Plant Responses to Stress Combinations

Subjects: Plant Sciences

Contributor: Zeyao Jing , Na Liu , Zongxian Zhang , Xiangyang Hou

Stress combinations describe the simultaneous exposure of plants to two or more stresses. In the past, stress combinations were defined as simple combinations of two or at most three different stresses, and extensive research has been conducted in this realm. Given the escalating environmental complexity arising from heightened levels of various pollutants and erratic weather patterns due to climate change, studies indicate a substantial decline in plant growth and survival even when each stressor is at a relatively low level, as the number of stressors amplifies their effects. Therefore, studying plant responses to basic stress combinations alone is inadequate for intricate environments.Therefore, the concept of stress combinations has recently broadened, introducing a novel approach to studying plant responses to combined stresses termed “multifactorial stress combinations”(MFSCs). This term denotes combinations of three or more ($n \geq 3$) stressors affecting the plant simultaneously or in succession. The simultaneous impacts on plants come from a multitude of stressors such as anthropogenic and non-anthropogenic biotic factors, climatic drivers, and soil-related abiotic factors.

plants stress combinations multifactorial stress combinations

1. Simple Stress Combinations

1.1. Abiotic Stress Combinations

Several scholars have focused on stress combinations and conducted a great deal of research. Many scholars have focused on abiotic stress combinations to address specific stress combinations relevant to their crop or region of interest. These include staple crops such as *Zea mays* and *Glycine max* under a combination of drought and heat stress [1], and trees in the Mediterranean region, which are vulnerable to drought and acute ozone [2]. Numerous studies have highlighted the profound effects of stress interactions on plants. Combinations of drought and heat waves, drought and ozone, or high temperature and salt have been found to have significantly more pronounced negative effects on plants than individual stress components applied in isolation [2][3][4][5]. Studies have also highlighted the positive effects of the interplay between two distinct stresses on plants. For instance, mild salt addition alleviates plant damage caused by low-temperature stresses [6][7].

The coupling of drought and high-temperature stress has led to a catastrophic decline in agricultural productivity. Consequently, more research has focused on understanding the effects of combined high temperatures and drought on plant growth and productivity [8][9]. Recent studies have revealed that the convergence of drought and high-temperature stress has a more detrimental effect on plant and crop growth than either stress alone. This synergy significantly diminished crop yield, indicating a shared defense mechanism across various plants to compete with the combined challenges of drought and high temperatures [10]. Nevertheless, various plants exhibit distinct responses to stress combinations in terms of the degree and manner of impact. For instance, *Arabidopsis thaliana* demonstrated greater susceptibility to the combined stress of salt and high temperatures than *Solanum lycopersicum* [11]. Cereals try to compensate for yield losses during combined drought and high-temperature stress by greater reductions of nutrient growth and seed size compared to legumes [12][13]. The impact on numerous vital food crops intensifies notably when combined drought and high-temperature stresses occur during a plant's reproductive stages [5][8][13]. Recent studies have highlighted that the sequence in which drought and high-temperature stresses are applied does not change the plant's response to combined stress. The metabolism of reactive oxygen species (ROS) and stomatal responses are pivotal in the adaptation of plants to combinations of drought and high-temperature stress [6].

1.2. Abiotic and Biotic Stress Combinations

Amid climate change and heightened environmental intricacies, the intersection of abiotic and biotic stresses has become a key research focus. Numerous studies investigating combined stresses delve into the interplay between abiotic and biotic stressors, like the interactions between drought and pests, cadmium and pathogens, and drought and pathogens [14][15][16][17]. Reports are available indicating that certain abiotic stress conditions, such as ozone stress, can bolster plant resilience against pathogen attacks in certain cases. However, in most scenarios, prolonged exposure of plants to abiotic stresses, such as drought or nutrient deprivation, tends to weaken their defenses, making them more susceptible to pests or pathogens, such as arthropods [1][16][18]. Abiotic stresses play a pivotal role in modulating plant tolerance or susceptibility to pathogens through various mechanisms, resulting in altered plant–pathogen interactions, influenced by factors such as plant species, pathogen type, and stress intensity [4].

