;11(6):e0157522. https://doi.org/10.1371/journal.pone.0157522
15. Farvardin A, González-Hernández AI, Llorens E, García-Agustín P, Scalschi L, Vicedo B. The apoplast: a key player in plant survival. Antioxidants. 2020;9(7):604. https://doi.org/10.3390/antiox9070604
16. Rui Y, Dinneny JR. A wall with integrity: surveillance and maintenance of the plant cell wall under stress. New Phytol. 2020;225(4):1428-39. https://doi.org/10.1111/nph.16166
17. Atkinson NJ, Urwin PE. The interaction of plant biotic and abiotic stresses: from genes to the field. J Exp Bot. 2012;63(10):3523-43. https://doi.org/10.1093/jxb/ers100
18. Ramegowda V, Senthil-Kumar M. The interactive effects of

simultaneous biotic and abiotic stresses on plants: mechanistic understanding from drought and pathogen combination. J Plant Physiol. 2015;176:47-54. https://doi.org/10.1016/j.jplph.2014.11.008

19. Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, et al. Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol. 2006;9(4):436-42. https://doi.org/10.1016/j.pbi.2006.05.014
20. Kamatchi KM, Anitha K, Kumar KA, Senthil A, Kalarani MK, Djanaguiraman M. Impacts of combined drought and high-temperature stress on growth, physiology and yield of crops. Plant Physiol Rep. 2024;29(1):28-36. https://doi.org/10.1007/s40502-023-00754-4
21. Nankishore A, Farrell AD. The response of contrasting tomato genotypes to combined heat and drought stress. J Plant Physiol. 2016;202:75-82. https://doi.org/10.1016/j.jplph.2016.07.006
22. Farooq M, Hussain M, Wahid A, Siddique KH. Drought stress in plants: an overview. In: Plant responses to drought stress. Berlin, Heidelberg: Springer; 2012. p. 1-33. https://doi.org/10.1007/978-3-642-32653-0_1
23. Lobell DB, Bänziger M, Magorokosho C, Vivek B. Nonlinear heat effects on African maize as evidenced by historical yield trials. Nat Clim Change. 2011;1(1):42-5. https://doi.org/10.1038/nclimate1043
24. Siebers MH, Yendrek CR, Drag D, Locke AM, Rios Acosta L, Leakey ADB, et al. Heat waves imposed during early pod development in soybean (*Glycine max*) cause significant yield loss despite a rapid recovery from oxidative stress. Glob Change Biol. 2015;21(8):3114-25. https://doi.org/10.1111/gcb.12935
25. Prasad PV, Boote KJ, Allen LH Jr. Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. Agric For Meteorol. 2006;139(3-4):237-51. https://doi.org/10.1016/j.agrformet.2006.07.003
26. Passioura J. The drought environment: physical, biological and agricultural perspectives. J Exp Bot. 2007;58(2):113-7. https://doi.org/10.1093/jxb/erl212
27. Nishiyama Y, Murata N. Revised scheme for the mechanism of photoinhibition and its application to enhance the abiotic stress tolerance of the photosynthetic machinery. Appl Microbiol Biotechnol. 2014;98:8777-96. https://doi.org/10.1007/s00253-014-6020-0
28. Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez-Cadenas A. Plant adaptations to the combination of drought and high temperatures. Physiol Plant. 2018;162(1):2-12. https://doi.org/10.1111/ppl.12540
29. Pornsiriwong W, Estavillo GM, Chan KX, Tee EE, Ganguly D, Crisp PA, et al. A chloroplast retrograde signal, 3′-phosphoadenosine 5′-phosphate, acts as a secondary messenger in abscisic acid signaling in stomatal closure and germination. Elife. 2017;6:e23361. https://doi.org/10.7554/eLife.23361
30. Panikulangara TJ, Eggers-Schumacher G, Wunderlich M, Stransky H, Schöffl F. Galactinol synthase 1. A novel heat shock factor target gene responsible for heat-induced synthesis of raffinose family oligosaccharides in Arabidopsis. Plant Physiol. 2004;136(2):3148-58. https://doi.org/10.1104/pp.104.042606
31. Li W, Zheng F, Zhang S, Lv F. A comprehensive analysis of the *Arabidopsis thaliana* gene expression in response to osmotic, cold and heat stresses based on RNA-Seq data. Sci Rep. 2015;5:15178. https://doi.org/10.1038/srep15178
