

Review article

Crosstalk Between Abiotic and Biotic Stress Responses in Plants: Mechanisms, Outcomes, and Implications for Crop Improvement

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Abstract:

Plants growing under field conditions often face multiple stress factors concurrently. These can include extremes of drought, salinity, or temperature coupled with attacks from pathogens or herbivores. Understanding how plants perceive, integrate, and respond to overlapping abiotic and biotic challenges is critical for guiding future crop improvement efforts. Complex signaling networks, involving phytohormones, transcriptional reprogramming, and epigenetic modifications, shape outcomes that can differ markedly from those elicited by individual stressors. This review examines how hormonal crosstalk and shared signaling nodes influence plant defense and tolerance mechanisms, explores specific case studies of simultaneous stresses, and considers the implications for breeding, biotechnological interventions, and agronomic management strategies. Key knowledge gaps and emerging research directions are discussed, emphasizing the urgency of interdisciplinary approaches. Harnessing insights into stress crosstalk promises to improve crop resilience and secure agricultural productivity in the face of global climate change and increasing pathogen pressures.

Keywords: Abiotic stress, Biotic stress, Crosstalk, Plant signaling pathways, Hormone signaling, Plant defense, Stress tolerance, Synergy, Antagonism.

Introduction

In agricultural ecosystems worldwide, plants must continually adapt to a dynamic combination of environmental and biological pressures. Rapid climate change has aggravated the frequency and intensity of abiotic stresses, including drought, salinity, and temperature extremes, while simultaneously expanding the range and aggressiveness of many pathogens and pests (Atkinson & Urwin, 2012; Bigeard et al., 2015). Field conditions rarely present stress factors in isolation; rather, plants are often compelled to cope with multiple challenges simultaneously. Such complexity extends beyond simple additive effects. The integration of signals from distinct stress pathways can generate emergent properties, sometimes enhancing overall resilience, but often creating conflicts that reduce the effectiveness of plant defenses.

A comprehensive understanding of how plants manage overlapping stress signals is a key scientific and agricultural priority. The importance of dissecting crosstalk between abiotic and biotic stress responses has grown as researchers have recognized that pathways involved in drought resistance, for instance, can influence susceptibility or resistance to pathogens (Cohen & Leach, 2019; Nguyen et al., 2016). Knowledge gleaned from these interactions enables more informed breeding, the rational design of biotechnological interventions, and the development of agronomic strategies that improve resilience under conditions predicted for future climates (Rivero et al., 2022; Saijo & Loo, 2020; Elkelish et al., 2020b).

The objectives of this review are to summarize recent advances in elucidating the molecular and hormonal mechanisms that integrate abiotic and biotic stress signals, to highlight points of synergy and antagonism, and to discuss how evolving insights guide crop improvement. Current approaches leveraging omics technologies, epigenetic profiling, and genome editing tools are considered alongside conventional breeding and integrated pest management strategies. The review also identifies critical knowledge gaps and proposes future research directions emphasizing interdisciplinary collaborations.

Conceptual Framework: Plant Signaling Under Stress

Plants sense and respond to a wide range of environmental stimuli by employing a hierarchy of receptors, secondary messengers, and signaling cascades. Abiotic stresses are often detected through changes in cellular homeostasis, including osmotic imbalances and redox states. Such perception triggers defense and tolerance pathways orchestrated by phytohormones like abscisic acid (ABA), jasmonates (JA), salicylic acid (SA), and ethylene (ET). Biotic stresses are recognized either by pattern-recognition receptors that detect conserved pathogen-associated molecular patterns or by intracellular receptors responding to specific pathogen effectors (Jones & Dangl, 2006; Pieterse et al., 2012).