2. Multifactorial Stress Combinations

Several abiotic stresses occur simultaneously, which is more lethal to crops than specific stress conditions [1]. The escalating impact of climate change and environmental pollution has correspondingly heightened the multitude and intricacy of stresses encountered by plants [19]. The recent emergence of MFSCs has focused on the response of plants exposed to three or more stress combinations simultaneously or sequentially [20], which has yielded some important conclusions.

Studies investigating MFSCs in *Arabidopsis thaliana*, *Oryza sativa*, and *Zea mays* have revealed substantial detrimental effects on plants. These findings indicate that even when individual stress levels are relatively low, the cumulative effect significantly diminishes plant growth and survival as the number of stressors increases [21][22]. Additional studies have demonstrated that plants navigate multifaceted stress combinations through distinct pathways and specialized processes [21]. Analysis of various *Oryza sativa* genotypes reveled noteworthy genetic diversity within its response mechanism [22]. As the number of stressors in a multifactorial stress combination increased, a consistent trend was observed in plant soil and microbial communities. This trend is aligned with the increasing number of stress factors, showing a notable decline in diversity [20][23].

3. Response Mechanisms to Stress Combinations

3.1. Reactive Oxygen Species

ROS homeostasis plays a crucial role in plant survival under stress combinations, and mutants with impaired ROS regulation exhibit high sensitivity to stress combinations [21][24]. In response to stress combinations, ROS function as pivotal signaling molecules, enabling the rapid detection of various stimuli and activation of regulatory pathways, including stomatal movement, abscisic acid (ABA), and immune responses [25]. This adjustment aids in adapting coping strategies, establishing defense mechanisms, and restoring growth capacity [26][27]. Despite their role as signaling molecules, ROS are also toxic by-products of stress metabolism. Elevated ROS levels can initiate genetically programmed cell death [28][29]. Plants exhibiting higher antioxidant capacities or lower ROS accumulation typically demonstrate greater resilience to stress combinations [6]. Effective detoxification of ROS is assumed to play a key role in enhancing plant tolerance to stress combinations [19]. Recent studies on plant ROS during stress combinations have revealed that while ROS can benefit plants amidst abiotic stresses, this is contingent on cells maintaining sufficiently high energy reserves to detoxify ROS, which enables plants to modulate their metabolism and craft suitable adaptive responses [28]. Following exposure to stress combinations, components such as flavanols [19], amino acids, and polyamines [30] show heightened accumulation in plants. They act as antioxidants, preserve cellular ROS homeostasis, and mitigate plant damage caused by stress combinations.

ROS waves are another aspect of plant response to stress combinations. ROS are produced as signaling molecules after stress in plants and are coupled with Ca^{2+} and electrical signals to form rapid and widespread systemic signals called ROS waves [31][32]. The ROS wave transmits signals to neighboring or distant cells, collaborating with various signaling components to orchestrate a systemic response. This process effectively regulates how plants respond to stress combinations [33], during which plants can integrate various systemic signals, generated simultaneously, through ROS waves. These signals can be swiftly transmitted from damaged parts, whether the same or different, to the entire plant within a few minutes [34]. The speed and efficiency of ROS signaling are correlated with the specific site of damage [35]. ROS waves are considered crucial signals that traverse through plant vascular bundles and chloroplasts [36]; ROS waves serve as a warning system for cells and tissues, signaling imminent stress. They are often accompanied by other signals that may convey specificity, eliciting systemic acquired acquisitiveness (SAA) to safeguard against growth and defense responses. Notably, plants without ROS waves do not exhibit SAA [33]. Thus, ROS waves are crucial for plant responses to stress combinations.

