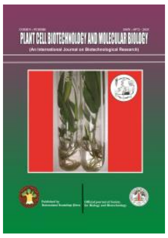

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Crosstalk in Plant Defense: Bridging Abiotic and Biotic Stresses

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Continuous exposure of plants to both biotic and abiotic stresses necessitate the use of an integrated signalling network for plant defence. Crosstalk signalling pathways of biotic and abiotic stresses result in antagonistic, synergistic interaction, which helps the plant respond differently from the single reaction of stress. Molecular mechanisms such as reactive oxygen species, calcium flux signalling, kinases, transcription factors and retrograde signalling, physiological mechanisms such as priming and defence and biotechnological strategies such as breeding, gene editing and chemicals, all are involved in crosstalk defence. Understanding and leveraging these interactions is critical for the production of varieties that can withstand the effects of both biotic and abiotic stresses with respect to climate change. ROS–Ca^{2+} signaling integrates biotic and abiotic stress response and activates MAPK cascades through defence gene regulation. Different hormonal pathways, such as JA, SA, and ethylene interactions help in cross-tolerance. These interconnected pathways help in shaping the plant's ability for defence signalling under combined stress conditions.

Keywords: Abiotic; biotic; crosstalk; cross-tolerance; defence and stress.

1. INTRODUCTION

Plants are sessile and cannot avoid exposure to environmental variation such as temperature extremes, shifts in water supply, salt rise, or disease or insect attack; hence, abiotic and biotic stresses frequently coexist. Crucial crops lose over 70% of their output due to unfavourable environmental conditions. This means that only 30% of the yield was obtained compared to the genetic potential yield (Zhang *et al*., 2020). Growing crop production needs and preserving high yield under adverse climatic circumstances necessitate massive expansion of plant stress resistance research endeavours. Global warming increases the frequency of a number of environmental stresses, including absorbed energy in excess (AEE), ultraviolet (UV) radiation, droughts and heat waves, which affect agricultural output. Climate change hampers the management strategies of plant by shifting the temperature of soil and moisture and helps in promoting pathogens infection (Akanksha *et al*., 2025) Signalling molecules, such as ethylene (ET), salicylic acid (SA), abscisic acid (ABA), jasmonic acid (JA), and reactive oxygen species (ROS), have been extensively studied in relation to the control of plant stress responses. Because of limited resources, overlapping damage, and competing demands for defence vs. expansion, the combination of stresses imposes a greater impact than single stresses (Nejat & Mantri, 2017). Crosstalk between abiotic and biotic response pathways enables plants to integrate information and prioritise responses, resulting in outcomes that differ from those predicted by single stress studies (Ramegowda & Senthil-Kumar, 2015; Fujita *et al*., 2006). This review summarizes the current state of knowledge on molecular signalling pathways, physiological consequences, and biotechnological approaches to exploit defensive crosstalk, as well as gaps and future directions.

2. CROSS-TOLERANCE

Plants become more resilient to various stresses when subjected to more than one type of stress because it can set off shared signals and pathways. An increase in adaptive fitness is linked with this process, which is known as cross-tolerance (Noctor & Foyer, 2016). Co-activating the plant's innate immune system, which consists of a network of stress-responsive pathways that cross the boundaries between biotic and abiotic stress, can help in achieving cross-tolerance. Abiotic stressors with cross-tolerance effects include heat, cold, drought, and salt stress (Mittler *et al*., 2012; Nejat & Mantri, 2017). Mitochondrial retrograde, nuclear anterograde and chloroplast signalling play an important role in cross tolerance by facilitating inter- and intracellular communication between the chloroplast and nucleus. Redox signal controls the gene expression encoded by the nucleus and chloroplast, which is necessary to mediate the signalling route of stress responses (Carvalho & Silveria, 2020; Leisner et al., 2023). Potential mediators of chloroplast-to-nucleus retrograde signalling that result in cross-tolerance include the WHIRLY protein family and the redox-responsive transcription factor 1 (RRTF1) (Jan *et al*., 2022). Several aerobic processes, such as hydrogen peroxide H2O2, have been linked to the induction of cross-tolerance and retrograde signalling (Jan *et al*., 2022). As an environmental sensor, chloroplasts interact with other cell compartments by using retrograde signalling and control gene expression in response to Ca2+ and reactive oxygen species stressors and developmental signals (Li & Kim, 2022; Elkelish & Abu-Elsaoud, 2024). Induced programmed cell death in cells is essential for stress response, leading to the induction of resistance against phytopathogens, thus helping plants survive under stress conditions (Bernacki *et al*., 2019; Gawronski *et al*., 2021). Systemic-acquired acclimation (SAA) processes of chloroplast retrograde signaling within and between plants help in programmed cell death induction (Zhang *et al*., 2022; Szechyńska-Hebda *et al*., 2022).

