

## STRESS RESPONSE CROSSTALK IN PLANTS - A REVIEW

NEENA ADICHIRATTLE<sup>1</sup>, MUHAMMAD MUNIR<sup>2\*</sup> AND BINU THOMAS<sup>1</sup>

<sup>1</sup>Centre for Post Graduate Studies and Research in Botany, St. Joseph's College (Autonomous), Devagiri, Calicut-673 008, Kerala, India

<sup>2</sup>Date Palm Research Center of Excellence, King Faisal University, Al-Ahsa, P.O. Box 31982, Saudi Arabia

\*Corresponding author's email: [mmunir@kfu.edu.sa](mailto:mmunir@kfu.edu.sa)

### Abstract

There are different levels at which abiotic and biotic stress can interact, depending on the type of stress (ionic or osmotic), the lifestyle, the pathogen infection strategy (biotrophic or necrotrophic, infection by direct penetration through stomata, etc.), and the stage of pathogenesis. Scientists have primarily studied plant responses to individual stress, but few have explored the complex stress response in plants against combined or sequential abiotic stresses and their interaction. Understanding the regulatory networks in agronomically important crops can help design strategies for developing plants with tolerance to multiple stress combinations, considering the world population's current food needs. Stress-tolerant plant varieties can develop when one stress can mask the effects of another stress, allowing for better growth and resistance to environmental stressors. This review provides a comprehensive overview of recent studies that examine the interactive effects of combined and sequential stresses on crop plants. We assume that this work will ameliorate our understanding and elucidate the mechanism of stress tolerance in plants. Additionally, it will provide valuable insights for plant physiologists, agronomists, and molecular biologists.

**Key words:** Stress crosstalk, Stress signaling, Abiotic stress, Drought, Salinity, Combinatorial stress, Plant response.

### Introduction

By 2050, the world's population is projected to approach 10 billion. Ensuring food security for the emerging population is one of the major challenges for the future. The population expansion will significantly increase food demand, making it a significant challenge to ensure sufficient production (Ranganathan *et al.*, 2018). There are several factors that can hinder crop production. These factors can be categorized into biotic and abiotic factors, which are known as plant stresses. In a complex environment, plants have to cope with a multitude of stress factors and have developed a variety of defence responses to adapt, survive, and reproduce under stress (Pieterse *et al.*, 2009). Crops produce only about half of their potential yield under field conditions due to abiotic stresses such as drought, salinity, temperature extremes, pollution, poor soil quality, and flooding (Hatfield & Walthall, 2015). Abiotic stress also contributes significantly to the yield gap, with field losses to insect pests estimated at more than 10% (Kerchev *et al.*, 2011) and rising to 50–80% in the absence of control measures (Bruce, 2010). Insects, fungi, bacteria, viruses, and other pathogens can attack crops, causing damage to leaves, stems, roots, and fruits. They can reduce plant vigor, inhibit photosynthesis, and transmit diseases that can significantly reduce crop yields (Kumar & Rathor, 2020). Weed plants also compete with crops for resources such as light, water, nutrients, and space, leading to reduced crop growth and yield loss (Sardana *et al.*, 2017).

Researchers have extensively examined the signaling and response pathways of plants to biotic and abiotic stresses, aiming to alleviate various agricultural limitations (Foyer *et al.*, 2016). With the advancement of omics technologies and ongoing experiments on functional characterizations of individual genes, it has become evident that environmental adaptation is under strict regulation, which is critical for plant survival (López *et al.*, 2008). This regulatory network, also known as the signal transduction pathway, involves various components in

responding to various stresses, which may function antagonistically or prioritize certain responses over others, thereby compromising plant resistance to multiple stresses simultaneously (Glazebrook, 2005; Yasuda *et al.*, 2008).

Reactive oxygen species (ROS) signaling (Miller *et al.*, 2008), plant hormones (Bari & Jones, 2009; Peleg & Blumwald, 2011), changes in redox status (Munné-Bosch *et al.*, 2013), and inorganic ion fluxes such as Ca<sup>2+</sup> (Martí *et al.*, 2013; Vivek *et al.*, 2013) are some of the most important parts of the regulatory networks that help plants adapt to environmental stress, recognize pathogens, and defend themselves. According to omics data analyses, these components appear to be at least partially shared between both abiotic and biotic stress signaling, indicating crosstalk and convergence of mechanisms in these pathways, as well as the existence of a general stress response (Walley *et al.*, 2007). The overlapping signaling pathway, or signal crosstalk, ultimately produces a response distinct from the individual response's outcome (Pastori & Foyer, 2002). This combined stress response is of great significance because the positive crosstalk between the stress signals results in a combinatorial effect that allows the plants to withstand the dreadful stress condition and produce resistant varieties over time. Various genes upregulate in response to these stress factors, mitigating the impact of stress and adjusting the cellular milieu and plant tolerance. In nature, stress does not generally come in isolation, and many stresses act hand in hand with each other. In response to these stress signals that crosstalk with each other, nature has developed a variety of pathways for combating and tolerating them. These pathways act in cooperation to reduce stress (Mahajan & Tuteja, 2005).

In contrast, under field conditions, numerous stresses can occur in combination or simultaneously and may specifically alter plant metabolism compared to individual stress treatments (Rizhsky *et al.*, 2002). Due to the higher frequency of concurrent occurrences of multiple stresses under field conditions, the plant response may differ from that tested under laboratory conditions (Tambussi *et al.*,

2020). Therefore, to understand the holistic survival mechanism of plants, it is essential to study the combined and sequential abiotic stresses under the natural environment, which is still far less investigated (Sewelam *et al.*, 2020). Despite a significant surge in abiotic stress-related studies over the past decade, the majority of these experiments have focused on how plants react to individual stress treatments under controlled conditions. Our knowledge of the molecular basis of the additive responses to combined and sequential abiotic stresses is considerably less (Obata *et al.*, 2015).

### What is a plant stress?

Selye introduced the concept of stress in 1956, defining it as any unfavorable changes and environmental constraints that negatively affect a plant and cause severe damage. Plants under stress experience adverse environmental factors or internal disturbances that disrupt their normal physiological functions and growth. Abiotic stress results in a reduction of up to >50% in almost all plant species under stress (Wang *et al.*, 2005). Insects, mites, nematodes, and pathogens like fungi, bacteria, and viruses cause biotic stress, which can damage plant tissues, consume plant nutrients, cause diseases, and affect plant health (Lal *et al.*, 2018). Internal plant disturbances, such as hormonal imbalances, genetic abnormalities, metabolic disruptions, or physiological disorders, can cause stress, such as excessive ROS production leading to oxidative stress (Raza *et al.*, 2022). A biological condition, which may be stressful for one plant, may be optimal for another plant. The most practical definition of biological stress is an adverse force or condition that inhibits the normal functioning and well-being of a biological system, such as plants (Jones *et al.*, 1989).