32. Obata T, Witt S, Lisec J, Palacios-Rojas N, Florez-Sarasa I, Yousfi S, et al. Metabolite profiles of maize leaves in drought, heat and combined stress field trials reveal the relationship between metabolism and grain yield. Plant Physiol. 2015;169(4):2665-83. https://doi.org/10.1104/pp.15.01164
33. Conde A, Silva P, Agasse A, Conde C, Gerós H. Mannitol transport and mannitol dehydrogenase activities are coordinated in *Olea europaea* under salt and osmotic stresses. Plant Cell Physiol. 2011;52(10):1766-75. https://doi.org/10.1093/pcp/pcr121
34. Munns R. Comparative physiology of salt and water stress. Plant Cell Environ. 2002;25(2):239-50. https://doi.org/10.1046/j.0016-8025.2001.00808.x
35. Yoon HS, Kim SY, Kim IS. Stress response of plant H^+-PPase-expressing transgenic *Escherichia coli* and *Saccharomyces cerevisiae*: a potentially useful mechanism for the development of stress-tolerant organisms. J Appl Genet. 2013;54:129-33. https://doi.org/10.1007/s13353-012-0117-x
36. Miller G, Shulaev V, Mittler R. Reactive oxygen signaling and abiotic stress. Physiol Plant. 2008;133(3):481-9. https://doi.org/10.1111/j.1399-3054.2008.01090.x
37. Lugan R, Niogret MF, Leport L, Guégan JP, Larher FR, Savouré A, et al. Metabolome and water homeostasis analysis of *Thellungiella salsuginea* suggests that dehydration tolerance is a key response to osmotic stress in this halophyte. Plant J. 2010;64(2):215-29. https://doi.org/10.1111/j.1365-313X.2010.04323.x
38. Rivero RM, Mestre TC, Mittler RO, Rubio F, Garcia-Sanchez FR, Martinez V. The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. Plant Cell Environ. 2014;37(5):1059-73. https://doi.org/10.1111/pce.12199
39. Song L, Jiang Y, Zhao H, Hou M. Acquired thermotolerance in plants. Plant Cell Tissue Organ Cult. 2012;111:265-76. https://doi.org/10.1007/s11240-012-0198-6
40. Takahashi S, Murata N. How do environmental stresses accelerate photoinhibition? Trends Plant Sci. 2008;13(4):178-82. https://doi.org/10.1016/j.tplants.2008.01.005
41. Kumar RR, Goswami S, Sharma SK, Singh K, Rai GK, Singh M, et al. Differential expression of heat shock protein and alteration in osmolyte accumulation under heat stress in wheat. Plant Biochem Biotechnol. 2013;22(4):16-26. https://doi.org/10.1007/s13562-012-0106-5
42. Rahman MM, Hasanuzzaman M, Anee TI, Fujita M. Jasmonic acid priming augments antioxidant defense and mitigates oxidative damage in soybean under combined heat and drought stress. Plant Physiol Biochem. 2024;202:107908. https://doi.org/10.1016/j.plaphy.2023.108193
43. Chen L, Yang H, Fang Y, Guo W, Chen H, Zhang X, et al. Overexpression of GmMYB14 improves high-density yield and drought tolerance of soybean through regulating plant architecture mediated by the brassinosteroid pathway. Plant Biotechnol J. 2021;19(4):702-16. https://doi.org/10.1111/pbi.13496
44. Singh S, Parihar P, Singh R, Singh VP, Prasad SM. Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics and ionomics. Front Plant Sci. 2016;6:1143. https://doi.org/10.3389/fpls.2015.01143
45. Emamverdian A, Ding Y, Mokhberdoran F, Xie Y. Heavy metal stress and some mechanisms of plant defense response. Sci World J. 2015;2015:756120. https://doi.org/10.1155/2015/756120
46. Rivero L, Scholl R, Holomuzki N, Crist D, Grotewold E, Brkljacic J, et al. Signal integration under combined stress: hierarchy and trade-offs. Trends Plant Sci. 2022;27(5):498-510. https://doi.org/10.1016/j.tplants.2022.03.007
47. Gupta A, Rico-Medina A, Caño-Delgado AI. ABA-pathway dominance in drought-pathogen cross-talk. New Phytol. 2020;227(1):54-69. https://doi.org/10.1111/nph.16451
48. Pieterse CMJ, Van der Does D, Zamioudis C, Leon-Reyes A, Van Wees SCM. Networking by small-molecule hormones in plant immunity. Annu Rev Phytopathol. 2014;52:1-28. https://doi.org/10.1146/annurev-phyto-082712-102340

