

Crosstalk in Plant Defense: Bridging Abiotic and Biotic Stresses

Abstract

Continuous exposure of plants to both biotic and abiotic stresses, necessitates the use of an integrated signalling network for plant defence. Crosstalk signalling pathways of biotic and abiotic stresses result in antagonistic or synergistic interactions, which help the plant respond differently from a single reaction to 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 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. ✓

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 agricultural 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 harbour 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) ✓. 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 for various stresses when subjected to more than one type of stress because it can set off shared signals and pathways. An increase in the 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 (Johnson & Puthur, 2021) ✓. Mitochondrial retrograde, nuclear anterograde and chloroplast signalling plays important role in cross tolerance by facilitating inter and intracellular communication between the chloroplast and nucleus. Redox signal controls the gene expression encoded by nucleus and chloroplast, which is necessary to mediate signalling

route of stress responses (Carvalho & Silveria, 2010). 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. Ref?

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 and ~~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 is 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 mitochondrial matrix, whereas SOD 1 is found in the cytosol and intermembrane space between the mitochondria. Superoxide dismutases stop superoxide from building up, which deactivate 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

damages, whereas its timely scavenging allows defence without damage (Verma *et al.*, 2016) (Table 1, Figure 1).

3.2 Calcium (Ca²⁺) signalling

Both abiotic and biotic stress can lead to changes in cytosolic Ca²⁺ 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 Ca²⁺ signature in PAMP and PTI (Erdenee & Ting, 2022) (Figure 2).

3.3 Hormonal crosstalk

Abscisic acid (ABA) is a key hormone in response of 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 (Nguyen *et al.*, 2016). For 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 is osmotic and ionic stress or ✓ pathogen molecular patterns and start downstream crosstalk between them by using common signalling components (Elkelish & Abu-Elsaoud, 2024) (Table 2). ✓

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; Nguyen *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). Similarly, when stress is protracted, allocating assimilates to defensive proteins or secondary metabolite production, which results in delayed development of the plant (Elkelish & Abu-Elsaoud, 2024).

4.2 Priming, memory and cross tolerance

Priming is a condition ~~where a previous~~ exposure to one stress ~~may be~~ biotic or abiotic, ~~enhances~~ increases 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, increased resistance to pathogen attack or accelerated reactive oxygen stress scavenging response to pathogen stress (Elkelish & Abu-Elsaoud, 2024).

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 moreover, it 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} ~~is~~ example of metabolic shifts (Nguyen *et al.*, 2016; Elkelish & Abu-Elsaoud, 2024).

5. Biotechnological approaches

5.1 Genetic engineering and gene editing

Regulators like kinases, hormone biosynthesis, signalling genes, transcription factors (WRKY, MYB, NAC, ERB) provides targets for genetic engineering to improve combined stress tolerance (Elkelish & Abu-Elsaoud, 2024). These genes can be precisely modified using CRISPER/Cas and gene editing technologies for improvement in disease resistance and abiotic stress tolerance traits (Verma *et al.*, 2016; Ku *et al.*, 2018). Better resilience under combinatorial stress may be achieved by engineering elements of reactive oxygen species detoxification pathways, retrograde signalling (Elkelish & Abu-Elsaoud, 2024).

5.2 Marker-assisted selection (MAS)

Approach in traditional breeding that takes advantage of natural variation in genes that function well under both biotic and abiotic stress (Nguyen *et al.*, 2016). 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 (Elkelish & Abu-Elsaoud, 2024). 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 (Elkelish & Abu-Elsaoud, 2024) (Figure 3). ✓

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). Cross tolerance can be induced by elicitors of pathogens, beneficial microorganism 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 nutrients supplements, modified irrigation and planting can be ✓adopted (Elkelish & Abu-Elsaoud, 2024).

5.4 Modelling approaches

Key regulatory nodes and network that shared by several stresses is being aided by transcriptomics, proteomics, and metabolomics under combined stress setting (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 enable the ✓prediction of emergent behaviour under combinatorial stress (Ku *et al.*, 2018; Elkelish & Abu-Elsaoud, 2024) (Table 3). ✓

6. Gaps, challenges, and future directions

Instead of accurately capturing field realities through dynamic stress combinations, ~~many~~ ^{much} research ^{continues} continue to concentrate on individual or sequential stress treatments (Nejat & ✓Mantri, 2017). In many plant systems, the temporal dynamics which stress happens first, how ^{namely,} 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). Further layer of complexity are added by interactions with the microbiome and

endophytes, soil conditions and 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.