### Stress signaling: An overview

The receptors present on the plant cell membrane first perceive the stress. The downstream transduction of the signal generates second messengers such as calcium, ROS, and inositol phosphates. Second messengers amplify the stress signal; that is, they will prevent signal sequestration. These second messengers, such as inositol phosphates, further modulate the intracellular calcium level (Jain *et al.*, 2018). Calcium-binding proteins, also known as Ca<sup>2+</sup> sensors, sense this perturbation in cytosolic Ca<sup>2+</sup> levels. Examples of calcium-sensing proteins include calmodulin-like proteins (CAM), calcium-dependent kinases (CDPKs), calcineurin B like proteins (CBLs). These sensors apparently lack any enzymatic activity and change their conformation in a calcium-dependent manner. These sensory proteins then interact with their respective interacting partners, often initiating a phosphorylation cascade and targeting the major stress-responsive genes or the transcription factors controlling these genes. The products of these stress genes ultimately lead to plant adaptation, which helps the plant survive and overcome unfavorable conditions. Thus, plants respond to stresses as individual cells and synergistically as a whole organism (Raina *et al.*, 2021). Stress-induced changes in gene expression may contribute to the production of hormones

such as ABA, salicylic acid, and ethylene. These molecules may amplify the initial signal and initiate a second round of signaling that may follow the same pathway or use altogether different components of the signaling pathway (Divi *et al.*, 2010). Certain molecules, also known as accessory molecules, may not directly participate in signaling but may contribute to the modification or assembly of signaling components. Protein modifiers, such as enzymes for myristoylation, glycosylation, methylation, and ubiquitination, may co-translationally add these proteins to signaling proteins (Partridge, 2009). We can broadly categorize the various stress-responsive genes into early-induced and late-induced groups. At the end, a stress signal can ultimately result in the plant's acclimation or death (Fig. 1).

Minutes after the perception of a stress signal, early induced genes initiate and frequently exhibit transient expression. The genes include various transcription factors, as their induction does not require the synthesis of new proteins, and signaling components are already primed (Kilian *et al.*, 2007). On the other hand, the late-induced category encompasses most other genes that activate slowly, typically after hours of stress perception. These genes often maintain their expression over time. These genes include the major stress-responsive genes RD (responsive to dehydration)/KIN (cold-induced), induced)/COR (cold-responsive), which encode and modulate the proteins needed for synthesis, such as LEA-like proteins (late embryogenesis abundant), antioxidants, membrane-stabilizing proteins, and the synthesis of osmolytes (Mahajan & Tuteja, 2005; Gallino *et al.*, 2018).

### Stress crosstalk: Synergistic and antagonistic effects on plants

The first physiological effect in plants under combined drought and high-temperature stress was reduced water uptake and increased canopy temperature through reduced stomatal conductance. Reactive oxygen species (ROS) accumulated in most of the combined stresses due to their involvement in cell signalling and defence process activation. Researchers discovered that both drought and high temperatures stress plants, leading to an increase in ROS. This makes the membranes more damaged through lipid peroxidation, which slows down the rate of photosynthesis. More photoinhibition, the deactivation of RuBisco (ribulose bisphosphate carboxylase/oxygenase), disruption in electron transport, and damage to the chloroplast's ultrastructure all contribute to the lower carbon uptake. However, combined drought and high-temperature stress increased the respiration rate. Under combined stresses, decreased synthesis and increased utilization of carbohydrates can result in reduced crop growth and grain yield. Various reproductive processes, including micro- and mega-sporogenesis, anthesis, pollination and fertilization, and embryo and seed development, experienced adverse effects under combined stress. The response to combined stress is complex and entails the contribution of various signalling molecules, transcription factors, hormones, and secondary metabolites for tolerance or susceptibility (Awasthi *et al.*, 2014; Annadurai *et al.*, 2023; Kamatchi *et al.*, 2024).

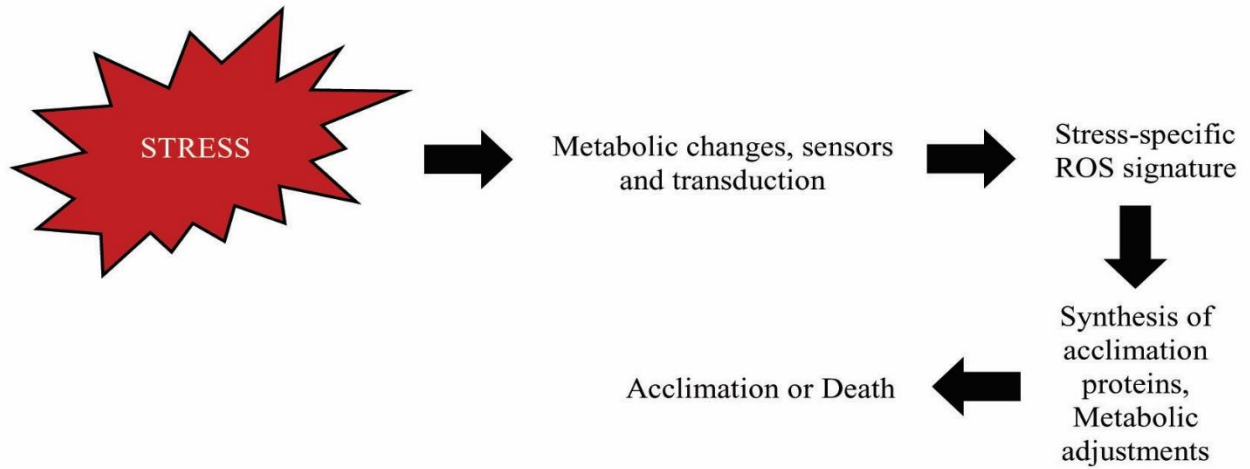


Fig. 1. A general presentation of plant stress response in plants.