49. Choudhary A, Senthil-Kumar M. Drought attenuates plant defence against bacterial pathogens by suppressing the expression of CBP60g/SARD1 during combined stress. Plant Cell Environ. 2022;45(4):1127-45. https://doi.org/10.1111/pce.14275
50. Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. Abiotic and biotic stress combinations. New Phytol. 2014;203(1):32-43. https://doi.org/10.1111/nph.12797
51. Anderson JP, Badruzsaufari E, Schenk PM, Manners JM, Bowles DJ, Dixon RA. Antagonistic interaction between abscisic acid and salicylic acid signaling pathways modulates basal resistance of tomato to *Botrytis cinerea*. Plant Physiol. 2004;136(2):522-31. https://doi.org/10.1105/tpc.104.025833
52. Das P, Khare P, Singh RP, Yadav V, Tripathi P, Kumar A, et al. Arsenic-induced differential expression of oxidative stress and secondary metabolite content in two genotypes of *Andrographis paniculata*. J Hazard Mater. 2021;406:124302. https://doi.org/10.1016/j.jhazmat.2020.124302
53. Dixit S, Sivalingam PN, Baskaran RM, Senthil-Kumar M, Ghosh PK. Plant responses to concurrent abiotic and biotic stress: unravelling physiological and morphological mechanisms. Plant Physiol Rep. 2024;29(1):6-17. https://doi.org/10.1007/s40502-023-00766-0
54. Mayek-Pérez N, García-Espinosa R, López-Castañeda C, Acosta-Gallegos JA, Simpson J. Water relations, histopathology and growth of common bean during pathogenesis of *Macrophomina phaseolina* under drought stress. Physiol Mol Plant Pathol. 2002;60(4):185-95. https://doi.org/10.1006/pmpp.2001.0388
55. Ramegowda V, Senthil-Kumar M, Ishiga Y, Kaundal A, Udayakumar M, Mysore KS. Drought stress acclimation imparts tolerance to *Sclerotinia sclerotiorum* and *Pseudomonas syringae* in *Nicotiana benthamiana*. Int J Mol Sci. 2013;14(5):9497-513. https://doi.org/10.3390/ijms14059497
56. Asselbergh B, De Vleesschauwer D, Höfte M. Global switches and fine-tuning—ABA modulates plant pathogen defense. Mol Plant Microbe Interact. 2008;21(6):709-19. https://doi.org/10.1094/MPMI-21-6-0709
57. de Torres-Zabala M, Truman W, Bennett MH, Lafforgue G, Mansfield JW, Egea PR, et al. *Pseudomonas syringae* pv. tomato hijacks the *Arabidopsis* abscisic acid signalling pathway to cause disease. EMBO J. 2007;26:1434-43. https://doi.org/10.1038/sj.emboj.7601575
58. Mohr PG, Cahill DM. Abscisic acid influences the susceptibility of *Arabidopsis* to *Pseudomonas syringae* pv. tomato and *Peronospora parasitica*. Funct Plant Biol. 2003;30(4):461-9. https://doi.org/10.1071/FP02231
59. Asselbergh B, Curvers K, França SC, Audenaert K, Vuylsteke M, Van Breusegem F, et al. Resistance to Botrytis cinerea in *sitiens*, an abscisic acid-deficient tomato mutant, involves timely production of hydrogen peroxide and cell wall modifications in the epidermis. Plant Physiol. 2007;144(4):1863-77. https://doi.org/10.1104/pp.107.099226
60. Kusajima M, Yasuda M, Kawashima A, Nojiri H, Yamane H, Nakajima M, et al. Suppressive effect of abscisic acid on systemic acquired resistance in tobacco plants. J Gen Plant Pathol. 2010;76:161-7. https://doi.org/10.1007/s10327-010-0218-5
61. Anderson JP, Badruzsaufari E, Schenk PM, Manners JM, Desmond OJ, Ehlert C, et al. Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in *Arabidopsis*. Plant Cell. 2004;16(12):3460-79. https://doi.org/10.1105/tpc.104.025833
62. Sánchez-Vallet A, López G, Ramos B, Delgado-Cerezo M, Riviere MP, Llorente F, et al. Disruption of abscisic acid signaling constitutively activates *Arabidopsis* resistance to the necrotrophic fungus *Plectosphaerella cucumerina*. Plant Physiol. 2012;160(4):2109-24. https://doi.org/10.1104/pp.112.200154