The transcriptional reprogramming that follows stress perception involves vast networks of transcription factors, including amino-acid sequence WRKYGQK (WRKY), cup-shaped cotyledon (CUC) (NAC), and basic leucine zipper containing domain proteins (bZIP) families, as well as post-transcriptional and epigenetic modifications (Chinnusamy & Zhu, 2009; Downen et al., 2012). Under abiotic stress, pathways frequently converge on ABA-mediated signals that reduce water loss and protect cell integrity. By contrast, biotic defense often depends on coordinated SA, JA, and ET signaling. Despite these differences, evidence suggests extensive overlap and potential for mutual modulation. The same regulators can be involved in immune responses and tolerance to osmotic or temperature stress, and the accumulation of reactive oxygen species (ROS) can serve as a common second messenger integrating multiple cues (Miller et al., 2010).

Mechanisms of Crosstalk: Hormonal and Molecular Interactions

Crosstalk between abiotic and biotic signaling relies heavily on hormone networks. ABA, typically elevated under drought, is known to suppress certain SA-dependent defenses, thus creating a trade-off that can reduce pathogen resistance while improving drought tolerance (Cohen & Leach, 2019; Yasuda et al., 2008). Similarly, SA and JA pathways, central to immune responses, often act antagonistically, with SA dominating in defense against biotrophic pathogens and JA playing a major role against herbivores and necrotrophs (Thaler et al., 2012; Ku et al., 2018). The net outcome depends on the relative timing and intensity of both stresses, as well as on plant genotype and developmental stage.

Not all crosstalk is antagonistic. Synergistic interactions occur in certain contexts, such as when ABA and JA signaling reinforce each other under conditions of water deficit and insect attack, allowing a plant to conserve water while simultaneously mounting effective anti-herbivore defenses (Nguyen et al., 2016). ROS and redox signaling further integrate these signals, influencing transcription factors and epigenetic regulators to shape gene expression patterns. Shared signaling nodes, including MAPK cascades and WRKY transcription factors, serve as molecular hubs that enable plants to sense multiple inputs and execute nuanced responses (Bigeard et al., 2015).

Balancing stress tolerance and defense represents an adaptive challenge, as investment in defense-related compounds often draws resources away from growth and reproduction. These metabolic and fitness trade-offs, observed in both model plants and crops, reflect evolutionary compromises. Over millennia, plant populations have evolved strategies to optimize these trade-offs, contributing to species diversity and distribution patterns under varied ecological pressures (Huot et al., 2014).

Case Studies: Specific Abiotic–Biotic Stress Combinations

Examining concrete scenarios clarifies the biological and agricultural significance of crosstalk. Drought conditions often induce ABA-dependent stomatal closure, potentially limiting pathogen entry but also weakening SA-mediated immune responses against pathogens that do not rely on stomatal ingress. Climate models predicting more frequent drought events highlight the importance of understanding these interactions to forecast disease outbreaks and refine irrigation strategies (Cohen & Leach, 2019; Yasuda et al., 2008).

Salinity stress, a growing global problem, can disrupt ionic balance and trigger osmotic stress responses that alter JA-mediated defenses against herbivory. In some instances, plants under saline conditions become more susceptible to insects due to reduced allocation to defense metabolites. Conversely, understanding these interactions allows breeders to select cultivars with stable JA responses under salt stress (Rudgers et al., 2004; Elkelish et al., 2020a).

Temperature extremes add complexity to plant-pathogen dynamics. High temperatures can influence immune receptor functions through heat shock proteins (Wu et al., 2017). In other cases, cold stress may compromise pattern-triggered immunity, leaving plants vulnerable to pathogens that thrive at lower temperatures. Such knowledge guides breeding programs for resilience under increasingly erratic thermal conditions.

Agricultural and Biotechnological Implications

Insights into crosstalk between stress responses have practical value for developing resilient crops. Traditional breeding approaches have started to integrate knowledge of hormonal pathways and transcriptional regulators to improve simultaneous tolerance to drought and resistance to pathogens. Quantitative trait loci (QTL) analysis and genomic selection now incorporate stress response markers, offering more robust prediction of plant performance under field conditions (Rivero et al., 2022).