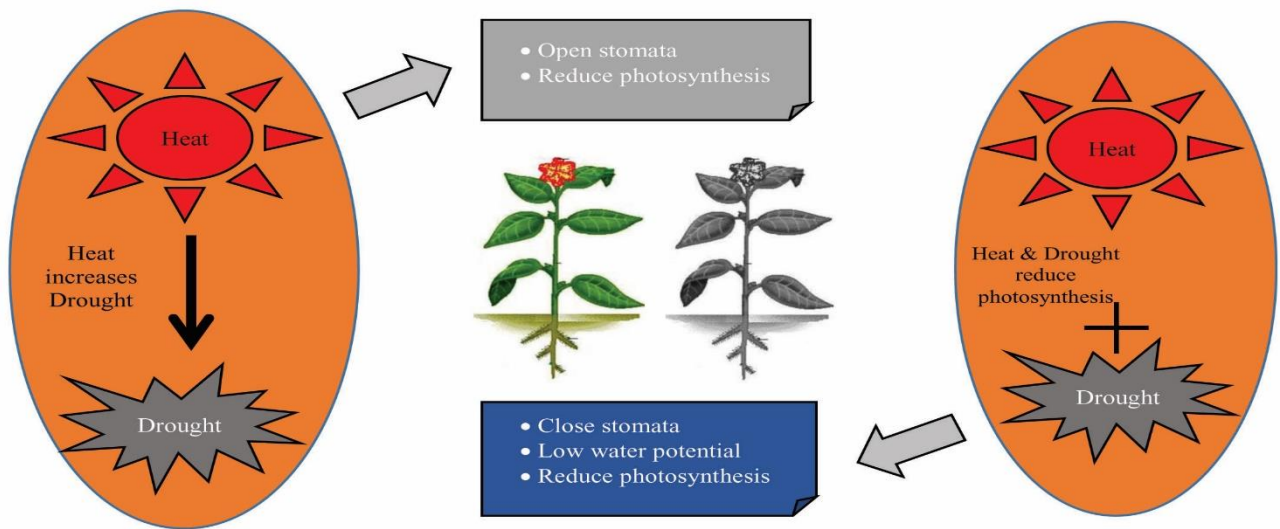


Fig. 2. Schematic representation showing the effects of combined stress on plants. The effect of combined stresses on plants expressed by heat and drought stressors. Combinatorial effect of both stressors trigger the retardation of physiological processes such as photosynthesis.

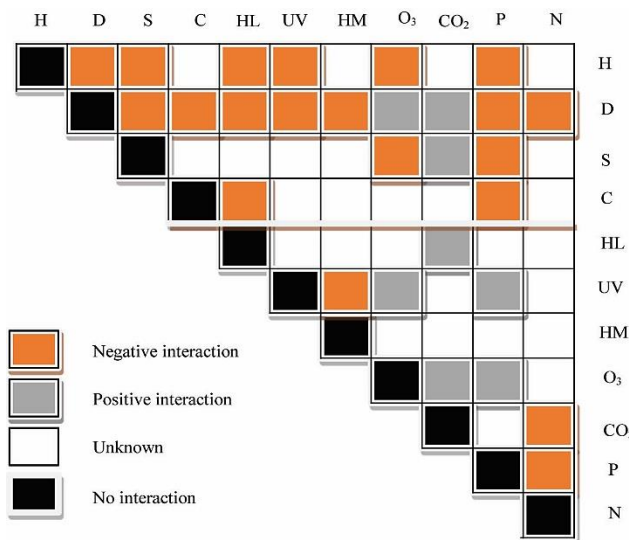


Fig. 3. A stress matrix indicating the interaction of different stress factors. Here H-Heat, D-Drought, S-Salinity, C-Chilling, HL-High light, UV-Ultra violet rays, HM-Heavy metal, O<sub>3</sub>-Ozone, CO<sub>2</sub>-High concentration of carbon dioxide, P-Pathogen attack, and N-Nutrient.

Almost all environmental stressors have corresponding consequences and reactions, including reduced photosynthetic activity and development, oxidative damage, hormonal changes, and accumulation of stress-related proteins (Aroca *et al.*, 2011). The ability of plants to absorb water from the roots plays a crucial role in minimizing growth loss caused by dehydration, together with the closing of stomata (Christmann *et al.*, 2007). Investigating the collective impact of heat and drought stress is crucial, particularly in regions that are affected by drought and have arid/semi-arid climate. This is because these two stressors often coexist in field conditions (Raja *et al.*, 2020). Several studies have examined combined effects of heat and drought stress on the growth and production of various grasses, barley, maize, and sorghum (Osakabe *et al.*, 2014). The co-occurrence of heat stress and drought is likely to have a substantial impact on the physiological and morphological attributes, as well as the metabolism, particularly photosynthesis (Rollins *et al.*, 2013) (Fig. 2).

The concurrent occurrence of drought and heat resulted in the accumulation of substantial quantities of proline, glycine betaine, sugar, inositol, and mannitol in the leaves of

*Mentha piperita* and *Catharanthus roseus*. This suggests that osmotic adjustment serves as a mechanism for stress tolerance in these plants (Alhaithloul *et al.*, 2019). Plants under drought and heat stress accumulated sucrose and other sugars, including maltose and glucosamine, according to metabolic profiling of plants exposed to drought, heat stress, or a combination of drought and heat stress (Kumar *et al.*, 2021; Choudhary *et al.*, 2022). Similarly, researchers discovered that the combined effects of heat and drought on *Arabidopsis thaliana* were different from those on plants that only received one type of stress treatment (drought or heat stress). Transcriptome analysis revealed a new pattern of defence response in plants that had experienced both drought and heat stress. Two multigene defence pathways (drought and heat stress) partially combine in this pattern, along with 454 transcripts specifically expressed in plants during a combination of drought and heat stress. The physiological and molecular characterization revealed many similarities between the responses of *Arabidopsis* and tobacco to this stress combination, indicating that different plants share this mode of defence response (Rizhsky *et al.*, 2004). Water deficit and high temperature on *Arabidopsis* plants resulted in additive effects in root allocation, reproductive allocation, hyponasty, and specific leaf area (Vile *et al.*, 2011). Heat, drought, and turnip mosaic virus stressors in *Arabidopsis* resulted in the expression of 23 particularly regulated genes, 11 differently regulated genes, and a reduced R-gene-mediated response (Giraud *et al.*, 2008). High temperatures and pathogen infection in *Arabidopsis* also caused changes in the R-like gene SNC1 and the R gene N, which alter the temperature sensitivity of defence responses (Zhu *et al.*, 2010). High temperature and drought significantly impact photosynthetic rate, transpiration rate, transcriptome, and metabolome in Masson pine. Starch and sucrose metabolism become pivotal carbon metabolic pathways, with Trehalose, *PmTPS1*, *PmTPS5*, and *PmTPPD* genes playing crucial roles as metabolites and regulators within these pathways (Li *et al.*, 2024). High temperature and drought stress are expected to decrease crop growth and yields and threaten food security. The study found that combined heat and drought significantly impacted physiological and yield traits of wheat cultivars, with single grain weight reduced by 13%-27% under drought stress and 43%-83% under combined heat and drought stress. Heat stress significantly decreased grain number, yield, and straw yield. Wheat cultivar responses were similar for heat but different for drought and combined heat and drought treatments (Mahrookashani *et al.*, 2017). In another study, high temperature and drought had a considerable impact on two wheat varieties. For leaf chlorophyll content, grain counts, and harvest index, the combined effects of high temperature and drought were larger than the additive effects of high temperature or drought alone. High temperature stress and its combination with drought stress resulted in the overexpression of EF-Tu in spring wheat cultivars (Prasad *et al.*, 2011). Combined drought and high temperature negatively affected the *Zea mays* in different aspects, such as dry weight, length, surface area, root mass ratio, and seminal lateral root production (Vescio *et al.*, 2020).