63. Robertson WK, McClanahan E, Smith MS. Nematode-induced root damage and its influence on insect feeding. J Nematol. 2008;40(1):25-32.
64. Yang J, Duan G, Li C, Liu L, Han G, Zhang Y, et al. The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses. Front Plant Sci. 2019;10:1349. https://doi.org/10.3389/fpls.2019.01349
65. Jiang Z, van Zanten M, Sasidharan R. Mechanisms of plant acclimation to multiple abiotic stresses. Commun Biol. 2025;8:655. https://doi.org/10.1038/s42003-025-08077-w
66. Berens ML, Wolinska KW, Spaepen S, Ziegler J, Nobori T, Nair A, et al. Leaf age-dependent variation in stress hormone cross-talk. Proc Natl Acad Sci USA. 2019;116(6):2364-73. https://doi.org/10.1073/pnas.1817233116
67. Saijo Y, Loo EP. Plant immunity in signal integration between biotic and abiotic stress responses. New Phytol. 2020;225(1):87-104. https://doi.org/10.1111/nph.15989
68. Li W, Zhang Q, Sun J, Wang L, Chen D, Liu Y, et al. PBS3: a versatile player in and beyond salicylic acid signaling. New Phytol. 2023;237(3):1027-1042. https://doi.org/10.1111/nph.18558
69. Prasch CM, Sonnewald U. Heat, drought and virus stress alter signaling in Arabidopsis. Plant Physiol. 2013;162(4):1849-66. https://doi.org/10.1104/pp.113.221044
70. Zarattini M, Farjad M, Launay A, Cannella D, Soulié MC, Bernacchia G, et al. Abiotic stress effects on gene expression in plant-pathogen interactions. J Exp Bot. 2021;72(4):1020-33. https://doi.org/10.1093/jxb/eraa531
71. Onaga G, Wydra KD, Koopmann B, Séré Y, von Tiedemann A. Elevated temperature increases in planta expression levels of virulence related genes in *Magnaporthe oryzae* and compromises resistance in *Oryza sativa* cv. Nipponbare. Funct Plant Biol. 2016;44(3):358-71. https://doi.org/10.1071/FP16151
72. Anfoka G, Moshe A, Fridman L, Amrani L, Rotem OR, Kolot M, et al. Tomato yellow leaf curl virus infection mitigates the heat stress response of plants grown at high temperatures. Sci Rep. 2016;6:19715. https://doi.org/10.1038/srep19715
73. Hamann E, Blevins C, Franks SJ, Jameel MI, Anderson JT. Climate change alters plant-herbivore interactions. New Phytol. 2021;229(4):1894-910. https://doi.org/10.1111/nph.17036
74. Javed T, Shabbir R, Ali A, Martel G, Ren X, Kousar R, Rao AQ, Shahid AA, Chung G, Siddique KH, Liu S. Transcription Factors in Plant Stress Responses: Current and Future Prospects. Int J Mol Sci. 2020;21(7):2738. https://doi.org/10.3390/plants9040491
75. Zandalinas SI, Fichman Y, Devireddy AR, Sengupta S, Azad RK, Mittler R. Systemic signaling during abiotic stress combination. Proc Natl Acad Sci USA. 2020;117(24):13810-20. https://doi.org/10.1073/pnas.2005077117
76. Lata C, Prasad M. Role of DREBs in regulation of abiotic stress responses in plants. J Exp Bot. 2011;62(14):4731-48. https://doi.org/10.1093/jxb/err210
77. Brotman Y, Landau U, Pnini S, Lisec J, Balazadeh S, Mueller-Roeber B, et al. The LysM receptor-like kinase LysM RLK1 is required to activate defense and abiotic-stress responses induced by overexpression of fungal chitinases in *Arabidopsis* plants. Mol Plant. 2012;5(5):1113-24. https://doi.org/10.1093/mp/sss021
78. Kim YS, An C, Park S, Gilmour SJ, Wang L, Renna L, et al. CAMTA-mediated regulation of salicylic acid immunity pathway genes in *Arabidopsis* exposed to low temperature and pathogen infection. Plant Cell. 2017;29(10):2465-77. https://doi.org/10.1105/tpc.16.00865
79. Bibi F, Rahman A. Climate change impacts on agriculture and mitigation strategies. Agriculture. 2023;13(8):1508. https://doi.org/10.3390/agriculture13081508