3.2. Plant Hormones

Plant hormones are other signaling molecules that plants use in response to stress combinations, coordinating multiple signal transduction pathways under stress combinations [37]. They play key roles in plant responses to stress combinations [38]. Various combinations of stress trigger distinct physiological and molecular responses in plants. These responses lead to alterations in the phytohormone and ROS levels, which subsequently influence each other [28]. Therefore, the ability of phytohormones to regulate antioxidant defense systems may be crucial for plant adaptation to stress combinations [9][37]. Hormones such as ABA, jasmonic acid (JA), salicylic acid (SA), and melatonin (MET) have previously been identified to play important roles in plant responses to stress combinations [39].

ABA is a major hormone in plant responses to stress combinations, regulating stomata and altering adaptor protein expression [40], which plays an important role in plant adaptation to stress combinations [9]. ABA serves as a pivotal regulator, controlling various response networks and bolstering plant resilience against stress combinations [41]. For example, ABA plays a crucial role in regulating the accumulation of vital proteins during high temperature and drought stress combinations [42]. Mutants deficient in ABA metabolism and signaling exhibit higher susceptibility than wild-type plants to combinations of salinity and high temperature [11], as well as salinity and intense light stress combinations [39]. ABA accumulation is affected by stress combinations [14], and interactions with ROS have important effects on plant adaptation to stress combinations [11][28].

Various stresses within a combination trigger hormone-signaling interactions. Other hormones, such as JA, SA, and MET, also participate in plant responses to stress combinations, contributing significantly to systemic signaling integration in plants [35]. JA plays a key role in the plant response of *Arabidopsis thaliana* to the combination of high-light and high-temperature stresses [43], and SA mitigates the damaging effects of combined drought, high-temperature, and salinity stresses by improving the antioxidant system [44]. Conversely, MET may function primarily as an antioxidant under stress combinations [45][46]; increased levels of MET under salinity and heat stress combinations enhance ROS detoxification and improve the acclimatization of *Solanum lycopersicum* by specifically regulating the expression of antioxidant-related genes, and the exogenous application of MET achieves a similar effect [29].

3.3. Transcription Factors

Transcription factors (TFs) are pivotal in the regulation of transcriptional processes, have broad involvement in plant growth and development, and are crucial in responding to stress combinations. Employing TFs to modulate the expression of specific genes proves to be an effective strategy for inducing plant tolerance [47][48][49]. Recent studies on *Arabidopsis thaliana* and *Zea mays*, under stress combinations, have revealed that these combinations induce distinct transcriptional changes that cannot be anticipated by plant responses to individual stressors [10][12]. In addition, transcriptome analyses of different soybean tissues under drought and high-temperature stress combinations showed that each tissue responded differently to the stress combinations [50].

Studies on *Oryza sativa*, *Helianthus annuus*, and *Triticum aestivum* have shown that plants express specific genes under stress combinations compared to single stresses, and that the responses to different stress combinations can be regulated by specific TFs [51][52][53]. Nevertheless, recent studies on several different stress combinations involving heat have shown that some TF families, such as heat shock factors (HSFs), myeloblastosis (MYB), and ethylene response factors (ERFs), may be used to enhance plant tolerance to different types of stress combinations involving heat when stress combinations with the same factor are involved [54][55][56]. These TFs play unique roles in stress combinations, whether they are specific TFs in stress combinations or common to different stress combinations, and in-depth studies on their own functions and regulatory pathways may be an effective means to reveal the regulatory pathways of stress combinations.

