

EDITORIAL

Stress combination: from genes to ecosystems

In nature, or under field conditions, plants and crops are routinely subjected to a combination of different abiotic and/or biotic stress conditions that may affect them simultaneously or sequentially (e.g., drought and heat, flooding and heat, nutrient deficiency and drought, flood followed by salinity stress, and many other stress combinations that include pathogens, increasing levels of CO₂, and other stress factors; Figure 1). Past climatic events and ongoing research have taught us that different stress combinations can have a dramatic and devastating impact on wild and cultivated plants, as well as on different ecosystems and their associated microbiomes. Notable examples are the drought and heat wave episodes that occurred during the summers of 1980 and 1988 in the US and resulted in yield losses estimated at 39 and 53 billion dollars to agriculture, respectively (<https://www.ncei.noaa.gov/access/billions/events>). As the frequency and intensity of many abiotic and/or biotic stresses, and their combinations, are gradually increasing due to global warming and climate change (<https://climate.nasa.gov/extreme-weather/>), a deeper understanding of the molecular mechanisms, physiological responses, and overall ecological processes involved in plant responses and acclimation to stress combinations is needed. With the overall goal of increasing the awareness of the plant research community to this emerging challenge, we organized this Special Issue focused on “Stress combination: From genes to ecosystems.”

The special issue comprises five research papers, two resource papers, and nine reviews. In the first research paper, Balfagon et al. (2024) reported on the transcription factor WRKY48 which functions as a key suppressor of plant responses specific to a combination of high light and heat stress. The authors further showed that WRKY48 expression is attenuated by jasmonic acid (JA) during the stress combination and identified putative genes that function downstream to WRKY48. This paper is significant as it is likely the first to identify a transcription factor that has a function specific to a set of two different stresses combined. Another research paper is that of Li et al. (2024) who studied the synergistic regulation at morphological, physiological, transcriptional, and metabolic levels of different tomato genotypes subjected to a combination of heat and salinity. These authors further identified the oxidative phosphorylation pathway and alternative oxidase 1 as potentially playing a key role in this stress combination. In the third

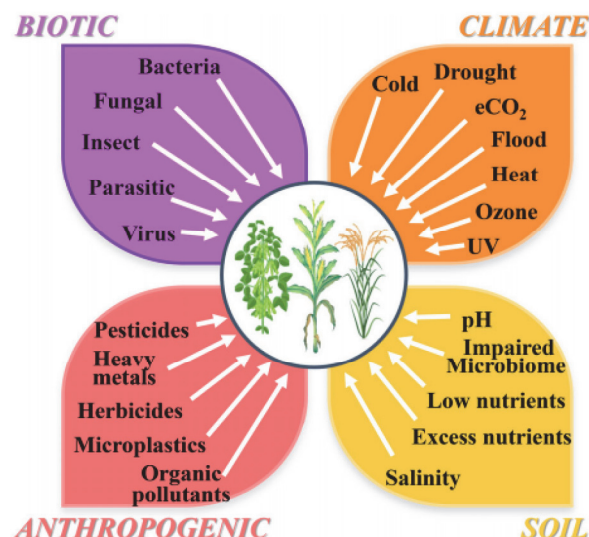


Figure 1. The concept of stress combination. Different abiotic and/or biotic stresses may occur together in different combinations in nature or the field (e.g., drought and heat stress, or salinity and pathogen infection), triggering in plants different stress-response pathways, that may be conflicting or synergistic, and causing an overall reduction in plant growth, yield, and in some cases survival. Different stresses can also impact crops sequentially (e.g., drought followed by cold stress, or flood followed by fungal infection), also impacting crops negatively. In some cases, three or more different stresses may impact plants simultaneously or sequentially, causing a “multifactorial stress combination” that could have a much higher negative effect on plant growth, yield, and survival. As our climate is changing, the frequency and intensity of stress combination events increase making this subject of research highly important for plant biology.

research paper of the special issue, Ludwig et al. (2024) studied phenotypic variation in the response of 149 accessions of *Brachypodium* to heat, drought, and drought combined with heat. Using GWAS and SNP analyses the authors identified different loci associated with plant responses to stress combination, revealing that these responses are not simply the additive effects of drought and heat, as they differ qualitatively from the responses to drought or heat alone. In the fourth research paper, Koch et al. (2024) studied the interactions between heat stress and excess nitrogen fertilization in potato. Using transgenic potato plants, they showed that yield reduction caused by elevated temperatures and high nitrogen fertilization can be mitigated by overexpression of SELF-PRUNING 6A (SP6A), a homolog of FLOWERING LOCUS T, that functions as a

tuberigen in potato. This is a significant finding as it proposes a new avenue in mitigating nutrient and heat stress combination in potato. In the fifth research paper, DeLoose, Cho, et al. (2024) also focused on nutrient stress combination, however, with a focus on iron and phosphate stress interactions in Arabidopsis. Using a GWAS analysis the authors of this exciting research paper determined that PDR9 allelic variation and MYB63 function modulate nutrient-dependent coumarin homeostasis in Arabidopsis to regulate the interactions between iron and phosphate.