80. Rai N, Rai SP, Sarma BK. Prospects for abiotic stress tolerance in crops utilizing phyto- and bio-stimulants. Front Sustain Food Syst. 2021;5:754853. https://doi.org/10.3389/fsufs.2021.754853

81. Vives-Peris V, De Ollas C, Gómez-Cadenas A, Pérez-Clemente RM. Root exudates: from plant to rhizosphere and beyond. Plant Cell Rep. 2020;39(1):3-17. https://doi.org/10.1007/s00299-019-02447-5

82. Evelin H, Giri B, Kapoor R. Contribution of *Glomus intraradices* inoculation to nutrient acquisition and mitigation of ionic imbalance in NaCl-stressed *Trigonella foenum-graecum*. Mycorrhiza. 2012;22:203-17. https://doi.org/10.1007/s00572-011-0392-0

83. Liu C, Ravnskov S, Liu F, Rubæk GH, Andersen MN. Arbuscular mycorrhizal fungi alleviate abiotic stresses in potato plants caused by low phosphorus and deficit irrigation/partial root-zone drying. J Agric Sci. 2018;156(1):46-58. https://doi.org/10.1017/S0021859618000023

84. Moradtalab N, Hajiboland R, Aliasgharzad N, Hartmann TE, Neumann G. Silicon and the association with an arbuscular-mycorrhizal fungus (*Rhizophagus clarus*) mitigate the adverse effects of drought stress on strawberry. Agronomy. 2019;9(1):41. https://doi.org/10.3390/agronomy9010041

85. Begum N, Qin C, Ahanger MA, Raza S, Khan MI, Ashraf M, et al. Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. Front Plant Sci. 2019;10:1068. https://doi.org/10.3389/fpls.2019.01068

86. Gupta A, Rai S, Bano A, Khanam A, Sharma S, Pathak N. Comparative evaluation of different salt-tolerant plant growth-promoting bacterial isolates in mitigating the induced adverse effect of salinity in *Pisum sativum*. Biointerfae Res Appl Chem. 2021;11(5):13141-54. https://doi.org/10.33263/BRIAC115.1314113154