Drought significantly reduced chlorophyll content, photosynthesis rate, stomatal conductance, transpiration,

and leaf water content in the date palm cultivars Khalas, Reziz, and Sheshi; however, leaf intercellular CO<sub>2</sub> concentration and water use efficiency increased. This study revealed that 1118 expressed sequence tags (ESTs), specifically 345 from Khalas, 391 from Reziz, and 382 from Sheshi, were sensitive to drought. To mitigate drought stress, these cultivars used a multivariate approach. About half of the ESTs were linked to photosynthesis regulation, structure, signal transduction, auxin biosynthesis, osmoregulation, stomatal conductance, protein synthesis, and cell structure modulation (Alhajhoj *et al.*, 2022). In another study, the date palm cultivar Khalas did well in terms of growth, productivity, and fruit quality when it was exposed to a 25% drought (75% ETc) (Alnaim *et al.*, 2022). In the date palm cultivar Sukary, reducing or increasing irrigation water to 100% ETc reduced physiological traits such as photosynthesis, stomatal conductance, and transpiration (Ghazzawy *et al.*, 2023). Severe drought conditions (40 and 60% ETc) significantly reduced leaf growth, plant dry biomass, and physiological and biochemical traits of date palm cultivars; however, moderate drought conditions (80% ETc) had a minimal effect. The study also revealed that the drought-related characteristics decreased gradually with an increase in water stress duration over 24 months (Ali-Dinar *et al.*, 2023). In *Robinia pseudoacacia* seedlings, drought and salinity significantly decreased leaf water potential and stomatal conductance. Drought increased stomatal density but decreased stomatal area, while salinity alone and combined with drought decreased stomatal length or width. Additionally, salinity and drought decreased xylem specific hydraulic conductivity, while percent loss of conductivity increased. The net photosynthetic rate and transpiration rate decreased, while leaf water use efficiency increased. The chlorophyll content index and maximum light quantum efficiency both decreased. Soluble sugars, starch, and total non-structural carbohydrates decreased in drought (Fan *et al.*, 2024). Another study found that onion cultivars Elit and Hazar had higher H<sub>2</sub>O<sub>2</sub>, maximum damage to pigments, and least accumulation of phenolics and osmolytes under drought and salinity stress conditions. Cultivar Şampiyon performed better under salt stress but had poor antioxidant defense under drought. Resilient cultivars had higher accumulation of osmolytes, antioxidants, and phenolics, and showed higher transcript levels of superoxide dismutase, ascorbate oxidase, and transcription factors (Chaudhry *et al.*, 2024). Two wheat genotypes exhibited a significant shift in plant growth and biomass (shoot and root dry weights) when exposed to drought and salt alone, and their combination (Dugasa *et al.*, 2018). Compared to individual drought or salinity stress, combined stress on maize caused a considerable reduction in primary root length (Li *et al.*, 2021). Photosynthetic efficiency, particularly the PSII activity of sugarcane was substantially affected by drought and cold (Sales *et al.*, 2013).

Low and high temperature stresses can potentially alter the antioxidative defense system's effects by altering the relationship between drought and salt stresses. Root and shoot elongation of wheat seedlings decreases under drought and salt stresses, while growth inhibition is observed under salt stress. Low temperature stress increases ascorbic acid,

catalase, and glutathione reductase activities, while high temperature stress increases carotenoids and glutathione reductase activities. The  $\alpha$ -tocopherol content increases under drought and salt stresses but decreases under high temperature stress (Keleş & Öncel, 2002). A study found that combined stress of salinity and high temperature significantly inhibited CO<sub>2</sub> assimilation and photosystem II efficiency, specifically promoting the expression of nucleoside diphosphate kinase 1 in *Suaeda salsa* (Li *et al.*, 2011). High temperature and ozone stress in silver birch decrease root shoot ratio in it (Kasurinen *et al.*, 2012). Salinity and pathogen stress in rice downregulated *OsMAPK5* expression increased pathogenesis-related genes expression and resistance to fungal and bacterial pathogens, while reduced tolerance to drought, salt, and cold, while overexpression increased *OsMAPK5* kinase activity and stress tolerance (Xiong & Yang, 2003).

Drought and low nitrogen levels in wheat seedlings have significant interaction in regulation of nitrate signaling, uptake, and assimilation genes, while low nitrogen stress leads to ABA accumulation (Mahmoud *et al.*, 2020). Red maple plants under drought and heavy metal stress experienced significant reductions in photosynthesis, stomatal conductance, transpiration, water use efficiency, and phosphorus uptake in seed and shoot (de Silva *et al.*, 2012). In another study, Mungbean under drought and low phosphorus stress showed significant reductions in photosynthesis, stomatal conductance, transpiration, water use efficiency, and phosphorus uptake in seed and shoot (Meena *et al.*, 2021). The study by Alameda *et al.* (2012) found that tobacco plants exposed to drought, compacted soil, and mechanical stress had a negative cumulative effect, resulting in reduced growth and fine roots, while xylem and root diameter increased. The combined stress of drought and UV-B radiation can lead to antagonistic, additive, or synergistic responses due to the interplay between metabolic shuts in plants (Bandurska *et al.*, 2013). Similarly, high temperatures and UV C stresses reduced total sugar content in strawberries, suggesting the benefits of applying each treatment separately and potentially extending postharvest life (Pan *et al.*, 2004). Drought and high light in *Arabidopsis* resulted in mutant seedlings, deficient in alternative oxidase, exhibited anthocyanin accumulation, altered photosynthetic efficiency, increased superoxide radical, and reduced root (Giraud *et al.*, 2008). Higher number of gene expression was observed when sunflower plants were exposed to high light (89 genes), high temperature (113 genes), and their combination (186 genes) treatments (Hewezi *et al.*, 2008). High temperature exposure to elevated CO<sub>2</sub> concentration in soybeans and maize leads to increased photosynthetic rates, potentially reducing the impact of moderately elevated temperatures on crop yield (Sicher & Bunce, 2015).

Low temperature inhibits both virus- and transgene-triggered RNA silencing in plants. Thus, plants become more susceptible to viruses. Transgenic plants lose their RNA-silencing-based phenotypes. However, temperature does not influence the accumulation of micro (mi) RNAs, which play a role in the developmental regulation (Szittyá *et al.*, 2003). *Dunaliella salina*, exposed to low temperature and bright light, experienced photo-oxidative stress. However, high light, low temperature, and their combination increased the total ascorbate and glutathione

pools without affecting their redox status (Haghjou *et al.*, 2009). A study by Amtmann *et al.* (2008) found that low potassium stress triggered physical and metabolic changes in *Arabidopsis*, which enhanced the defence system against pathogens and insects. UV B and heavy metals stress had an inhibitory influence on PSII activity, which reduced the effectiveness of photosynthetic processes in pea plants (Srivastava *et al.*, 2012). *Panicum maximum*, under nutrient and high CO<sub>2</sub> stress, increased productivity and required more nitrogen, calcium, and sulphur nutrients (Carvalho *et al.*, 2020).

