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A stressful life: How plants cope with multiple biotic and abiotic adverse factors☆

In natural and agricultural ecosystems, plants quickly respond to abiotic and biotic stress factors, alone or in their combinations, by complex acclimation processes and, over long-term, by evolving adaptation strategies. Future climate change scenarios are expected to increase the effects of abiotic stresses on plants, and further enhance the virulence and diffusion of the existing pathogens and pests, thus negatively affecting crop yields and plant survival. Indeed, global warming is producing several and sometimes contrasting effects on global and regional climate, exposing plants to higher temperatures, higher vapor pressure deficit, more frequent and intense drought, but also to anomalous frost events, flooding and so on. Most importantly, plants will be facing a complex array of simultaneous stress factors that will challenge their persistence in some habitats, and sometimes favor their expansion in new geographical ranges. In this view, understanding plants' resistance and resilience mechanisms to the complex and variegated effects of climate change is and urgent task.

Within certain limits, plants are known to cope with multiple stress factors via complex adjustments of their physiological and phenotypic traits. Furthermore, plants can respond to environmental challenges by shaping their own microbiome to establish commensal or even mutualistic relationships. The importance of plants and their ecto- and endophytes acting as a unique organism (the so-called holobiont) and interacting with the surrounding environment to withstand stressful conditions has been increasingly recognized. Understanding the complex interactions between plants, the environment, and the associated microbes is challenging. Thanks to the wide diffusion of -omics approaches, these complex interactions have started to be uncovered. In the future, a mechanistic understanding of the processes underlying the plant-microbe response to climate change and a multi-faceted and interdisciplinary approach will be crucial for developing successful climate mitigation strategies to reduce chemical, water, and energy consumption. The unraveled beneficial plant-microbe interactions and holobiont responses to climate challenges will open new options to sustain agriculture and recover natural ecosystems under threat. In this context, (Juurakko et al., 2021) reviewed how diverse plant species have evolved complex and intricate signaling networks, molecular mechanisms, and physiological changes, in addition to symbiotic relationships with root-associated microbiota, to survive low temperatures.

The articles published in this special issue provide novel experimental insights or review the responses of several crops (e.g. rice, canola, woody trees, sorghum) to diverse stress conditions (water deficit, cold stress, salinity stress, moisture, heat and combined stress), using different approaches (large scale or targeted) in a multidisciplinary fashion. In the last decades, advances in -omics have greatly contributed to deciphering the mechanisms involved in stress responses, generating and interrelating a huge quantity of data at many levels contemporaneously. Baldoni (2022) focused the attention on comparative transcriptomics in rice, suggesting that it can be considered a powerful tool for the identification of increasing numbers of functional genes and the corresponding molecular mechanisms, leading to gain crucial information to successfully transfer the biological knowledge from the bench to the field in a timely manner. Rice is particularly sensitive to water deficit and the development of drought-tolerant cultivars represents a key strategy for breeding programs. The article highlights how information from comparative transcriptomic studies can support breeders in the identification of interesting genomic traits in rice, to enhance drought tolerance and yield. In addition to transcriptomics, the understanding of the metabolic profile might lead to useful information for improving target traits directly related to the phenotype. Non-targeted metabolite profiling analysis helped understanding the overall changes in the primary metabolism in canola seedling tissues exposed to heat, waterlogging, drought and salt stresses (Viana et al., 2022). Abiotic stress factors can severely constrain canola, which is an important oilseed crop worldwide that needs further efforts in identifying specific traits underlying stress resilience. Using a GC-MS approach, these authors profiled organic acids, free amino acid and sugars in diverse tissues, demonstrating that these metabolites differently accumulate in shoots and roots under abiotic stresses, with differences among shoot tissues that presented greater variation in metabolites content in response to abiotic stresses in comparison to roots. A role for the metabolite mimosine, which is considered an osmoprotectant with antioxidant properties, has been suggested in giant leucaena (*Leucaena leucocephala* subsp. Glabrata) as a stress response molecule, where it increases or decreases its concentration in response to favorable or unfavorable environmental conditions (Honda and Borthakur, 2021). Among abiotic stresses, cold is a major environmental factor that negatively affects food and feed production, leading to morphological, physiological, biochemical and molecular changes that plants use to adapt and survive in non-optimal conditions. Additionally, low-temperatures are frequently coupled with other abiotic and biotic stresses, including pathogen attacks. Considering the importance of rice (*Oryza sativa* L.) as a primary source of food worldwide, Martini et al. (2022) studied the effects of cold stress and bispyribac-sodium herbicide application on gene expression and physiological patterns in rice seedlings, identifying a peculiar cross-talk in molecular responses of cold and herbicide application at early planting date with negative effects on its

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selectivity of rice seedling. This study highlights the importance of precisely tailoring agronomic practices in light of the ongoing climate change events.