87. Sarkar J, Chakraborty B, Chakraborty U. Plant growth promoting rhizobacteria protect wheat plants against temperature stress through antioxidant signalling and reducing chloroplast and membrane injury. J Plant Growth Regul. 2018;37(4):1396-412. https://doi.org/10.1007/s00344-018-9789-8

88. Singh RK, Singh P, Li HB, Yang LT, Li YR. Soil–plant–microbe interactions: use of nitrogen-fixing bacteria for plant growth and development in sugarcane. In: Plant-microbe interactions in agro-ecological perspectives. Singapore: Springer; 2017. p. 35-59. https://doi.org/10.1007/978-981-10-5813-4_3

89. Alori ET, Glick BR, Babalola OO. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. Front Microbiol. 2017;8:971. https://doi.org/10.3389/fmicb.2017.00971

90. Grobelak A, Napora A, Kacprzak MJ. Using plant growth-promoting rhizobacteria (PGPR) to improve plant growth. Ecol Eng. 2015;84:22-8. https://doi.org/10.1016/j.ecoleng.2015.07.019

91. Khanna K, Kohli SK, Ohri P, Bhardwaj R, Al-Huqail AA, Siddiqui MH, et al. Microbial fortification improved photosynthetic efficiency and secondary metabolism in *Lycopersicon esculentum* plants under Cd stress. Biomolecules. 2019;9(10):581. https://doi.org/10.3390/biom9100581

92. Bicer S, Erdinc C, Comlekcioglu N. A comparative analysis of co-inoculation of microbial biostimulants at different irrigation levels under field conditions on the cucumber growth. Gesunde Pflanzen. 2023;75(4):1237-56. https://doi.org/10.1007/s10343-022-00804-1

93. Hamidian M, Movahhedi-Dehnavi M, Sayyed RZ, Almalki WH, Gafur A, Fazeli-Nasab B. Co-application of Mycorrhiza and methyl jasmonate regulates morpho-physiological and antioxidant responses of *Crocus sativus* (Saffron) under salinity stress conditions. Sci Rep. 2023;13(1):7378. https://doi.org/10.1038/s41598-023-34359-6

94. Goicoechea N, Antolín MC. Increased nutritional value in food crops. Microb Biotechnol. 2017;10(5):1004-7. https://doi.org/10.1111/1751-7915.12764

95. Bijalwan P, Jeddi K, Saini I, Sharma M, Kaushik P, Hessini K. Mitigation of saline conditions in watermelon with mycorrhiza and silicon application. Saudi J Biol Sci. 2021;28(7):3678-84. https://doi.org/10.1016/j.sjbs.2021.05.019

96. Hashem A, Abd_Allah EF, Alqarawi AA, Al Huqail AA, Egamberdieva D, Wirth S. Alleviation of cadmium stress in *Solanum lycopersicum* L. by arbuscular mycorrhizal fungi via induction of acquired systemic tolerance. Saudi J Biol Sci. 2016;23(2):272-81. https://doi.org/10.1016/j.sjbs.2015.11.002

97. Nogales A, Ribeiro H, Nogales-Bueno J, Hansen LD, Gonçalves EF, Coito JL, et al. Response of mycorrhizal 'Touriga Nacional' variety grapevines to high temperatures measured by calorespirometry and near-infrared spectroscopy. Plants. 2020;9(11):1499. https://doi.org/10.3390/plants9111499

98. De Oliveira VH, Montanha GS, Carvalho HW, Mazzafera P, de Andrade SA. Mycorrhizal symbiosis alleviates Mn toxicity and downregulates Mn transporter genes in *Eucalyptus tereticornis* under contrasting soil phosphorus. Plant Soil. 2023;489(1):361-83. https://doi.org/10.1007/s11104-023-06024-4

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