The combination of drought and ozone stress led to an increase in nitrogen concentration in the birch leaves, resulting in thicker upper epidermal cell wall, more pectinaceous projections on mesophyll cell walls, and the formation of vacuolar tannin-like depositions and phenolic droplets, all of which are considered indicators of activated stress defence mechanisms. Both drought and ozone caused an increase in specific foliage mass, cytoplasmic lipids in younger leaves, and a condensed appearance of the upper epidermal mucilaginous layer (Paakkonen *et al.*, 1998). In beech trees, a linear relationship was found between ozone stress and cumulative ozone uptake (COU) under humid conditions. These findings support the hypothesis that drought protects plants from ozone injury by stomatal closure, restricting ozone influx into leaves and decoupling COU from high external ozone levels. Similarly, *Medicago truncatula* cultivar Jemalong, sensitive to drought and ozone stress, showed greater tolerance to combined treatment (Löw *et al.*, 2006). High CO<sub>2</sub> and drought in C<sub>3</sub> plants increase leaf and canopy photosynthesis, reduce transpiration, increase biomass without altering dry matter partitioning, and improve water use efficiency. However, these changes have a site-specific effect on agronomic performance and crop water use. Nutrient uptake directly correlates with overall biomass, with root surface area significantly influencing this relationship (Brouder & Volence, 2008). The combination of heat and salinity significantly protects tomato plants from the negative effects of salinity. This study revealed that plants react differently to stress combination, accumulating glycine betaine, and trehalose. This accumulation maintains a high potassium concentration, lower Na<sup>+</sup>/K<sup>+</sup> ratio, and improves cell water status and photosynthesis performance compared to salinity alone (Rivero *et al.*, 2013). Hypoxia and salinity stress in *Salix* spp. enhance root biomass production, increasing root number and elongation (Quiñones Martorello *et al.*, 2019). Similarly, the study by Pérez-López *et al.*, (2015) found that the high light treatment increased green-leaf lettuce production but not red-leaf lettuce. Elevated CO<sub>2</sub> combined with salinity or high light increased antioxidant capacity, while high light treatment alone increased red-leaf lettuce's antioxidant capacity. A study discovered that plants exhibit very similar cellular responses when exposed to pathogens and UV stress. This similarity in responses may explain why plants that are resistant to one stress are often also tolerant to other stresses (Bowler & Fluhr, 2000). Rice yield increased by elevated CO<sub>2</sub>, with reasonable grain mass and higher panicle and grain number. However, rice grown in ozone-exposed air showed a decrease in yield, affecting various yield determinants such as photosynthesis, biomass, leaf area index, grain number, and mass (Ainsworth *et al.*, 2008). In *Zea mays*, boron can

directly influence membrane components' activity under salt stress, regulating water uptake and transport through aquaporin isoforms (Martinez-Ballesta *et al.*, 2008). Fig. 3 showed the interaction of different stress factors in the form of a stress matrix.

## Conclusion

Major studies on plant stress response have primarily focused on investigating individual stressors within controlled laboratory settings. While these studies have provided valuable insights into the mechanisms underlying stress responses, there is a critical need to expand our understanding by thoroughly examining the combined and sequential stress responses that plants encounter in their natural environments. By doing so, we can gain a more comprehensive and realistic understanding of plant stress adaptation under in vivo conditions.

Previous research has already revealed that combined and sequential stresses can elicit different or similar responses compared to individual stressors, often activating distinct signaling pathways. Moreover, these stress conditions disrupt the delicate balance of phytohormones and nutrient assimilation patterns, leading to oxidative stress, as well as reduced growth and yield in plants. The fact that stress-responsive transcripts, proteins, and metabolites differ during single, combined, and sequential stresses suggests that cells have evolved diverse mechanisms to protect themselves from various stressors. However, the detailed analysis of the pathways and associated genes involved in these stress responses still remains largely unpredictable.

The emerging information on signal integration and stress-signaling pathways holds promise for enhancing our understanding of gene functions and developing advanced breeding programs aimed at generating stress-tolerant plant varieties. By unraveling the intricate network of pathways and genes involved in individual, combined, and sequential stress responses, researchers can identify key molecular players that confer resistance and develop targeted strategies to improve stress tolerance in crops.

Despite significant strides in elucidating abiotic sensing mechanisms, there is an ongoing need to identify valid sensing mechanisms during individual, combined, and sequential abiotic stresses. Unraveling these mechanisms will not only shed light on the intricate cellular signaling pathways activated during complex environmental conditions but also enable the discovery of novel genes responsible for stress resistance. Such knowledge is crucial for the development of stress-tolerant crop varieties through genetic engineering and selective breeding approaches.

## Acknowledgments

The authors extend their gratitude to the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Kingdom of Saudi Arabia, for funding the publication of this work under the Reviewing Researcher program (GrantA315).

## References

- Ainsworth, E.A., A. Rogers and A.D. Leakey. 2008. Targets for crop biotechnology in a future high-CO<sub>2</sub> and high-O<sub>3</sub> world. *Plant Physiol.*, 147(1): 13-19.
- Alameda, D., N.P. Anten and R. Villar. 2012. Soil compaction effects on growth and root traits of tobacco depend on light, water regime and mechanical stress. *Soil Tillage Res.*, 120: 121-129.
- Alhaithloul, H.A., M.H. Soliman, K.L. Ameta, M.A. El-Esawi and A. Elkelish. 2019. Changes in ecophysiology, osmolytes, and secondary metabolites of the medicinal plants of *Mentha piperita* and *Catharanthus roseus* subjected to drought and heat stress. *Biomolecules*, 10(1): 43. <https://doi.org/10.3390/biom10010043>.
- Alhajhoj, M.R., M. Munir, B. Sudhakar, H.M. Ali-Dinar and Z. Iqbal. 2022. Common and novel metabolic pathways related ESTs were upregulated in three date palm cultivars to ameliorate drought stress. *Sci. Rep.*, 12(1): 15027. <https://doi.org/10.1038/s41598-022-19399-8>
- Ali-Dinar, H., M. Munir and M. Mohammed. 2023. Drought-tolerance screening of date palm cultivars under water stress conditions in arid regions. *Agronomy*, 13(11): 2811. <https://doi.org/10.3390/agronomy13112811>
- Alnaim, M.A., M.S. Mohamed, M. Mohammed and M. Munir. 2022. Effects of automated irrigation systems and water regimes on soil properties, water productivity, yield and fruit quality of date palm. *Agriculture*, 12(3): 343. <https://doi.org/10.3390/agriculture12030343>
- Amtmann, A., S. Troufflard and P. Armengaud. 2008. The effect of potassium nutrition on pest and disease resistance in plants. *Physiol. Plant.*, 133(4): 682-691.
- Annadurai, M.K.K., S. Alagarsamy, K.M. Karuppasami, S. Ramakrishnan, M. Subramanian, P.R. Venugopal, R. Muthurajan, G. Vellingiri, V. Dhashnamurthi, R. Veerasamy and B. Parasuraman. 2023. Melatonin decreases negative effects of combined drought and high temperature stresses through enhanced antioxidant defense system in tomato leaves. *Horticulturae*, 9(6): 673.
- Aroca, R.R. Porcel and J.M. Ruiz-Lozano. 2011. Regulation of root water uptake under abiotic stress conditions. *J. Exp. Bot.*, 63(1): 43-57.
- Awasthi, R., N. Kaushal, V. Vadez, N.C. Turner, J. Berger, K.H. Siddique and H. Nayyar. 2014. Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. *Fun. Plant Biol.*, 41(11): 1148-1167.
- Bandurska, H., J. Niedziela, and T. Chadzinikolau. 2013. Separate and combined responses to water deficit and UV-B radiation. *Plant Sci.*, 213: 98-105.
- Bari, R. and J.D.G. Jones. 2008. Role of plant hormones in plant defence responses. *Plant Mol. Biol.*, 69(4): 473-488.
- Bowler, C. and R. Fluhr. 2000. The role of calcium and activated oxygens as signals for controlling cross-tolerance. *Trends Plant Sci.*, 5(6): 241-246.
- Brouder, S. M. and J.J. Volenc. 2008. Impact of climate change on crop nutrient and water use efficiencies. *Physiol. Plant.*, 133(4): 705-724.
- Bruce, T.J.A. 2010. Tackling the threat to food security caused by crop pests in the new millennium. *Food Secur.*, 2(2): 133-141.
- Carvalho, J. M., R.F. Barreto, R.D.M. Prado, E. Habermann, R.B.F. Branco and C.A. Martinez. 2020. Elevated CO<sub>2</sub> and warming change the nutrient status and use efficiency of *Panicum maximum* Jacq. *PLOS One*, 15(3): e0223937.
- Chaudhry, U.K., Z.N. Öztürk and A.F. Gökçe. 2024. Assessment of salt and drought stress on the biochemical and molecular functioning of onion cultivars. *Mol. Biol. Rep.*, 51(1): 37. <https://doi.org/10.1007/s11033-023-08923-2>