References

1. Mittler, R. Abiotic Stress, the Field Environment and Stress Combination. Trends Plant Sci. 2006, 11, 15–19.
2. Cotrozzi, L.; Pellegrini, E.; Guidi, L.; Landi, M.; Lorenzini, G.; Massai, R.; Remorini, D.; Tonelli, M.; Trivellini, A.; Vernieri, P.; et al. Losing the Warning Signal: Drought Compromises the Cross-Talk of Signaling Molecules in Quercus Ilex Exposed to Ozone. Front. Plant Sci. 2017, 8, 1020.
3. Lopez-Delacalle, M.; Camejo, D.M.; García-Martí, M.; Nortes, P.A.; Nieves-Cordones, M.; Martínez, V.; Rubio, F.; Mittler, R.; Rivero, R.M. Using Tomato Recombinant Lines to Improve Plant Tolerance to Stress Combination Through a More Efficient Nitrogen Metabolism. Front. Plant Sci. 2019, 10, 1702.
4. Pandey, P.; Ramegowda, V.; Senthil-Kumar, M. Shared and Unique Responses of Plants to Multiple Individual Stresses and Stress Combinations: Physiological and Molecular Mechanisms. Front. Plant Sci. 2015, 6, 723.
5. Sinha, R.; Fritschi, F.B.; Zandalinas, S.I.; Mittler, R. The Impact of Stress Combination on Reproductive Processes in Crops. Plant Sci. 2021, 311, 111007.
6. Zandalinas, S.I.; Mittler, R.; Balfagón, D.; Arbona, V.; Gómez-Cadenas, A. Plant Adaptations to the Combination of Drought and High Temperatures. Physiol. Plant 2018, 162, 2–12.
7. Zhou, X.; Yin, Y.; Wang, G.; Amombo, E.; Li, X.; Xue, Y.; Fu, J. Mitigation of Salt Stress on Low Temperature in Bermudagrass: Resistance and Forage Quality. Front. Plant Sci. 2022, 13, 1042855.
8. Sinha, R.; Zandalinas, S.I.; Fichman, Y.; Sen, S.; Zeng, S.; Gómez-Cadenas, A.; Joshi, T.; Fritschi, F.B.; Mittler, R. Differential Regulation of Flower Transpiration during Abiotic Stress in Annual Plants. New Phytol. 2022, 235, 611–629.
9. Balfagón, D.; Zandalinas, S.I.; Mittler, R.; Gómez-Cadenas, A. High Temperatures Modify Plant Responses to Abiotic Stress Conditions. Physiol. Plant 2020, 170, 335–344.
10. Guo, Q.; Li, X.; Niu, L.; Jameson, P.E.; Zhou, W. Transcription-Associated Metabolomic Adjustments in Maize Occur during Combined Drought and Cold Stress. Plant Physiol. 2021, 186, 677–695.