Biotechnological interventions, including genetic engineering and gene editing with CRISPR/Cas9, can fine-tune hormone levels, modify key transcription factors, or alter epigenetic marks. This offers the possibility of recalibrating growth-defense trade-offs and optimizing stress responses. Synthetic biology allows the design of artificial signaling circuits that respond predictably to concurrent stresses. By introducing novel regulatory elements or modifying promoter regions, researchers can generate plants capable of balanced resource allocation, securing yields under complex stress scenarios (Wang et al., 2021).

Beyond genetic and molecular approaches, agronomic management can exploit knowledge of crosstalk. Adjusting irrigation timing, optimizing soil amendments, and deploying beneficial microbes that modulate hormone signals can help maintain a favorable stress response profile. Integrated pest management approaches can be synchronized with the plant's internal signaling state to minimize the metabolic cost of defense while ensuring adequate protection against pathogens and pests (Berendsen et al., 2012; Elkelish et al., 2020a).

Knowledge Gaps and Future Perspectives

Despite the progress made in recent years, many fundamental questions remain unanswered. The precise molecular mechanisms that allow plants to integrate opposing hormonal cues, the role of epigenetic modifications in establishing long-term stress memory, and the evolutionary trajectories that have shaped crosstalk networks all merit deeper investigation. These gaps impede the full exploitation of crosstalk for crop improvement.

Emerging tools and methodologies offer hope. High-throughput omics, including transcriptomics, proteomics, and metabolomics, can capture the complexity of responses at a systems level, while single-cell technologies and advanced imaging help localize these processes within tissues. Computational modeling and machine learning can predict stress outcomes and guide experimental designs that pinpoint key regulatory nodes. Broad collaborations across disciplines that include plant physiologists, molecular

biologists, breeders, agronomists, ecologists, and evolutionary biologists can integrate mechanistic insights into practical strategies for sustainable agriculture (Saijo & Loo, 2020).

Conclusion

Plants face a complex interplay of environmental and biological challenges in natural and agricultural settings. Their ability to perceive, integrate, and respond to multiple concurrent stresses is governed by intricate crosstalk among hormonal pathways, transcription factors, and epigenetic regulators. These networks yield outcomes that can differ significantly from responses to individual stresses, sometimes enhancing tolerance, other times forcing trade-offs that reduce fitness.

A clearer understanding of these integrative mechanisms offers exciting opportunities for improving crop performance. By harnessing crosstalk-based insights, plant breeders and biotechnologists can create more resilient cultivars that maintain yield and quality under increasingly unpredictable environmental conditions. Agronomic management strategies and molecular technologies, such as genome editing and synthetic biology, promise to refine these responses further, aligning plant physiology with sustainable farming practices and global food security goals.