Conclusion

A complex network of molecular signals ~~as~~ **including -** the 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 has the potential to increase resilience **crops** for crops under climate change.

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Those colored are not in the text. Incorporate them at appropriate places.

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Table 1. ROS signalling in abiotic vs biotic stress ✓

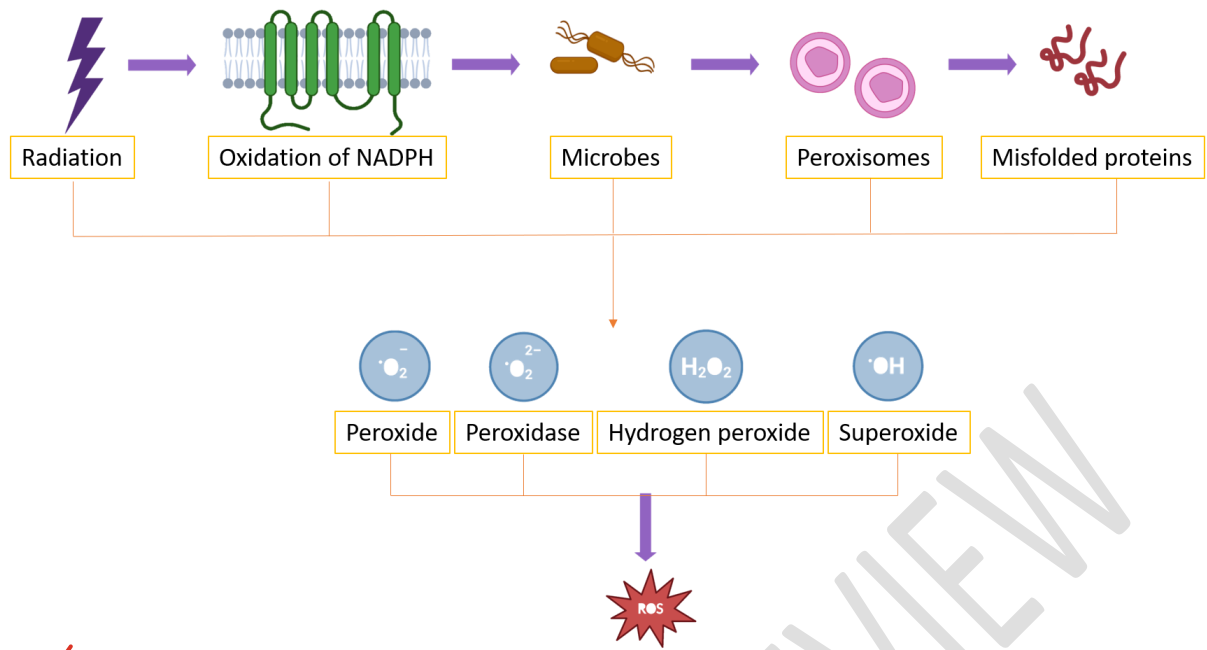
Source of ROS	Major Enzymes	Function in Abiotic Stress	Function in Biotic Stress	Reference
Chloroplasts	NADPH oxidase (RBOH), peroxidases	Controls photosynthetic electron flow, stress acclimation	Signals hypersensitive response, defence activation	Verma <i>et al.</i> , 2016
Apoplast	Peroxidases, SOD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