11. Suzuki, N.; Bassil, E.; Hamilton, J.S.; Inupakutika, M.A.; Zandalinas, S.I.; Tripathy, D.; Luo, Y.; Dion, E.; Fukui, G.; Kumazaki, A.; et al. ABA Is Required for Plant Acclimation to a Combination of Salt and Heat Stress. PLoS ONE 2016, 11, e0147625.
12. Rizhsky, L.; Liang, H.; Shuman, J.; Shulaev, V.; Davletova, S.; Mittler, R. When Defense Pathways Collide. The Response of Arabidopsis to a Combination of Drought and Heat Stress. Plant Physiol. 2004, 134, 1683–1696.
13. Cohen, I.; Zandalinas, S.I.; Huck, C.; Fritschi, F.B.; Mittler, R. Meta-Analysis of Drought and Heat Stress Combination Impact on Crop Yield and Yield Components. Physiol. Plant 2021, 171, 66–76.
14. Ngumbi, E.; Dady, E.; Calla, B. Flooding and Herbivory: The Effect of Concurrent Stress Factors on Plant Volatile Emissions and Gene Expression in Two Heirloom Tomato Varieties. BMC Plant Biol. 2022, 22, 536.
15. Peng, P.; Li, R.; Chen, Z.-H.; Wang, Y. Stomata at the Crossroad of Molecular Interaction between Biotic and Abiotic Stress Responses in Plants. Front. Plant Sci. 2022, 13, 1031891.
16. Arbona, V.; Ximénez-Embún, M.G.; Echavarri-Muñoz, A.; Martin-Sánchez, M.; Gómez-Cadenas, A.; Ortego, F.; González-Guzmán, M. Early Molecular Responses of Tomato to Combined Moderate Water Stress and Tomato Red Spider Mite Tetranychus Evansi Attack. Plants 2020, 9, 1131.
17. Bidzinski, P.; Ballini, E.; Ducasse, A.; Michel, C.; Zuluaga, P.; Genga, A.; Chiozzotto, R.; Morel, J.-B. Transcriptional Basis of Drought-Induced Susceptibility to the Rice Blast Fungus Magnaporthe Oryzae. Front. Plant Sci. 2016, 7, 1558.
18. Chávez-Arias, C.C.; Ligarreto-Moreno, G.A.; Ramírez-Godoy, A.; Restrepo-Díaz, H. Maize Responses Challenged by Drought, Elevated Daytime Temperature and Arthropod Herbivory Stresses: A Physiological, Biochemical and Molecular View. Front. Plant Sci. 2021, 12, 702841.
19. Martinez, V.; Mestre, T.C.; Rubio, F.; Girones-Vilaplana, A.; Moreno, D.A.; Mittler, R.; Rivero, R.M. Accumulation of Flavonols over Hydroxycinnamic Acids Favors Oxidative Damage Protection under Abiotic Stress. Front. Plant Sci. 2016, 7, 838.
20. Pascual, L.S.; Segarra-Medina, C.; Gómez-Cadenas, A.; López-Climent, M.F.; Vives-Peris, V.; Zandalinas, S.I. Climate Change-Associated Multifactorial Stress Combination: A Present Challenge for Our Ecosystems. J. Plant Physiol. 2022, 276, 153764.
21. Zandalinas, S.I.; Sengupta, S.; Fritschi, F.B.; Azad, R.K.; Nechushtai, R.; Mittler, R. The Impact of Multifactorial Stress Combination on Plant Growth and Survival. New Phytol. 2021, 230, 1034–1048.
22. Sinha, R.; Peláez-Vico, M.Á.; Shostak, B.; Nguyen, T.T.; Pascual, L.S.; Ogden, A.M.; Lyu, Z.; Zandalinas, S.I.; Joshi, T.; Fritschi, F.B.; et al. The Effects of Multifactorial Stress Combination on

Rice and Maize. Plant Physiol. 2023, kiad557.

23. Rillig, M.C.; Ryo, M.; Lehmann, A.; Aguilar-Trigueros, C.A.; Buchert, S.; Wulf, A.; Iwasaki, A.; Roy, J.; Yang, G. The Role of Multiple Global Change Factors in Driving Soil Functions and Microbial Biodiversity. Science 2019, 366, 886–890.
24. Rivero, R.M.; Mittler, R.; Blumwald, E.; Zandalinas, S.I. Developing Climate-Resilient Crops: Improving Plant Tolerance to Stress Combination. Plant J. 2022, 109, 373–389.
25. Qi, J.; Song, C.-P.; Wang, B.; Zhou, J.; Kangasjärvi, J.; Zhu, J.-K.; Gong, Z. Reactive Oxygen Species Signaling and Stomatal Movement in Plant Responses to Drought Stress and Pathogen Attack. J. Integr. Plant Biol. 2018, 60, 805–826.
26. Katano, K.; Honda, K.; Suzuki, N. Integration between ROS Regulatory Systems and Other Signals in the Regulation of Various Types of Heat Responses in Plants. Int. J. Mol. Sci. 2018, 19, 3370.
27. Guo, Z.; Chen, Q.; Liang, T.; Zhou, B.; Huang, S.; Cao, X.; Wang, X.; Ding, Z.; Tu, J. Functionalized Carbon Nano-Enabled Plant ROS Signal Engineering for Growth/Defense Balance. Nano Today 2023, 53, 102045.
28. Choudhury, F.K.; Rivero, R.M.; Blumwald, E.; Mittler, R. Reactive Oxygen Species, Abiotic Stress and Stress Combination. Plant J. 2017, 90, 856–867.
29. Martinez, V.; Nieves-Cordones, M.; Lopez-Delacalle, M.; Rodenas, R.; Mestre, T.C.; Garcia-Sanchez, F.; Rubio, F.; Nortes, P.A.; Mittler, R.; Rivero, R.M. Tolerance to Stress Combination in Tomato Plants: New Insights in the Protective Role of Melatonin. Molecules 2018, 23, 535.
30. Zandalinas, S.I.; Balfagón, D.; Gómez-Cadenas, A.; Mittler, R. Plant Responses to Climate Change: Metabolic Changes under Combined Abiotic Stresses. J. Exp. Bot. 2022, 73, 3339–3354.
31. Miller, G.; Schlauch, K.; Tam, R.; Cortes, D.; Torres, M.A.; Shulaev, V.; Dangl, J.L.; Mittler, R. The Plant NADPH Oxidase RBOHD Mediates Rapid Systemic Signaling in Response to Diverse Stimuli. Sci. Signal. 2009, 2, ra45.
32. Lecourieux, D.; Mazars, C.; Pauly, N.; Ranjeva, R.; Pugin, A. Analysis and Effects of Cytosolic Free Calcium Increases in Response to Elicitors in Nicotiana plumbaginifolia Cells. Plant Cell 2002, 14, 2627–2641.
33. Fichman, Y.; Mittler, R. Rapid Systemic Signaling during Abiotic and Biotic Stresses: Is the ROS Wave Master of All Trades? Plant J. 2020, 102, 887–896.
34. Fichman, Y.; Rowland, L.; Oliver, M.J.; Mittler, R. ROS Are Evolutionary Conserved Cell-to-Cell Stress Signals. Proc. Natl. Acad. Sci. USA 2023, 120, e2305496120.