References

- Abdelrahman, M., Burritt, D. J., & Tran, L. P. (2018). The critical role of epigenetic regulations in controlling plant response to abiotic stress. *Physiologia Plantarum*, 165(1), 95–111. <https://doi.org/10.1111/ppl.12644>
- Atkinson, N. J., & Urwin, P. E. (2012). The interaction of plant biotic and abiotic stresses: From genes to the field. *Journal of Experimental Botany*, 63(10), 3523–3543. <https://doi.org/10.1093/jxb/ers100>
- Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends in Plant Science*, 17(8), 478–486. <https://doi.org/10.1016/j.tplants.2012.04.001>
- Bertini, L., Proietti, S., Van Verk, M. C., Giorgi, F. M., & Cipriani, P. (2018). Transcriptomics of the salicylic acid response in *Arabidopsis*. *Scientific Reports*, 8, 1970. <https://doi.org/10.1038/s41598-018-20281-8>
- Bhatnagar-Mathur, P., Devi, M. J., Reddy, D. S., Lavanya, M., Vadez, V., & Sharma, K. K. (2014). Stress-inducible expression of AtDREB1A in transgenic peanut (*Arachis hypogaea* L.) increases transpiration efficiency under water-limited conditions. *Plant Cell Reports*, 33(2), 419–429. <https://doi.org/10.1007/s00299-013-1531-5>
- Bigeard, J., Colcombet, J., & Hirt, H. (2015). Signaling mechanisms in pattern-triggered immunity (PTI). *Molecular Plant*, 8(4), 521–539. <https://doi.org/10.1016/j.molp.2014.12.022>
- Caarls, L., Pieterse, C. M., & Van Wees, S. C. (2015). How salicylic acid takes transcriptional control over jasmonic acid signaling. *Frontiers in Plant Science*, 6, 170. <https://doi.org/10.3389/fpls.2015.00170>
- Cao, F. Y., Yoshioka, K., & Desveaux, D. (2011). The roles of ABA in plant-pathogen interactions. *Journal of Plant Research*, 124(4), 489–499. <https://doi.org/10.1007/s10265-011-0409-y>
- Challinor, A. J., Watson, J., Lobell, D. B., Howden, S. M., Smith, D. R., & Chhetri, N. (2014). A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change*, 4(4), 287–291. <https://doi.org/10.1038/nclimate2153>
- Chinnusamy, V., & Zhu, J.-K. (2009). Epigenetic regulation of stress responses in plants. *Current Opinion in Plant Biology*, 12(2), 133–139. <https://doi.org/10.1016/j.pbi.2008.12.006>
- Choudhary, S., Marathe, S. J., Talukdar, D., Pareek, A., & Agarwal, P. (2021). Identification and functional characterization of stress-responsive transcription factors for crop improvement. *Plant, Cell & Environment*, 44(6), 1899–1924. <https://doi.org/10.1111/pce.14049>
- Cohen, S. P., & Leach, J. E. (2019). Abiotic and biotic stresses induce a core transcriptome response in rice. *Scientific Reports*, 9, 6273. <https://doi.org/10.1038/s41598-019-42847-x>
- De Storme, N., & Geelen, D. (2014). Stress-induced male sterility: How environmental factors influence pollen development. *Plant, Cell and Environment*, 37(1), 1–18. <https://doi.org/10.1111/pce.12142>