- Choudhary, A., A. Kumar, N. Kaur and H. Kaur. 2022. Molecular cues of sugar signaling in plants. *Physiol. Plant.*, 174(1): e13630.
- Christmann, A., E.W. Weiler, E. Steudle, and E. Grill. 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *Plant J.*, 52(1): 167-174.
- de Silva, N. D. G., E. Cholewa and P. Ryser. 2012. Effects of combined drought and heavy metal stresses on xylem structure and hydraulic conductivity in red maple (*Acer rubrum* L.). *J. Exp. Bot.*, 63(16): 5957-5966.
- Divi, U.K., T. Rahman and P. Krishna. 2010. Brassinosteroid-mediated stress tolerance in *Arabidopsis* shows interactions with abscisic acid, ethylene and salicylic acid pathways. *BMC Plant Biol.*, 10: 1-14.
- Dugasa, M. T., F. Cao, W. Ibrahim and F. Wu. 2018. Differences in physiological and biochemical characteristics in response to single and combined drought and salinity stresses between wheat genotypes differing in salt tolerance. *Physiol. Plant.*, 165(2): 134-143.
- Fan, Y., J. Wang, M. Yan, X. Wang, G. Du, H. Li, M. Li and B. Si. 2024. Salt addition mitigate mortality risk and prolong survival of *Robinia pseudoacacia* subjected to drought stress. *Agronomy*, 14: 439. <https://doi.org/10.3390/agronomy14030439>
- Foyer, C.H., B. Rasool, J.W. Davey and R.D. Hancock. 2016. Cross-tolerance to biotic and abiotic stresses in plants: A focus on resistance to aphid infestation. *J. Exp. Bot.*, 67(7): 2025-2037.
- Gallino, J.P., C. Ruibal, E. Casaretto, A.L. Fleitas, V. Bonnacarrère, O. Borsani and S. Vidal. 2018. A dehydration-induced eukaryotic translation initiation factor iso4G identified in a slow wilting soybean cultivar enhances abiotic stress tolerance in *Arabidopsis*. *Front. Plant Sci.*, 9: 344702.
- Ghazzawy, H.S., N. Alqahtani, M. Munir, N.S. Alghanim and M. Mohammed. 2023. Combined impact of irrigation, potassium fertilizer, and thinning treatments on yield, skin separation, and physicochemical properties of date palm fruits. *Plants*, 12(5): 1003. <https://doi.org/10.3390/plants12051003>
- Giraud, E., L.H. Ho, R. Clifton, A. Carroll, G. Estavillo, Y.F. Tan, K.A. Howell, A. Ivanova, B.J. Pogson, A.H. Millar and J. Whelan. 2008. The absence of ALTERNATIVE OXIDASE1a in *Arabidopsis* results in acute sensitivity to combined light and drought stress. *Plant Physiol.*, 147(2): 595-610.
- Glazebrook, J. 2005. Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. *Annu. Rev. Phytopathol.*, 43(1): 205-227.
- Haghjou, M.M., M. Shariati and N. Smirnov. 2009. The effect of acute high light and low temperature stresses on the ascorbate-glutathione cycle and superoxide dismutase activity in two *Dunaliella salina* strains. *Physiol. Plant.*, 135(3): 272-280.
- Hatfield, J.L. and C.L. Walthall. 2015. Meeting Global Food Needs: Realizing the Potential via Genetics × Environment × Management Interactions. *Agronomy*, 107(4): 1215-1226.
- Hewezi, T., M. Léger and L. Gentzittel. 2008. A comprehensive analysis of the combined effects of high light and high temperature stresses on gene expression in sunflower. *Ann. Bot.*, 102(1): 127-140.
- Jain, M., P. Nagar, P. Goel, A.K. Singh, S. Kumari and A. Mustafiz. 2018. Second messengers: central regulators in plant abiotic stress response. In: (Eds.): Zargar, S.M. and M.Y. Zargar. *Abiotic Stress-Mediated Sensing and Signaling in Plants: An Omics Perspective*, Springer, Cham. pp. 47-94.
- Jones, H.G., T.J. Flowers and M.B. Jones. 1989. Plant under stress. Society for Experimental Botany. Seminar Series 39.
- Kamatchi, K.M., K. Anitha, K.A. Kumar, A. Senthil, M.K. Kalarani and M. Djanaguiraman. 2024. Impacts of combined drought and high-temperature stress on growth, physiology, and yield of crops. *Plant Physiol. Rep.*, 29(1): 28-36. <https://doi.org/10.1007/s40502-023-00754-4>
- Kasurinen, A., C. Biasi, T. Holopainen, M. Rousi, M. Maenpää and E. Oksanen. 2012. Interactive effects of elevated ozone and temperature on carbon allocation of silver birch (*Betula pendula*) genotypes in an open-air field exposure. *Tree Physiol.*, 32(6): 737-751.
- Keleş, Y and I. Öncel. 2002. Response of antioxidative defence system to temperature and water stress combinations in wheat seedlings. *Plant Sci.*, 163(4): 783-790.
- Kerchev, P. I., B. Fenton, C.H. Foyer and R.D. Hancock. 2011. Plant responses to insect herbivory: interactions between photosynthesis, reactive oxygen species and hormonal signalling pathways. *Plant Cell Environ.*, 35(2): 441-453.
- Kilian, J., D. Whitehead, J. Horak, D. Wanke, S. Weinl, O. Batistic, C. D'Angelo, E. Bornberg-Bauer, J. Kudla and K. Harter. 2007. The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. *The Plant J.*, 50(2): 347-363.
- Kumar, M., M.K. Patel, N. Kumar, A.B. Bajpai and K.H. Siddique. 2021. Metabolomics and molecular approaches reveal drought stress tolerance in plants. *Int. J. Mol. Sci.*, 22(17): 9108.
- Kumar, R. and V.S. Rathor. 2020. Nature and types of damage by insect pests. *J. Entomol. Res.*, 44(4): 639-646.
- Lal, M.A., R. Kathpalia, R. Sisodia and R. Shakya. 2018. Biotic stress. In: (Eds.): Bhatla, S.C. and M.A. Lal. *Plant Physiology, Development and Metabolism*. Springer, Cham. pp. 1029-1095.
- Li, L., Y. Li and G. Ding. 2024. Response mechanism of carbon metabolism of *Pinus massoniana* to gradient high temperature and drought stress. *BMC Genom.*, 25(1): 166. <https://doi.org/10.1186/s12864-024-10054-2>
- Li, P.C., X.Y. Yang, H.M. Wang, T. Pan, J.Y. Yang, Y.Y. Wang, Y. Xu, Z.F. Yang and C.W. Xu. 2021. Metabolic responses to combined water deficit and salt stress in maize primary roots. *J. Integr. Agri.*, 20(1): 109-119.
- Li, W., C. Zhang, Q. Lu, X. Wen and C. Lu. 2011. The combined effect of salt stress and heat shock on proteome profiling in *Suaeda salsa*. *J. Plant Physiol.*, 168: 1743-1752.
- López, M.A., G. Bannenberg and C. Castresana. 2008. Controlling hormone signaling is a plant and pathogen challenge for growth and survival. *Curr. Opin. Plant Biol.*, 11(4): 420-427.
- Löw, M., K. Herbinger, A.J. Nunn, K.H. Häberle, M. Leuchner, C. Heerdt, H. Werner, P. Wipfler, H. Pretzsch, M. Tausz and R. Matyssek. 2006. Extraordinary drought of 2003 overrules ozone impact on adult beech trees (*Fagus sylvatica*). *Trees*, 20(5): 539-548.
- Mahajan, S. and N. Tuteja. 2005. Cold, salinity and drought stresses: An overview. *Arch. Biochem. Biophys.*, 444(2): 139-158.
- Mahmoud, D. R. Pandey, L. Sathee, M. Dalal, M.P. Singh and V. Chinnusamy. 2020. Regulation of expression of genes associated with nitrate response by osmotic stress and combined osmotic and nitrogen deficiency stress in bread wheat (*Triticum aestivum* L.). *Plant Physiol. Reports*, 25(2): 200-215.
- Mahrookashani, A., S. Siebert, H. Hüging and F. Ewert. 2017. Independent and combined effects of high temperature and drought stress around anthesis on wheat. *J. Agron. Crop Sci.*, 203(6): 453-463.