35. Zandalinas, S.I.; Fichman, Y.; Devireddy, A.R.; Sengupta, S.; Azad, R.K.; Mittler, R. Systemic Signaling during Abiotic Stress Combination in Plants. Proc. Natl. Acad. Sci. USA 2020, 117, 13810–13820.
36. Zandalinas, S.I.; Mittler, R. Vascular and Nonvascular Transmission of Systemic Reactive Oxygen Signals during Wounding and Heat Stress. Plant Physiol. 2021, 186, 1721–1733.
37. Raza, A.; Salehi, H.; Rahman, M.A.; Zahid, Z.; Madadkar Haghjou, M.; Najafi-Kakavand, S.; Charagh, S.; Osman, H.S.; Albaqami, M.; Zhuang, Y.; et al. Plant Hormones and Neurotransmitter Interactions Mediate Antioxidant Defenses under Induced Oxidative Stress in Plants. Front. Plant Sci. 2022, 13, 961872.
38. Suzuki, N. Hormone Signaling Pathways under Stress Combinations. Plant Signal. Behav. 2016, 11, e1247139.
39. Segarra-Medina, C.; Alseekh, S.; Fernie, A.R.; Rambla, J.L.; Pérez-Clemente, R.M.; Gómez-Cádenas, A.; Zandalinas, S.I. Abscisic Acid Promotes Plant Acclimation to the Combination of Salinity and High Light Stress. Plant Physiol. Biochem. 2023, 203, 108008.
40. Kumazaki, A.; Suzuki, N. Enhanced Tolerance to a Combination of Heat Stress and Drought in Arabidopsis Plants Deficient in ICS1 Is Associated with Modulation of Photosynthetic Reaction Center Proteins. Physiol. Plant 2019, 165, 232–246.
41. Danquah, A.; de Zelicourt, A.; Colcombet, J.; Hirt, H. The Role of ABA and MAPK Signaling Pathways in Plant Abiotic Stress Responses. Biotechnol. Adv. 2014, 32, 40–52.
42. Zandalinas, S.I.; Rivero, R.M.; Martínez, V.; Gómez-Cadenas, A.; Arbona, V. Tolerance of Citrus Plants to the Combination of High Temperatures and Drought Is Associated to the Increase in Transpiration Modulated by a Reduction in Abscisic Acid Levels. BMC Plant Biol. 2016, 16, 105.
43. Balfagón, D.; Sengupta, S.; Gómez-Cadenas, A.; Fritschi, F.B.; Azad, R.K.; Mittler, R.; Zandalinas, S.I. Jasmonic Acid Is Required for Plant Acclimation to a Combination of High Light and Heat Stress. Plant Physiol. 2019, 181, 1668–1682.
44. Torun, H. Time-Course Analysis of Salicylic Acid Effects on ROS Regulation and Antioxidant Defense in Roots of Hulled and Hulless Barley under Combined Stress of Drought, Heat and Salinity. Physiol. Plant 2019, 165, 169–182.
45. Pardo-Hernández, M.; López-Delacalle, M.; Rivero, R.M. ROS and NO Regulation by Melatonin Under Abiotic Stress in Plants. Antioxidants 2020, 9, 1078.
46. Wang, Y.; Cheng, P.; Zhao, G.; Li, L.; Shen, W. Phytomelatonin and Gasotransmitters: A Crucial Combination for Plant Physiological Functions. J. Exp. Bot. 2022, 73, 5851–5862.
47. Yan, Z.; Li, K.; Li, Y.; Wang, W.; Leng, B.; Yao, G.; Zhang, F.; Mu, C.; Liu, X. The ZmbHLH32-ZmIAA9-ZmARF1 Module Regulates Salt Tolerance in Maize. Int. J. Biol. Macromol. 2023, 253,