3. MOLECULAR MECHANISM IN DEFENCE CROSSTALK

3.1 Reactive oxygen species (ROS) and Redox signalling

ROS produced under both stresses that is biotic and abiotic and serve as early indicators of downstream responses (Verma *et al*., 2016). Extreme environmental conditions such as high light intensity, heat and salinity trigger the generation of ROS in chloroplasts, mitochondria and peroxisomes, affecting gene expression (Nejat & Mantri, 2017). During the biotic stress, oxidative burst is an early defence, with the functioning of ROS as pathogen inhibitors (Ku *et al*., 2018). Superoxide, NADPH oxidases, which are produced by mitochondria, are converted to H2O2 (Brand, 2010). Superoxide is produced when molecular oxygen undergoes a one-electron reduction. SOD 1 and 2 (Superoxide dismutase) transform superoxide into H2O2 inside the cell. Superoxide dismutase 2 is found in the mitochondrial matrix, whereas SOD 1 is found in the cytosol and intermembrane space between the mitochondria. Superoxide dismutases stop superoxide from building up, which deactivates proteins with iron sulphur clusters (Fridovich, 1997). Consequently, superoxide buildup is linked to oxidative stress more than redox signalling. The equilibrium between production of ROS and its scavenging is crucial because excessive buildup of ROS causes cellular damage, whereas its timely scavenging allows defence without damage (Verma *et al*., 2016). Cross-tolerance is initiated through crosstalk between the ROS signaling pathway in generating defense responses (Imran *et al*., 2022). Antioxidant defense systems accumulation, like production of secondary metabolites like flavonoids, which help in scavenging excess ROS and balance the cellular redox state, is shown by plants to abiotic stress (Chen & Raji, 2020) (Table 1, Fig. 1).