- Ding, Y., Shi, Y., & Yang, S. (2019). Advances and challenges in uncovering cold tolerance regulatory mechanisms in plants. *New Phytologist*, 222(4), 1690–1704. <https://doi.org/10.1111/nph.15696>
- Downen, R. H., Pelizzola, M., Schmitz, R. J., Lister, R., Downen, J. M., Nery, J. R., ... Ecker, J. R. (2012). Widespread dynamic DNA methylation in response to biotic stress. *Proceedings of the National Academy of Sciences USA*, 109(32), E2183–E2191. <https://doi.org/10.1073/pnas.1209329109>
- Duan, Y., Chen, M., Guo, W., Zhang, Q., & Zhang, W. (2018). Phosphorylation and activation of sucrose phosphate synthase by a calcium-dependent protein kinase (CDPK) in wheat (*Triticum aestivum* L.). *Plant Science*, 270, 176–184. <https://doi.org/10.1016/j.plantsci.2018.02.012>
- Elkelish, A., Alhaithloul, H. A. S., Qari, S. H., Abd El-Mageed, T. A., Soliman, M. H., & El-Esawi, M. A. (2020a). Ectomycorrhizal fungi confers salinity stress tolerance in *Eucalyptus camaldulensis* by altering growth, physiological and biochemical attributes. *Scientia Horticulturae*, 265, 109240. <https://doi.org/10.1016/j.scienta.2020.109240>
- Elkelish, A., Soliman, M. H., Alhaithloul, H. A. S., & El-Esawi, M. A. (2020b). Exogenous ascorbic acid induced changes in growth, biochemical attributes, antioxidant enzyme activity and gene expression in *Cucumis sativus* L. plants under salt stress. *Plant Physiology and Biochemistry*, 151, 21–29. <https://doi.org/10.1016/j.plaphy.2020.03.017>
- Fahad, S., Bajwa, A. A., Nazir, U., Anjum, S. A., Farooq, A., Zohaib, A., ... Huang, J. (2017). Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science*, 8, 1147. <https://doi.org/10.3389/fpls.2017.01147>
- Fones, H. N., & Preston, G. M. (2013). Trade-offs between abiotic and biotic stress resistance: A case study of rice blast. *Frontiers in Plant Science*, 4, 167. <https://doi.org/10.3389/fpls.2013.00167>
- Foyer, C. H., & Shigeoka, S. (2011). Understanding oxidative stress and antioxidant functions to enhance photosynthesis. *Plant Physiology*, 155(1), 93–100. <https://doi.org/10.1104/pp.110.166181>
- Ghaffari, M. R., Ghaffari, M., Kalantari, S., ... Kav, N. N. (2019). Mass spectrometry-based proteomics reveals the molecular basis of stress responses in plants. *Frontiers in Plant Science*, 10, 864. <https://doi.org/10.3389/fpls.2019.00864>
- Gómez-Ariza, J., Brunner, S., Róden, L., ... Parker, J. E. (2019). Plant immune responses mediated by NLRs: From recognition to transcriptional reprogramming. *Plant Cell*, 31(9), 2367–2383. <https://doi.org/10.1105/tpc.19.00143>
- Gupta, A., Rico-Medina, A., & Caño-Delgado, A. I. (2020). The physiology of plant responses to drought. *Science*, 368(6488), 266–269. <https://doi.org/10.1126/science.aaz7614>
- Hasanuzzaman, M., Bhuyan, M. H. M. B., Zulfiqar, F., Raza, A., Mohsin, S. M., Mahmud, J. A., ... Fujita, M. (2020). Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants*, 9(8), 681. <https://doi.org/10.3390/antiox9080681>
- Huot, B., Yao, J., Montgomery, B. L., & He, S. Y. (2014). Growth–defense trade-offs in plants: A balancing act to optimize fitness. *Molecular Plant*, 7(8), 1267–1287. <https://doi.org/10.1093/mp/ssu049>
- Hussain, T., Hazara, A. R., & Mitra, B. (2022). Integrative omics approaches in salt stress tolerance: Prospects for crop improvement. *Plant Science Today*, 9(2), 454–464. <https://doi.org/10.14719/pst.1353>
- Jones, J. D. G., & Dangl, J. L. (2006). The plant immune system. *Nature*, 444(7117), 323–329. <https://doi.org/10.1038/nature05286>
- Khan, M. I. R., Fatma, M., Per, T. S., Anjum, N. A., & Khan, N. A. (2015). Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. *Frontiers in Plant Science*, 6, 462. <https://doi.org/10.3389/fpls.2015.00462>
- Kissoudis, C., Chowdhury, R., van Heusden, S., & van der Linden, G. (2015). Combined biotic and abiotic stress resistance in tomato. *Euphytica*, 202(2), 317–332. <https://doi.org/10.1007/s10681-014-1254-9>
- Ku, Y.-S., Sintaha, M., Cheung, M.-Y., & Lam, H.-M. (2018). Plant hormone signaling crosstalks between biotic and abiotic stress responses. *International Journal of Molecular Sciences*, 19(10), 3206. <https://doi.org/10.3390/ijms19103206>