Table 2. Key transcription factors regulating dual stress responses ✓

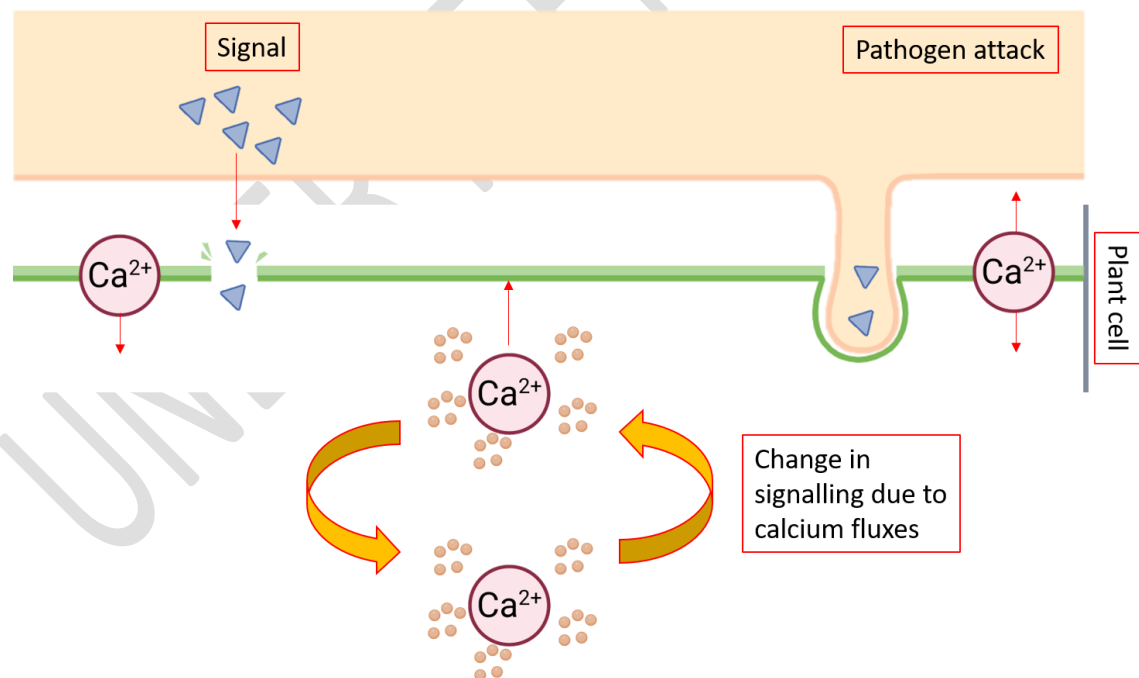
TF Family	Stress Type Regulated	Function in Abiotic Stress	Function in Biotic Stress	Reference
WRKY	Drought, Pathogens	Interacts with MAPK pathway; regulates PR genes	WRKY33	Verma <i>et al.</i> , 2016
NAC	Drought, Cold, Biotic	Controls ROS balance, senescence	SNAC1	Nejat & Mantri, 2017
AP2/ERF	Salinity,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

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 <i>et al.</i> , 2016 ✓
CRISPR knockout	PP2C genes	Improved ABA-mediated drought resistance	Arabidopsis	Ku <i>et al.</i> , 2018
Priming with SA/JA	Hormone signalling	Cross-tolerance induction	Wheat	Elkelish & Abu-Elsaoud, 2024 ✓



✓ Figure 1. A schematic illustration of oxidative stress caused by internal and external stimuli. Extracellular ROS sources include radiation, NADPH, microbes 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.



✓ Figure 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.

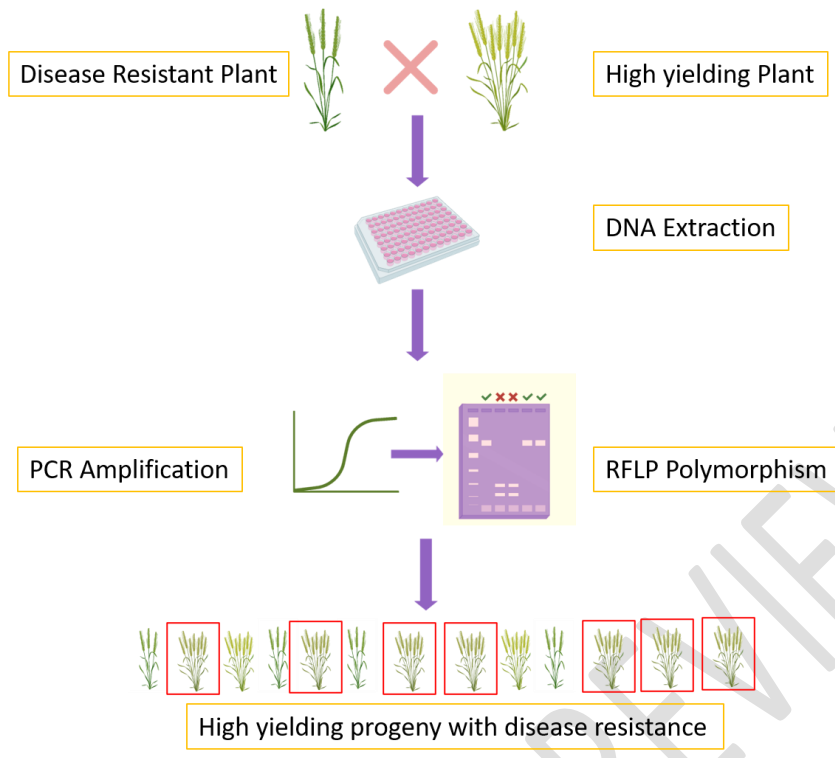


Figure 3. A schematic illustration of Marker-Assisted Selection (MAS) in plant breeding.

✓ At the seedling stage, desired genotypes for disease resistance and high yield was 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.