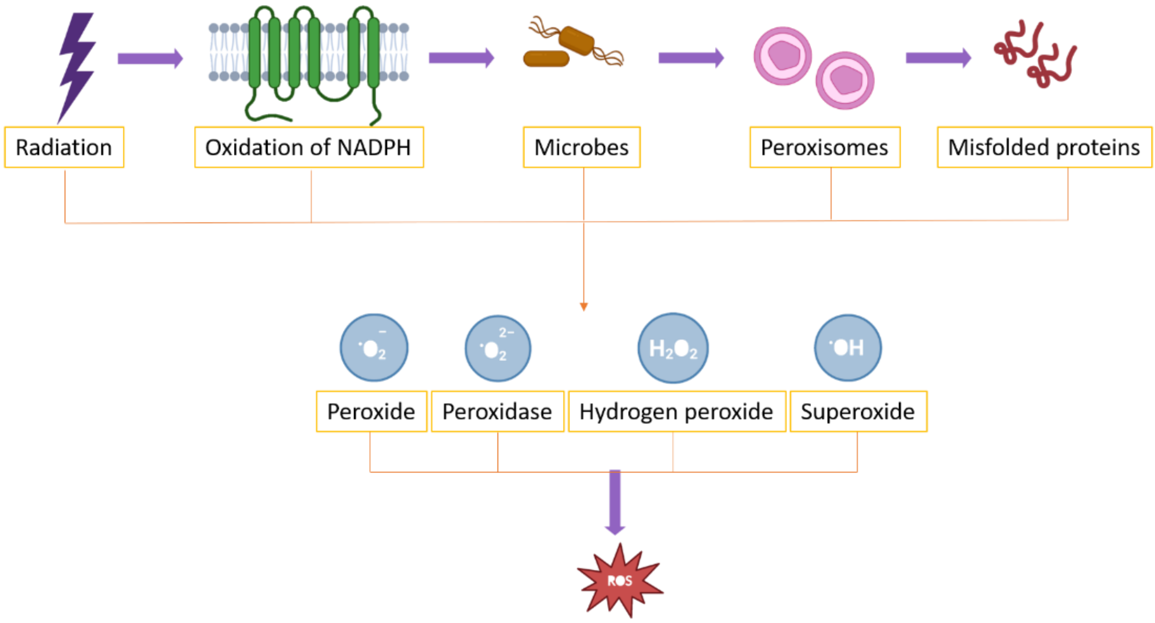

Fig. 1. A schematic illustration of oxidative stress caused by internal and external stimuli. Extracellular ROS sources include radiation, NADPH, microbial exposure and misfolded proteins. Intracellular ROS are produced in other organelles, such as the peroxisome. These sources lead to the production of peroxide, peroxidase, hydrogen peroxide and superoxide

Table 1. ROS signalling in abiotic vs biotic stress

Source of ROS	Major Enzymes	Function in Abiotic Stress	Function in Biotic Stress	Reference
Chloroplasts	NADPH oxidase (RBOH), peroxidases	Controls photosynthetic electron flow, stress acclimation	Signals hypersensitive response, defence activation	Verma *et al*., 2016
Apoplast	Peroxidases, SOD	Modulates cell wall rigidity, ion transport	PAMP-triggered immunity (PTI)	Ku *et al*., 2018
Mitochondria	AOX, SOD	Maintains respiration under stress	Induces systemic acquired resistance (SAR)	Nejat & Mantri, 2017; Choudhary & Varma, 2016; Durrant & Dong, 2004.

3.2 Calcium (Ca^{2+}) Signalling

Both abiotic and biotic stress can lead to changes in cytosolic Ca^{2+} concentration (Verma *et al*., 2016). Calcium sensors such as calcineurin-B-like proteins (CBLs) and CBL-interacting protein kinases (CIPKs) mediate signal responses to abiotic stimuli such as salt, water stress and pathogen-triggered immunity (Ku *et al*., 2018). Calcium-dependent protein kinases (CDPKs) and calmodulin-dependent kinase modulate transcription factors and hormone signalling response to biotic and abiotic stresses (Ku *et al*., 2018). Pathogen-associated molecular patterns (PAMPs) and microbe-associated molecular patterns (MAMPs) detected by pattern recognition receptors (PRRs) cause a rise in calcium influx, which results in a pathogen-triggered immunity (PTI) specific Ca^{2+} signature in PAMP and PTI (Fig. 2).

3.3 Hormonal Crosstalk

Abscisic acid (ABA) is a key hormone in response to abiotic stresses, controlling closure of stomata, osmotic adjustments and gene expression during water and salt stress (Verma *et al*., 2016). Salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) play a key role in biotic stress responses by recognizing pathogens, acquiring resistance and activating defence-related genes (Ku *et al*., 2018). Interactions between abscisic acid, SA, JA and ET are complicated as ABA can inhibit SA-mediated defence against pathogens (Verma *et al*., 2016). JA and ET pathways on the other side affect abiotic stress tolerance, such as JA affects drought or cold tolerance by altering stomatal behaviour, secondary metabolites synthesis and antioxidant enzymes. For the regulation of plant development under stress conditions, cytokinin interacts with auxins and ABA and counteracts the effects of ABA or aids in recovery once stress is alleviated (Verma *et al*., 2016).