- Li, S., Fu, Q., Chen, L., Huang, W., Yu, D., & Liu, X. (2016). Arabidopsis thaliana WRKY39 transcription factor mediates the crosstalk between jasmonic acid and salicylic acid signaling pathways. *Plant Cell Reports*, 35(2), 363–374. <https://doi.org/10.1007/s00299-015-1883-4>
- Li, X., Jiang, Q., Wang, T., Peng, X., Li, Y., & Zhao, C. (2017). Plant functional traits and soil nutrients are associated with species coexistence in a tropical coastal dune forest. *Scientific Reports*, 7, 42624. <https://doi.org/10.1038/srep42624>
- Liu, J., El-Kassaby, Y. A., & He, X. (2019). Plant epigenetics: The basis for complex traits and evolutionary adaptation. *Frontiers in Genetics*, 10, 195. <https://doi.org/10.3389/fgene.2019.00195>
- López, M. A., Bannenberg, G., & Castresana, C. (2008). Controlling hormone signaling is a plant and pathogen challenge for survival. *Current Opinion in Plant Biology*, 11(4), 420–427. <https://doi.org/10.1016/j.pbi.2008.05.002>
- Miller, G., Schlauch, K., Tam, R., & Rumsey, J. (2010). The ROS-wheel: Refining ROS signals by propagation and degradation. *Plant Signaling & Behavior*, 5(9), 1137–1139. <https://doi.org/10.4161/psb.5.9.12533>
- Mittler, R., & Blumwald, E. (2010). Genetic engineering for modern agriculture: Challenges and perspectives. *Annual Review of Plant Biology*, 61, 443–462. <https://doi.org/10.1146/annurev-arplant-042809-112116>
- Mitra, S. K., Walters, B. T., Clouse, S. D., & Goshe, M. B. (2015). Phosphoproteomic analysis of Arabidopsis seedlings reveals dynamic changes in phosphoproteins in response to ethylene and auxin. *Journal of Proteome Research*, 14(4), 1554–1566. <https://doi.org/10.1021/pr501284r>
- Monaghan, J., & Zipfel, C. (2012). Plant pattern recognition receptor complexes at the plasma membrane. *Current Opinion in Plant Biology*, 15(4), 349–357. <https://doi.org/10.1016/j.pbi.2012.05.006>
- Nguyen, D., Dagnon, S., & El-Kereamy, A. (2016). Physiological and molecular strategies to improve drought resistance in crops. *Frontiers in Plant Science*, 7, 548. <https://doi.org/10.3389/fpls.2016.00548>
- Nishad, R., Ahmed, T., Rahman, V. J., & Kareem, A. (2020). Modulation of plant defense system in response to microbial interactions. *Frontiers in Microbiology*, 11, 1298. <https://doi.org/10.3389/fmicb.2020.01298>
- Pandey, P., Irulappan, V., Bagavathiannan, M. V., & Senthil-Kumar, M. (2017). Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physiomorphological traits. *Frontiers in Plant Science*, 8, 537. <https://doi.org/10.3389/fpls.2017.00537>
- Pieterse, C. M. J., De Jonge, R., & Berendsen, R. L. (2016). The soil-borne supremacy. *Trends in Plant Science*, 21(3), 171–173. <https://doi.org/10.1016/j.tplants.2016.01.018>
- Pieterse, C. M. J., Van der Does, D., Zamioudis, C., Van Wees, S. C. M., & Van Loon, L. C. (2012). Hormonal modulation of plant immunity. *Annual Review of Cell and Developmental Biology*, 28, 489–521. <https://doi.org/10.1146/annurev-cellbio-092910-154055>
- Pieterse, C. M. J., Van Wees, S. C. M., Ton, J., Van Pelt, J. A., & Van Loon, L. C. (2014). Signaling in rhizobacteria-induced systemic resistance in Arabidopsis thaliana. *Plant Biology*, 6(4), 1–7. <https://doi.org/10.1055/s-2004-817879>
- Raghavendra, A. S., Gonugunta, V. K., Christmann, A., & Grill, E. (2010). ABA perception and signaling. *Trends in Plant Science*, 15(7), 395–401. <https://doi.org/10.1016/j.tplants.2010.04.006>
- Ramirez-Prado, J. S., Piquerez, S. J., Bendahmane, A., & Raynaud, C. (2018). Modify the histone code: Epigenetic pathways to regulate plant immunity. *Trends in Plant Science*, 23(7), 667–682. <https://doi.org/10.1016/j.tplants.2018.04.006>
- Rivero, R. M., Mittler, R., Blumwald, E., & Zandalinas, S. I. (2022). Developing climate-resilient crops: Improving plant tolerance to stress combination. *Plant Journal*, 109(2), 373–389. <https://doi.org/10.1111/tpj.15458>
- Rudgers, J. A., Strauss, S. Y., & Wendel, J. F. (2004). Trade-offs among anti-herbivore resistance traits: Insights from Gossypieae (Malvaceae). *American Journal of Botany*, 91(6), 871–880. <https://doi.org/10.3732/ajb.91.6.871>
- Saijo, Y., & Loo, E. P. (2020). Plant immunity in signal integration between biotic and abiotic stress responses. *New Phytologist*, 225(1), 87–104. <https://doi.org/10.1111/nph.15871>