The two resource papers featured in the special issue include the paper by Peláez-Vico et al. (2024) that subjected soybean plants to a multifactorial stress combination (MFSC) of up to five different stresses (water deficit, salinity, low phosphate, acidity, and cadmium), in an increasing level of complexity and conducted an integrative transcriptomic-phenotypic analysis of their reproductive and vegetative tissues. This paper is highly important as it provides significant datasets for vegetative and reproductive tissues of a crop plant subjected to stress combination. In the second resource paper, Pardo-Hernández et al. (2024) provide important datasets for wild type and abscisic acid (ABA) deficient tomato plants subjected to a combination of heat and salinity stress, offering new insights into the ABA-dependent and ABA-independent responses of tomato to stress combination.

The nine different reviews included in the special issue address multiple aspects of plant, crop, and ecosystem responses to stress combination. In their review, DeLoose, Clúa, et al. (2024) discuss the response of plants to nutrient stress combinations with a focus on the regulation of phosphorous homeostasis in plants. The authors discuss deficiencies in phosphorous combined with other essential elements, such as nitrogen, iron, and zinc, as well as with non-essential elements such as aluminum and sodium. Rillig et al. (2024) describe in their review a new classification scheme that captures the different targets of global change factors along the ecological hierarchy. The authors discuss how effects can propagate across the levels of the ecological hierarchy, upwards and downwards, presenting new opportunities for explaining the non-additivity of effects of multiple factors. The conceptual framework described by these authors will help inform the next generation of plant-focused global change experiments, specifically aimed at the non-additivity of effects at the confluence of many factors. Sadras et al. (2024) review some of the very interesting aspects of virus-virus (inter-virus) and virus-drought combinations, discussing antagonistic, additive, and synergistic inter-virus relationships in double infections, as well as additive or antagonistic virus-drought interactions. They then relate these to crop yield in agriculture and crop fitness in the field. Zandalinas et al. (2024) tackle the challenging subject of MFSC. The authors explain how climate change, industrial pollution,

and global warming elevate the frequency, complexity, and intensity of multiple stress combinations, and discuss the impacts of MFSC on agriculture, microbiomes, and ecosystems worldwide. Chen et al. (2024) discuss in their review the combination of drought and salinity stresses. The authors address the challenges this stress combination poses to agriculture and compare some of the key traits that differentiate between xerophytes (naturally drought-tolerant plants) and mesophytes (majority of the crops). Finally, the authors propose ways of incorporating some of these traits into breeding practices to produce more drought- and salt-resistant crops. In their review, Renziehausen et al. (2024) address the highly important combination of flooding or waterlogging stress with other abiotic stresses such as heat stress. The authors discuss how flooding/anoxia signaling pathways are affected by other stresses and propose molecular mechanisms that could play a key role in stress combinations that include hypoxia and other stresses. Cagnola et al. (2024) analyzed the impact of combined abiotic stresses, such as water restriction and nitrogen deficiency, or water restriction and elevated temperatures, on crop yield per unit soil area in corn. They further address the highly important aspect of plant population density, which generates crowding stress during stress combination, and show that depending on different factors, the magnitude of the detrimental effects of two combined stresses on field-grown plants can be lower, similar, or higher than the sum of the individual stresses. In their review, Sato et al. (2024) provide a comprehensive overview of how drought, heat, and the combination of these stress conditions affect plants and crops by altering factors such as stomatal conductance, photosynthetic activity, cellular oxidative conditions, metabolomic profiles, and molecular signaling mechanisms. The authors further focus on stress-response regulatory factors such as transcription factors and other signaling components that play a key role during stress combination. Finally, Han et al. (2024) discuss in their review how plants coordinately respond to a combination of shade and environmental stresses such as drought, soil salinity, extreme temperatures, pathogens, and pests. They present these interactions with a focus on the shade avoidance syndrome, and the role of phytochrome B and the transcription factors PHYTOCHROME INTERACTING FACTORS (PIFs) in these responses.

We hope that the wide array of research, resource, and review articles on stress combination, included in this special issue, will spark interest in young scientists, highlight this important subject to the broad scientific community, and attract the attention of policy and decision makers. The timing of this special issue, approximately 20 years following the first molecular and physiological analyses of stress combination in plants (Mittler, 2006; Rizhsky et al., 2002, 2004), the over 1000 papers published on stress combination since, and the 2023 report on

climate change by IPCC (Lee & Romero, 2023; <https://www.ipcc.ch/report/ar6/syr/>), further highlights the importance of this subject, and its relevance to current events and the rapid changes in our climate and environment. As the impacts of global warming, climate change, and industrial/urban pollution, on plants and crops continue to grow on a yearly basis (e.g., Zandalinas et al., 2021, 2024), so will the importance of studying stress combination/MFSC. To truly develop Climate-, pathogen- and/or pollution-resilient crops, we must understand how plants and crops respond to and acclimate to stress combination.

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