3.4 Retrograde Signalling and Organelle to Nucleus Communication

Nucleus receives signals from chloroplast, such as redox reaction, reactive oxygen species, and plastoquinone pool changes in response to light, temperature, or oxidative stress. These signals help in the modification of gene expression that responds during stress (Ku *et al*., 2018). Retrograde signals are produced by peroxisomal and mitochondrial reactive oxygen species (Nejat & Mantri, 2017) and these signals help in coordinating energy balance, defensive metabolite synthesis, photosynthetic regulation and programmed cell death (PCD).

3.5 Transcription Factor, Kinases and Signal Cascades

Both abiotic and biotic stress signalling response relies on mitogen-activated protein kinase (MAPK) cascades (Ramegowda & Kumar, 2015). Both biotic and abiotic stresses are responsive to transcription factor families such as WRKY, MYB, NAC, ERF/AP2, which integrate upstream signals such as the generation of reactive oxygen species, hormone production and calcium influxes and regulate genes essential for stress tolerance and their defence (Nejat & Mantri, 2017; Ku *et al*., 2018). At the surface of the cell, some kinases and receptor-like kinases (RLKs) detect abiotic stress signals, that as osmotic and ionic stress or pathogen molecular patterns and start downstream crosstalk between them by using common signalling components (Kissoudis *et al*., 2014) (Table 2).

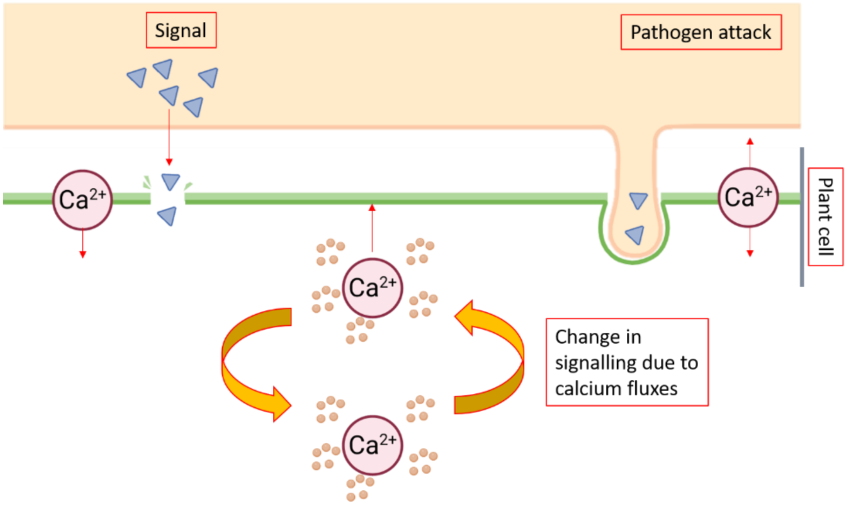

Fig. 2. Plant calcium flux signalling during stress. External signal (pathogen's effector) causes Ca^{2+} entry through membrane channels and release from internal storage, resulting in a distinct Ca^{2+} signature. This indicates that calcium flux plays a role in the signalling pathways triggered by fungal effectors during plant pathogen interactions

Table 2. Key transcription factors regulating dual stress responses

TF Family	Stress Type Regulated	Function in Abiotic Stress	Function in Biotic Stress	Reference
WRKY	Drought, Pathogens	Interacts with the MAPK pathway; regulates PR genes	WRKY33	Verma *et al*., (2016)
NAC	Drought, Cold, Biotic	Controls ROS balance, senescence	SNAC1	Nejat & Mantri, (2017)
AP2/ERF	Salinity, Pathogen	Ethylene and JA signalling integration	DREB2A	Ku *et al*. (2018)