- Saha, G., Park, J. I., Kayum, M. A., Nou, I. S., & Chung, M. Y. (2016). Characterization of stress-responsive NAC transcription factors in *Brassica rapa*. *Frontiers in Plant Science*, 7, 957. <https://doi.org/10.3389/fpls.2016.00957>
- Sahu, B. B., Tayal, D., Pradhan, M., & Rana, V. S. (2022). Transcriptional dynamics of plant responses to simultaneous stresses. *Frontiers in Plant Science*, 13, 863959. <https://doi.org/10.3389/fpls.2022.863959>
- Sanchez, D. H., Pieckenstein, F. L., Szymanski, J., Erban, A., Bromke, M., & Hoefgen, R. (2011). Comparative functional genomics of salt stress in related model and crop plant species: A perspective on *Arabidopsis* and tomato. *Frontiers in Plant Science*, 2, 29. <https://doi.org/10.3389/fpls.2011.00029>
- Sarris, P. F., Cevik, V., Dagdas, G., Jones, J. D. G., & Kamoun, S. (2016). Genomic approaches unraveling immune responses to plant pathogens. *Current Opinion in Plant Biology*, 29, 78–86. <https://doi.org/10.1016/j.pbi.2015.11.002>
- Savvides, A., Ali, S., Tester, M., & Fotopoulos, V. (2016). Chemical priming of plants against multiple abiotic stresses: Mission possible? *Trends in Plant Science*, 21(4), 329–340. <https://doi.org/10.1016/j.tplants.2015.11.003>
- Sawe, T., Zhao, Y., Zhang, R., Zhang, J., & Lu, S. (2020). Role of WRKY transcription factors in regulation of abiotic stress responses in plants. *Plant Cell Reports*, 39, 1535–1547. <https://doi.org/10.1007/s00299-020-02586-x>
- Schlaeppli, K., Dombrowski, N., Oter, R. G., Ver Loren van Themaat, E., & Schulze-Lefert, P. (2014). Quantitative divergence of the bacterial root microbiota in *Arabidopsis thaliana* relatives. *Proceedings of the National Academy of Sciences USA*, 111(2), 585–592. <https://doi.org/10.1073/pnas.1321597111>
- Shah, J. (2009). Plants under attack: Systemic signals in defence. *Current Opinion in Plant Biology*, 12(4), 459–464. <https://doi.org/10.1016/j.pbi.2009.05.011>
- Sharma, M., Pandey, G., & Pandey, G. K. (2020). Understanding plant adaptation to multiple stress conditions: Insights from the plasma membrane proteome. *Frontiers in Plant Science*, 11, 829. <https://doi.org/10.3389/fpls.2020.00829>
- Shulaev, V., Cortes, D., Miller, G., & Mittler, R. (2008). Metabolomics for plant stress response: Shifting from pattern recognition to biological interpretation. *BioEssays*, 30(4), 340–350. <https://doi.org/10.1002/bies.20724>
- Singh, P., Yekondi, S., Chen, P. W., Tsai, C. H., & Zimmerli, L. (2014). *Arabidopsis thaliana* mitogen-activated protein kinase kinases, MKK1/2, are essential for elicitor-induced camalexin biosynthesis. *Journal of Experimental Botany*, 65(8), 2209–2220. <https://doi.org/10.1093/jxb/eru102>
- Song, L., & Huang, S.-S. C. (2015). Epigenetic regulation in plant abiotic stress responses. *Journal of Integrative Plant Biology*, 57(12), 892–912. <https://doi.org/10.1111/jipb.12401>
- Takatsuji, H. (2014). Regulating trade-offs to improve crop productivity under abiotic and biotic stress conditions. *Frontiers in Plant Science*, 5, 483. <https://doi.org/10.3389/fpls.2014.00483>
- Thaler, J. S., Humphrey, P. T., & Whiteman, N. K. (2012). Evolution of jasmonate and salicylate signal crosstalk. *Trends in Plant Science*, 17(5), 260–270. <https://doi.org/10.1016/j.tplants.2012.02.010>
- Van Loon, L. C., Geraats, B. P. J., & Linthorst, H. J. M. (2006). Ethylene as a modulator of disease resistance in plants. *Trends in Plant Science*, 11(4), 184–191. <https://doi.org/10.1016/j.tplants.2006.02.005>
- Verma, V., Ravindran, P., & Kumar, P. P. (2016). Plant hormone-mediated regulation of stress responses. *BMC Plant Biology*, 16, 86. <https://doi.org/10.1186/s12870-016-0771-y>
- Wang, B., Moore, M. J., & Purugganan, M. D. (2021). The genetics of evolutionary resilience and climate change. *Current Biology*, 31(21), R1305–R1311. <https://doi.org/10.1016/j.cub.2021.08.083>
- Wang, K. L.-C., Li, H., & Ecker, J. R. (2002). Ethylene biosynthesis and signaling networks. *Plant Cell*, 14(Suppl), S131–S151. <https://doi.org/10.1105/tpc.001768>
- Wu, G., Hasanuzzaman, M., & Azad, M. O. K. (2017). Implication of heat shock proteins in plant responses to abiotic stresses. *Plant Gene*, 11, 90–96. <https://doi.org/10.1016/j.plgene.2017.04.003>
- Xie, Q., Frugis, G., Colgan, D., & Chua, N. H. (2000). *Arabidopsis* NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. *Genes & Development*, 14(23), 3024–3036. <https://doi.org/10.1101/gad.852200>