Acclimation is one of the best strategies that plants use to react against cold injuries. This process of implies a series of metabolic and physiological adjustments initiated by molecular signaling (Van Buskirk and Thomashow, 2006). Acclimation mechanisms on *Sorghum bicolor* [Moench (L.)] have been included in the review of Ndlovu et al. (2021) focused on morphological and physiological impact of single and combined abiotic stresses. This review reports a comprehensive overview of plant-mediated tolerance mechanisms including those from many genetic accessions, as a basis for accurate screening and future breeding programs. Acclimation is a common topic in diverse papers published in this special issue, both in herbaceous plants (Ndlovu et al., 2021) and woody plants such as walnut (*Juglans regia* L.; Karimi and Ehterami-Fini, 2021). Walnut is a drought and heat- susceptible plant species and these vulnerabilities are intensified in young plants grown in greenhouse nurseries. The mechanisms of acclimation and adaptation seem to be particularly important in trees, which are sessile long-living organisms, unable to rapidly shift their distribution range to escape from the worsening of environmental conditions (Bussotti and Pollastrini, 2021). Climate change projections suggests in fact that climate will change faster than plants can adapt or migrate, hypothesizing that, despite trees moved across the habitats in response to climate change, contemporary forest tree species and populations will need to migrate faster than their natural ability (Dyderski et al., 2018; Fadrique et al., 2018). In this respect, to prime tolerance responses against stresses thus favoring the acclimation, several so-called 'pretreatment' approaches have been discovered. For example, in the study of Karimi and Ehterami-Fini (2021), one-year-old greenhouse-grown walnut 'Chandler' trees were subjected to three different pretreatments to promote acclimation after transplantation: i) long-term water stress, ii) controlled salinity stress, and iii) foliar application of β-aminobutyric acid (BABA). The effectiveness of these pretreatments was evaluated on transplanted plants into hot and dry conditions. Investigating the responses of pretreated walnut plants for identifying the activation of adaptation mechanisms demonstrated that pretreatments induced osmotic adjustment (OA) in leaves, with the salinity pretreatment that was the most effective one in showing higher proline content and biomass than controls at the end of the experiment.

Recent evidence shows that plants respond to a combination of stresses by activating a reprogramming of gene expression, which differs from their single-stress response and is related to the exact environmental conditions encountered (Atkinson and Urwin, 2012). Understanding the mechanisms involved in plant responses to multiple simultaneous stresses is crucial for developing broad-spectrum strategies applicable for the development of stress-tolerant crops. In this special issue, the impact of a combined stress (salt and water stress) has been studied on *Aspidosperma pyrifolium* Mart. and Zucc., which is one of the main species of Caatinga biome, a seasonally dry tropical forest in Brazilian Semi-arid, is very promising for restoring degraded or decertified zones (da Conceição Sabino et al., 2021). The study investigated the effects of combined stress condition on morphological dynamics, biomass accumulation and gas exchange, concluding that this species is able to modulate its biomass to improve tolerance to salt and water stresses.

At biochemical level, it is worth noting under stressful conditions the pivotal role(s) of antioxidant signaling and molecules protecting cells by reactive oxygen species (ROS)-induced damage. Due to the importance of ROS scavenging in the response to stress conditions, a review article has focused on salt stress highlighted as recent research advancements, providing up-to-date information on how antioxidant defense machinery, antioxidant enzymes and non-antioxidant metabolites work together to alleviate the negative effects of ROS, as well as how reactive sulphur, nitrogen and carbonyl species can act as important signal molecules (Singh, 2022).

The concept of stress in forest trees at the time of global change as well as the issues for its monitoring have also been discussed in the review paper by Bussotti and Pollastrini (2021). The authors revisited the stress concept applied to forest trees looking at the capacity of these complex organisms to restore the disrupted equilibrium caused by the rapid climate change events. For these reasons, it is important to strictly monitor the stressful events to better define the new equilibrium composed by the photosynthetic efficiency and resilience capacity (in terms of non-structural carbohydrates levels). Furthermore, the authors also suggested the importance of predicting the possible changes in species composition and structure of communities and ecosystems. This is desirable to maintain and optimize the ecosystem services in a new environment and in consequence to the climate changing scenario.

Taken together, the studies and reviews collected in this special issue further improve our knowledge on plant responses to single or multiple stresses imposition. Researchers moving towards integrated studies at multiple levels from cellular signaling to whole plant responses exposing them to combined stresses as commonly occur in natural conditions. These findings will allow deciphering mechanisms at the basis of tolerance and acclimation for future sustainable strategies against environmental stresses. Surprisingly, despite the importance of the interactions with soil microorganisms in the tolerance to abiotic and biotic stress, there were no studies focused on the interactions between plants and microorganisms. It is important to note that plants are not alone in their environment, but they share it with a myriad of microbes. Therefore, several stress-related responses might be mediated by rhizosphere and root-associated microorganisms, including bacteria and fungi. Given the multitude and diversity of microorganisms on the planet and their importance in the plant-environment interaction, modulating the plant-microbe interactions in the rhizosphere will support plant fitness and improve plant resistance to biotic and abiotic stresses. In turn, this may help plants withstand climate change challenges.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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