4. PHYSIOLOGICAL AND CELLULAR MECHANISMS IN DEFENCE

4.1 Trade-Off Between Defence and Growth

Resources like energy, carbon and nutrients have a protective role in biomass accumulation or reproductive growth, activation of defence pathways, and frequently conflict with growth (Verma *et al*., 2016). For instance, stomatal closure decreases photosynthetic rate during drought conditions, which restricts reactions to insect and pathogen invasion (Nejat and Mantri, 2017; Miller *et al*., 2010). Similarly, when stress is protracted, the plant allocates assimilates to defensive proteins or secondary metabolite production, which results in delayed development of the plant (Kissoudis *et al*., 2014).

4.2 Priming, Memory and Cross Tolerance

Priming is a condition in which prior exposure to one stress, whether biotic or abiotic, enhances the rate of response to subsequent stresses. Through some signalling pathways and hormonal connections, cross tolerance occurs when abiotic stress increases resistance to biotic stress or vice versa (Ramegowda & Kumar, 2015). When plants are exposed to mild drought and salt conditions, they exhibit increased defensive gene expression, increase resistance to pathogen attack, or accelerate reactive oxygen stress, there by scavenging response to pathogen stress (Kissoudis *et al*., 2014).

4.3 Programmed Cell Death (PCD)

Plants undergo programmed cell death to sacrifice damaged tissues and to protect healthy tissue under extreme and combined stress conditions. This cell death is regulated by signalling molecules such as ROS, SA and ET and it is frequently influenced by ABA (Nejat & Mantri, 2017). Cell death must be balanced since little initiation of PCD can promote the spread of pathogens, whereas more production of PCD results in excessive tissue loss and hampers the survival of pathogens in plant tissues (Verma *et al*., 2016).

4.4 Antioxidant Systems

Oxidative stress is frequently regulated by abiotic stress, necessitating the overexpression of antioxidant enzymes such as peroxidase, superoxide dismutases and peroxidase as well as non-enzymatic antioxidants such as glutathione and ascorbate. These enzymes are also activated by biotic stress, especially when it comes to defence against pathogen attack and oxidative burst (Ku *et al*., 2018). Soluble sugars, osmolytes such as proline, glycine and specialized secondary metabolites that serve as both abiotic tolerance and pathogen deterrence are examples of metabolic shifts (Kissoudis *et al*., 2014).

5. BIOTECHNOLOGICAL APPROACHES

5.1 Genetic engineering and gene editing

Regulators like kinases, hormone biosynthesis, signalling genes, transcription factors (WRKY, MYB, NAC, ERB) provide targets for genetic engineering to improve combined stress tolerance (Kissoudis *et al*., 2014). These genes can be precisely modified using CRISPR/Cas and gene editing technologies for improvement in disease resistance and abiotic stress tolerance traits (Verma *et al*., 2016; Ku *et al*., 2018; Pandey *et al*., 2017). Better resilience under combinatorial stress may be achieved by engineering elements of reactive oxygen species detoxification pathways, retrograde signalling (Kissoudis *et al*., 2014).

5.2 Marker-Assisted Selection (MAS)

An approach in traditional breeding that takes advantage of natural variation in genes that function well under both biotic and abiotic stress. The pyramiding trait can be aided by marker-assisted selection, which targets resistant genes, QTLs linked to abiotic stress tolerance and transcription factors that control both stress types (Kissoudis *et al*., 2014). Genomic selection, mapping of stress tolerance combined traits such as high yield and tolerance to abiotic (drought, salinity) and biotic stresses (pathogen attack) are required for speeding up of robust cultivars (Kissoudis *et al*., 2014) (Fig. 3).