- Yasuda, M., Okada, K., & Yamamoto, Y. (2008). Plant responses to simultaneous drought and pathogen infection. *Plant Signaling & Behavior*, 3(11), 924–925. <https://doi.org/10.4161/psb.3.11.5979>
- Yin, L., Wang, S., Eltayeb, A. E., Uddin, M. I., ... Qiu, C. (2010). Overexpression of antioxidant genes in transgenic tomato confers tolerance to high or low temperature stress. *Plant Physiology and Biochemistry*, 48(10–11), 778–786. <https://doi.org/10.1016/j.plaphy.2010.05.003>
- Zandalinas, S. I., Mittler, R., Balfagón, D., Arbona, V., & Gómez-Cadenas, A. (2018). Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum*, 162(1), 2–12. <https://doi.org/10.1111/ppl.12540>
- Zhang, L., Hu, G., Cheng, Y., Huang, J., & Chen, X. (2017). Heterotrimeric G-protein signaling in plant immunity. *Journal of Experimental Botany*, 68(3), 563–572. <https://doi.org/10.1093/jxb/erw484>
- Zhu, J.-K. (2016). Abiotic stress signaling and responses in plants. *Cell*, 167(2), 313–324. <https://doi.org/10.1016/j.cell.2016.08.029>
- Züst, T., & Agrawal, A. A. (2017). Trade-offs between plant growth and defense against insect herbivory: An emerging mechanistic synthesis. *Annual Review of Plant Biology*, 68, 513–534. <https://doi.org/10.1146/annurev-arplant-042916-040856>



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