- Martí, M.C., M.A. Stancombe and A.A. Webb. 2013. Cell- and stimulus type-specific intracellular free  $\text{Ca}^{2+}$  signals in *Arabidopsis*. *Plant Physiol.*, 163(2): 625-634.
- Martinez-Ballesta, M.D.C., E. Bastías, C. Zhu, A.R. Schöffner, B. González-Moro, C. González-Murua and M. Carvajal. 2008. Boric acid and salinity effects on maize roots. Response of aquaporins ZmPIP1 and ZmPIP2, and plasma membrane  $\text{H}^+$ -ATPase, in relation to water and nutrient uptake. *Physiol. Plant.*, 132(4): 479-490.
- Meena, S.K., R. Pandey, S. Sharma, T. Kumar, M.P. Singh and H.K. Dikshit. 2021. Physiological basis of combined stress tolerance to low phosphorus and drought in a diverse set of Mungbean germplasm. *Agronomy*, 11(1): 99.
- Miller, G., V. Shulaev and R. Mittler. 2008. Reactive oxygen signaling and abiotic stress. *Physiol. Plant.*, 133(3): 481-489.
- Munné-Bosch, S., G. Queval and C.H. Foyer. 2012. The impact of global change factors on redox signaling underpinning stress tolerance. *Plant Physiol.*, 161(1): 5-19.
- Obata, T., S. Witt, J. Lisek, N. Palacios-Rojas, I. Florez-Sarasa, S. Yousfi and A.R. Fernie. 2015. Metabolite profiles of maize leaves in drought, heat, and combined stress field trials reveal the relationship between metabolism and grain yield. *Plant Physiol.*, 169(4): 2665-2683.
- Osakabe, Y., K. Osakabe, K. Shinozaki and L.S.P. Tran. 2014. Response of plants to water stress. *Front. Plant Sci.*, 5: 76566.
- Paakkonen, E., J. Vahala, M. Pohjola, T. Holopainen and L. Karenlampi. 1998. Physiological, stomatal and ultrastructural ozone responses in birch (*Betula pendula* Roth.) are modified by water stress. *Plant. Cell Environ.*, 21(7): 671-684.
- Pan, J., A.R. Vicente, G.A. Martínez, A.R. Chaves and P.M. Civeello. 2004. Combined use of UV-C irradiation and heat treatment to improve postharvest life of strawberry fruit. *J. Sci. Food Agri.*, 84(14): 1831-1838.
- Partridge, M. 2009. *Investigation of the Roles of a Membrane-Bound Caleosin in Higher Plants*. University of South Wales, United Kingdom.
- Pastori, G.M. and C.H. Foyer. 2002. Common components, networks, and pathways of cross-tolerance to stress. The central role of "redox" and abscisic acid-mediated controls. *Plant Physiol.*, 129(2): 460-468.
- Peleg, Z. and E. Blumwald. 2011. Hormone balance and abiotic stress tolerance in crop plants. *Curr. Opin. Plant Biol.*, 14(3): 290-295.
- Pérez-López, U., J. Miranda-Apodaca, M. Lacuesta, A. Mena-Petite and A. Muñoz-Rueda. 2015. Growth and nutritional quality improvement in two differently pigmented lettuce cultivars grown under elevated  $\text{CO}_2$  and/or salinity. *Sci. Hortic.*, 195: 56-66.
- Pieterse, C.M.J., A. Leon-Reyes, S. Van der Ent and S.C.M. Van Wees. 2009. Networking by small-molecule hormones in plant immunity. *Nat. Chem. Biol.*, 5(5): 308-316.
- Prasad, P.V.V., S.R. Pisipati, I. Momčilović and Z. Ristic. 2011. 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.*, 197(6): 430-441.
- Quiñones Martorello, A.S., M.E. Fernández, M.G. Monterubbianesi, M.N. Colabelli, P. Laclau and J.E. Gyenge. 2019. Effect of combined stress (salinity + hypoxia) and auxin rooting hormone addition on morphology and growth traits in six *Salix* spp. clones. *New Forests*, 51(1): 61-80.
- Raina, M., A.V. Kisku, S. Joon, S. Kumar and D. Kumar. 2021. Calmodulin and calmodulin-like  $\text{Ca}^{2+}$  binding proteins as molecular players of abiotic stress response in plants. In: (Ed.): Upadhyay, S.K. *Calcium Transport Elements in Plants*. Academic Press. pp. 231-248.
- Raja, V., S.U. Qadir, M.N. Alyemeni and P. Ahmad. 2020. Impact of drought and heat stress individually and in combination on physio-biochemical parameters, antioxidant responses, and gene expression in *Solanum lycopersicum*. *3 Biotech*, 10(5): 1-18.
- Ranganathan, J., R. Waite, T. Searchinger and C. Hanson. 2018. How to sustainably feed 10 billion people by 2050, in 21 charts. World Resources Institute, Washington, DC, United States. <https://www.wri.org/insights/how-sustainably-feed-10-billion-people-2050-21-charts> (accessed on 8 May 2024)
- Raza, A., H. Salehi, M.A. Rahman, Z. Zahid, M. Haghjoui, S. Najafi-Kakavand, S. Charagh, H.S. Osman, M. Albaqami, Y. Zhuang and K.H. Siddique. 2022. Plant hormones and neurotransmitter interactions mediate antioxidant defenses under induced oxidative stress in plants. *Front. Plant Sci.*, 13: 961872.
- Rivero, R.M., T.C. Mestre, R. Mittler, F. Rubio, F. Garcia-Sanchez and V. Martinez. 2013. The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. *Plant Cell Environ.*, 37(5): 1059-1073.
- Rizhsky, L., H. Liang and R. Mittler. 2002. The combined effect of drought stress and heat shock on gene expression in tobacco. *Plant Physiol.*, 130(3): 1143-1151.
- Rizhsky, L., H. Liang, J. Shuman, V. Shulaev, S. Davletova and R. Mittler. 2004. When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. *Plant Physiol.*, 134(4): 1683-1696.
- Rollins, J.A., E. Habte, S.E. Templer, T. Colby, J. Schmidt and M. Von Korff. 2013. Leaf proteome alterations in the context of physiological and morphological responses to drought and heat stress in barley (*Hordeum vulgare* L.). *J. Exp. Bot.*, 64(11): 3201-3212.
- Sales, C.R., R.V. Ribeiro, J.A. Silveira, E.C. Machado, M.O. Martins and A.M.M. Lagôa. 2013. Superoxide dismutase and ascorbate peroxidase improve the recovery of photosynthesis in sugarcane plants subjected to water deficit and low substrate temperature. *Plant Physiol. Biochem.*, 73: 326-336.
- Sardana, V., G. Mahajan, K. Jabran and B.S. Chauhan. 2017. Role of competition in managing weeds: An introduction to the special issue. *Crop Prot.*, 95: 1-7.
- Selye, H. 1956. What is stress? *Metabolism*, 5(5): 525-530.
- Sewelam, N., D. Brillhaus, A. Bräutigam, S. Alseekh, A.R. Fernie and V. G. Maurino. 2020. Molecular plant responses to combined abiotic stresses put a spotlight on unknown and abundant genes. *J. Exp. Bot.*, 71(16): 5098-5112.
- Sicher, R.C. and J.A. Bunce. 2015. The impact of enhanced atmospheric  $\text{CO}_2$  concentrations on the responses of maize and soybean to elevated growth temperatures. In: (Ed.): Mahalingam, R. *Combined Stresses in Plants: Physiological, Molecular, and Biochemical Aspects*. Springer, Cham. pp. 27-48.
- Srivastava, G., S. Kumar, G. Dubey, V. Mishra and S.M. Prasad. 2012. Nickel and ultraviolet-B stresses induce differential growth and photosynthetic responses in *Pisum sativum* L. seedlings. *Biol. Trace Elem. Res.*, 149(1): 86-96.
- Szittyá, G., D. Silhavy, A. Molnár, Z. Havelda, A. Lovas, L. Lakatos and J. Burgyán. 2003. Low temperature inhibits RNA silencing-mediated defence by the control of siRNA generation. *EMBO J.*, 22(3): 633-640.
- Tambussi, E.A., J.J. Guamet and C.G. Bartoli. 2020. Cross-tolerance to abiotic stress at different levels of organizations: Prospects for scaling-up from laboratory to field. In: (Eds.): Hossain, M.A., F. Liu and B. Huang. *Priming-Mediated Stress and Cross-Stress Tolerance in Crop Plants*. Academic Press. pp. 317-327. <https://doi.org/10.1016/B978-0-12-817892-8.00019-2>