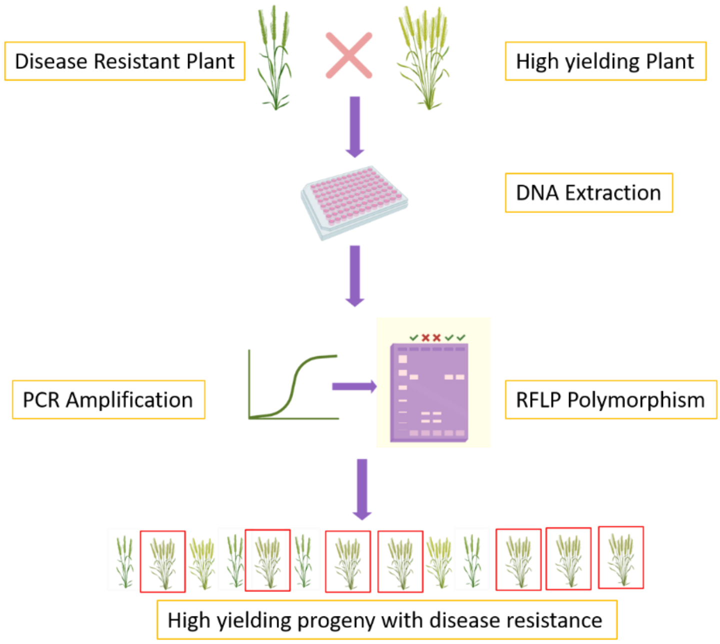

Fig. 3. A schematic illustration of Marker-Assisted Selection (MAS) in plant breeding. At the seedling stage, desired genotypes for disease resistance and high yield were selected for crossing, followed by DNA extraction, PCR amplification (disease-resistant associated marker) and verification with RFLP (Restriction fragment length polymorphism) selection. In contrast to phenotype-based selection, marker profiling enables early selection of individuals harbouring the advantageous allele or alleles, speeding up the breeding process and improving precision

Table 3. Biotechnological approaches enhancing dual stress tolerance

Strategy	Target	Outcome	Example	Reference
Overexpression of TFs	WRKY, NAC	Enhanced drought & pathogen resistance	Rice, Tomato	Verma *et al*., 2016
CRISPR knockout	PP2C genes	Improved ABA-mediated drought resistance	Arabidopsis	Ku *et al*., 2018
Priming with SA/JA	Hormone signalling	Cross-tolerance induction	Wheat	Kissoudis *et al*., 2014

5.3 Priming and Chemical Inducers

Priming to plants respond better to subsequent biotic stress by being exposed to minor abiotic stresses (heat, drought, salt) or chemical inducers (SA, JA, oxidative stress) (Verma *et al*., 2016; Atkinson & Urwin, 2012). Cross tolerance can be induced by elicitors of pathogens, beneficial microorganisms such as plant growth-promoting rhizobacteria (PGPR) that initiate ROS or hormone signalling (Aloo *et al*., 2023). To overcome the abiotic stress, suppressive effects on biotic resistance, agronomical practices like nutrient supplements, modified irrigation and planting can be adopted (Kissoudis *et al*., 2014).

5.4 Modelling Approaches

Key regulatory nodes and networks that are shared by several stresses are being aided by transcriptomics, proteomics, and metabolomics under combined stress settings (Verma *et al*., 2016; Nejat & Mantri, 2017). Targets that might not be apparent from single stress studies can be identified with the use of modelling techniques, network analysis, which enables the prediction of emergent behaviour under combinatorial stress (Ku *et al*., 2018; Kissoudis *et al*., 2014) (Table 3).

6. GAPS, CHALLENGES, AND FUTURE DIRECTIONS

Instead of accurately capturing field realities through dynamic stress combinations, much research continues to concentrate on individual or sequential stress treatments (Nejat & Mantri, 2017; Prasch & Sonnewald, 2015). In many plant systems, temporal dynamics, namely, stress happens first, how long it lasts, how intense it is and when it recovers are not well understood. In combined stress responses, little is known about epigenetic control (DNA methylation, histone changes, small RNAs). A further layer of complexity is added by interactions with the microbiome and endophytes, soil conditions and the actual field situation. Future studies should focus on field validation, integrating omics, conducting experiments under realistic multistress regimes and identifying signalling thresholds that tip the scales between fitness and defence costs.