126978.

48. Fang, L.; Wang, Z.; Su, L.; Gong, L.; Xin, H. Vitis Myb14 Confer Cold and Drought Tolerance by Activating Lipid Transfer Protein Genes Expression and Reactive Oxygen Species Scavenge. Gene 2024, 890, 147792.
49. Shen, L.; Xia, X.; Zhang, L.; Yang, S.; Yang, X. SmWRKY11 Acts as a Positive Regulator in Eggplant Response to Salt Stress. Plant Physiol. Biochem. 2023, 205, 108209.
50. Sinha, R.; Induri, S.P.; Peláez-Vico, M.; Tukuli, A.; Shostak, B.; Zandalinas, S.I.; Joshi, T.; Fritschi, F.B.; Mittler, R. The Transcriptome of Soybean Reproductive Tissues Subjected to Water Deficit, Heat Stress, and a Combination of Water Deficit and Heat Stress. Plant J. 2023, 116, 1064–1080.
51. Mittal, D.; Madhyastha, D.A.; Grover, A. Gene Expression Analysis in Response to Low and High Temperature and Oxidative Stresses in Rice: Combination of Stresses Evokes Different Transcriptional Changes as against Stresses Applied Individually. Plant Sci. 2012, 197, 102–113.
52. Hewezi, T.; Léger, M.; Gentzbittel, L. A Comprehensive Analysis of the Combined Effects of High Light and High Temperature Stresses on Gene Expression in Sunflower. Ann. Bot. 2008, 102, 127–140.
53. Liu, Z.; Xin, M.; Qin, J.; Peng, H.; Ni, Z.; Yao, Y.; Sun, Q. Temporal Transcriptome Profiling Reveals Expression Partitioning of Homeologous Genes Contributing to Heat and Drought Acclimation in Wheat (Triticum aestivum L.). BMC Plant Biol. 2015, 15, 152.
54. Zandalinas, S.I.; Fritschi, F.B.; Mittler, R. Signal Transduction Networks during Stress Combination. J. Exp. Bot. 2020, 71, 1734–1741.
55. Anfoka, G.; Moshe, A.; Fridman, L.; Amrani, L.; Rotem, O.; Kolot, M.; Zeidan, M.; Czosnek, H.; Gorovits, R. Corrigendum: Tomato Yellow Leaf Curl Virus Infection Mitigates the Heat Stress Response of Plants Grown at High Temperatures. Sci. Rep. 2016, 6, 25284.
56. Jacob, P.; Hirt, H.; Bendahmane, A. The Heat-Shock Protein/Chaperone Network and Multiple Stress Resistance. Plant Biotechnol. J. 2017, 15, 405–414.