- Vescio, R., M.R. Abenavoli and A. Soragonà. 2020. Single and combined abiotic stress in maize root morphology.-*Plants*, 10(1): 5. <https://doi.org/10.3390/plants10010005>
- Vile, D., M. Pervent, M. Belluau, F. Vasseur, J. Bresson, B. Muller, C. Granier and T. Simonneau. 2011. *Arabidopsis* growth under prolonged high temperature and water deficit: Independent or interactive effects? *Plant Cell Environ.*, 35(4): 702-718. <https://doi.org/10.1111/j.1365-3040.2011.02445.x>
- Vivek, P.J., N. Tuteja and E.V. Soniya. 2013. CDPK1 from ginger promotes salinity and drought stress tolerance without yield penalty by improving growth and photosynthesis in *Nicotiana tabacum*. *PLOS One*, 8(10): e76392.
- Walley, J., S Coughlan, M.E. Hudson, M.F. Covington, R. Kaspi, G. Banu, S.L. Harmer and K. Dehesh. 2007. Mechanical stress induces biotic and abiotic stress responses via a novel cis-element. *PLOS Genet.*, 3(10): e172.
- Wang, C., X. Cai and Z. Zheng. 2005. High humidity represses Cf-4/Avr4-and Cf-9/Avr9-dependent hypersensitive cell death and defense gene expression. *Planta*, 222(6): 947-956.
- Xiong, L. and Y. Yang. 2003. Disease resistance and abiotic stress tolerance in rice are inversely modulated by an abscisic acid-inducible mitogen-activated protein kinase. *Plant Cell*, 15: 745-759.
- Yasuda, M., A. Ishikawa, Y. Jikumaru, M. Seki, T. Umezawa, T. Asami, A. Maruyama-Nakashita, T. Kudo, K. Shinozaki, S. Yoshida and H. Nakashita. 2008. Antagonistic interaction between systemic acquired resistance and the abscisic acid-mediated abiotic stress response in *Arabidopsis*. *Plant Cell*, 20(6): 1678-1692.
- Zhu, Y., W. Qian and J. Hua. 2010. Temperature modulates plant defense responses through NB-LRR proteins. *PLOS Pathog.*, 6(4): e1000844.

(Received for publication 12 February 2023)