7. CONCLUSION

A complex network of molecular signals, including production of reactive oxygen species, calcium signalling, hormone production, transcription factor, retrograde signalling, physiological responses, trade-offs, priming and metabolic adjustments, work together to maximize plant survival under combined stress. This crosstalk between biotic and abiotic stresses is a part of the defence response. Biotechnological approaches such as gene editing, breeding, priming and use of beneficial microbes to exploit this crosstalk have the potential to increase resilience for crops under climate change.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

Akanksha, Sharma, S. K., Gupta, B. K., Rana, N., Sharma, A., & Verma, P. (2025). Biocontrol potential of *Trichoderma*-derived chitinase: Optimization, purification and antifungal activity against soilborne pathogens of apple. *Frontiers in Fungal Biology, 6*. https://doi.org/10.3389/ffunb.2025.1618728

Aloo, B. N., Dessureault-Rompré, J., Tripathi, V., Nyongesa, B. O., & Were, B. A. (2023). Signaling and crosstalk of rhizobacterial and plant hormones that mediate abiotic stress tolerance in plants. *Frontiers in Microbiology, 14*, 1171104. https://doi.org/10.3389/fmicb.2023.1171104

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

Bernacki, M. J., Czarnocka, W., Szechyńska-Hebda, M., Mittler, R., & Karpiński, S. (2019). Biotechnological potential of LSD1, EDS1, and PAD4 in the improvement of crops and industrial plants. *Plants, 8*, 290.

Brand, M. D. (2010). The sites and topology of mitochondrial superoxide production. *Experimental Gerontology, 45*(6), 466–472. https://doi.org/10.1016/j.exger.2010.01.003

Carvalho, F. E. L., & Silveira, J. A. G. (2020). H_2O_2-retrograde signaling as a pivotal mechanism to understand priming and cross-stress tolerance in plants. In D. K. Choudhary & A. Varma (Eds.), *Priming-mediated stress and cross-stress tolerance in crop plants* (pp. 57–78). Elsevier. DOI:10.1016/B978-0-12-817892-8.00004-0

Chen, Z., & Raji, M. (2020). Role of reactive oxygen species in modulating cross tolerance in plants via flavonoids. In *Priming-mediated stress and cross-stress tolerance in crop plants* (pp. 203–214). Elsevier.

Choudhary, D. K., & Varma, A. (2016). Microbial-mediated induced systemic tolerance in plants under combined stress. *Frontiers in Plant Science, 7*, 570. https://doi.org/10.3389/fpls.2016.00570

Durrant, W. E., & Dong, X. (2004). Systemic acquired resistance. *Annual Review of Phytopathology, 42*, 185–209. https://doi.org/10.1146/annurev.phyto.42.040803.140421

Elkelish, A., & Abu-Elsaoud, A. M. (2024). Crosstalk between abiotic and biotic stress responses in plants: Mechanisms, outcomes, and implications for crop improvement. *Spectrum Science Journal, 1*(1), 27–34.

Fridovich, I. (1997). Superoxide anion radical ($O_2^{-}\cdot$), superoxide dismutases, and related matters. *Journal of Biological Chemistry, 272*(30), 18515–18517. https://doi.org/10.1074/jbc.272.30.18515

Fujita, M., Fujita, Y., Noutoshi, Y., Takahashi, F., Narusaka, Y., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2006). Crosstalk between abiotic and biotic stress responses: A current view from the points of convergence in the stress signaling networks. *Current Opinion in Plant Biology, 9*(4), 436–442. https://doi.org/10.1016/j.pbi.2006.05.014

Gawronski, P., Burdiak, P., Scharff, L. B., Mielecki, J., Górecka, M., Zaborowska, M., Leister, D., Waszczak, C., & Karpiński, S. (2021). CIA2 and CIA2-LIKE are required for optimal photosynthesis and stress responses in *Arabidopsis thaliana*. *Plant Journal, 105*, 619–638.

Imran, Q. M., Shahid, M., Hussain, A., & Yun, B. W. (2022). NO and ROS crosstalk and acquisition of abiotic stress tolerance. In *Nitric oxide in plant biology* (pp. 477–491). Elsevier.

Jan, M., Liu, Z., Rochaix, J.-D., & Sun, X. (2022). Retrograde and anterograde signaling in the crosstalk between chloroplast and nucleus. *Frontiers in Plant Science, 13*, 980237. https://doi.org/10.3389/fpls.2022.980237

Kissoudis, C., van de Wiel, C., Visser, R. G., & van der Linden, G. (2014). Enhancing crop resilience to combined abiotic and biotic stress through the dissection of physiological and molecular crosstalk. *Frontiers in Plant Science, 5*, 207.

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

Leisner, C. P., Potnis, N., & Sanz-Saez, A. (2023). Crosstalk and trade-offs: Plant responses to climate change-associated abiotic and biotic stresses. *Plant, Cell & Environment, 46*(10), 2946–2963.

Li, M., & Kim, C. (2022). Chloroplast ROS and stress signaling. *Plant Communications, 3*(1), 100264. https://doi.org/10.1016/j.xplc.2021.100264

Miller, G., Suzuki, N., Ciftci-Yilmaz, S., & Mittler, R. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, Cell & Environment, 33*(4), 453–467. https://doi.org/10.1111/j.1365-3040.2009.02041.x

Mittler, R., Finka, A., & Goloubinoff, P. (2012). How do plants feel the heat? *Trends in Biochemical Sciences, 37*(3), 118–125. https://doi.org/10.1016/j.tibs.2011.11.007

Nejat, N., & Mantri, N. (2017). Plant immune system: Crosstalk between responses to biotic and abiotic stresses. *Current Issues in Molecular Biology, 23*(1), 1–16. https://doi.org/10.21775/cimb.023.001

Noctor, G., & Foyer, C. H. (2016). Intracellular redox compartmentation and ROS-related communication in regulation and signaling. *Plant Physiology, 171*(3), 1581–1592. https://doi.org/10.1104/pp.16.00346

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 physio-morphological traits. *Frontiers in Plant Science, 8*, 537. https://doi.org/10.3389/fpls.2017.00537

Prasch, C. M., & Sonnewald, U. (2015). Signaling events in plants: Stress factors in combination change the picture. *Environmental and Experimental Botany, 114*, 4–14. https://doi.org/10.1016/j.envexpbot.2014.06.020

Ramegowda, V., & Senthil-Kumar, M. (2015). The interactive effects of simultaneous biotic and abiotic stresses on plants: mechanistic understanding from drought and pathogen combination. Journal of plant physiology, 176, 47-54. https://doi.org/10.1016/j.jplph.2014.11.008

Szechyńska-Hebda, M., Lewandowska, M., Witoń, D., Fichman, Y., Mittler, R., & Karpiński, S. M. (2022). Aboveground plant-to-plant electrical signaling mediates network acquired acclimation. *Plant Cell, 34*, 3047–3065.

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

Zhang, H., Zhao, Y., & Zhu, J.-K. (2020). Thriving under stress: How plants balance growth and the stress response. *Developmental Cell, 55*(5), 529–543. https://doi.org/10.1016/j.devcel.2020.10.012

Zhang, H., Zhu, J., Gong, Z., & Zhu, J. K. (2022). Abiotic stress responses in plants. *Nature Reviews Genetics, 23*, 104–119.

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