

CHAPTER 17

Abiotic and biotic stress interactions in plants: A cross-tolerance perspective

Venkategowda Ramegowda, Maria Vera Jesus Da Costa, Sapna Harihar, Nataraja N. Karaba, Sheshshayee M. Sreeman

Department of Crop Physiology, University of Agricultural Sciences, Bangalore, India

17.1 Introduction

Abiotic and biotic stresses affect plant growth, development, and yield, thereby threatening global food security. Further, the ever-changing climate is continuously resetting the growing habitat of plants through increased frequency of occurrence and intensity of stresses. Therefore, the chances of plants encountering abiotic and biotic stresses, alone or in combination, are likely to be higher in the future and it is critical for plants to endure these stresses for survival.¹ So far, the majority of the research has been primarily focused on individual stressors under a highly controlled environment, which has no doubt helped us understand the key processes and signaling components of abiotic and biotic stress responses.^{2,3} However, less importance has been given to multiple stresses simultaneously occurring in field conditions. In the natural environment, plants have co-evolved with several abiotic and biotic stresses and hence have learnt to endure these factors through diverse and finely coordinated responses. These responses involve a multitude of mechanisms that have complex interactions, but share common signals, genes and products referred to as signaling crosstalk.^{4–9} The advancements in “omic” technologies (transcriptomic, proteomic, and metabolomic) have helped us to unravel the regulation of such interactions.^{10–12} These interactions primarily regulate cellular processes leading to physiological, biochemical, and molecular changes, resulting in either decreased or increased tolerance of plants.

Exposure of plants to one type of stress can activate common signals and pathways, resulting in enhanced tolerance to other different types of stresses; this is known as cross-tolerance.^{13–15} There is considerable information in the literature on cross-tolerance of plants to multiple abiotic stresses.^{16–18} Most abiotic stresses share similar stress signaling pathways and hence plants tolerant to one type of abiotic stress have been tested for their tolerance to other different types of abiotic stresses.² In most cases, increased tolerance to one abiotic stress increases tolerance to multiple other abiotic stresses.^{19–24} The same is true with biotic-biotic stress cross-tolerances.^{25–28} However, our understanding of cross-tolerance between abiotic and biotic stresses is limited, with several studies revealing the

existence of crosstalk resulting in either synergistic or antagonistic interactions.^{6,29–31} Recently, efforts have been made to understand plant interactions under abiotic and biotic stresses. Phytohormones are known to govern diverse physiological processes, including cross-tolerance between abiotic and biotic stresses.^{32,33} Generation of reactive oxygen species (ROS) is suggested to be another key process that is shared between abiotic and biotic stress responses.³⁴ Increasing gene expression data with the advancement of genome sequencing technologies and improved functional genomic tools to evaluate the role of these differentially expressed genes suggests the existence of common regulatory pathways controlling plant responses to both abiotic and biotic stresses.^{35–37} These studies have revealed that regulatory genes encoding kinases and phosphatases and transcription factors (TFs), are the major components of abiotic and biotic stress signaling networks.^{30,38} These regulatory genes are triggered by upstream molecules such as phytohormones and redox signaling components, resulting in complex interactions with frequent crosstalk.^{39,40} This chapter focuses on the current understanding of plant abiotic-biotic stress interactions, especially cross-tolerance mechanisms, and the approaches to improve cross-tolerance of plants to multiple abiotic-biotic stresses.

17.2 Abiotic and biotic stress interactions leading to cross-tolerance

17.2.1 Effect of abiotic stresses on plant disease resistance

Interaction between abiotic and biotic stress can either cause a positive or a negative effect on plant growth and metabolism.^{41,42} In most of the cases, abiotic stresses predispose plants to subsequent pathogen infection.^{43–45} However, abiotic stresses also have positive effects on plant tolerance to biotic stresses.^{46,47} Drought stressed *Nicotiana benthamiana* plants showed improved tolerance to necrotrophic fungus, *Sclerotinia sclerotiorum*, and also to hemibiotrophic bacterial pathogen, *Pseudomonas syringae* pv. *tabaci*. ROS-generated during drought acclimation have been shown to be key in priming the defense response of plants, resulting in improved tolerance to pathogens.¹³ In tomato, exposure of plants to drought stress resulted in a significant reduction in infection by the biotrophic fungus *Oidium neolycopersici* and the necrotrophic fungus *Botrytis cinerea*, which was associated with accumulation of higher abscisic acid (ABA).⁴⁷ Salt stress significantly reduced infection by *O. neolycopersici* with no effect on *B. cinerea*. However, there was no change in the concentration of ABA in salt treated plants.⁴⁷ These findings suggest that, in tomato, drought and salt stress stimulate different, but possibly overlapping, pathogen defense responses, which may not necessarily be through ABA.⁴⁷ Similarly, the drought tolerant grapevine (*Vitis vinifera*) genotype, Meski, showed reduced susceptibility to *B. cinerea* strain 630. This increased cross-tolerance was associated with homeostasis of polyamine related amino acids, phytoalexin accumulation, and upregulation of *pathogenesis-related* (PR)-genes. There was also reduced expression of *9-cis-epoxycarotenoid dioxygenase 2* (NCED2), suggesting that this cross-tolerance in grapevine was ABA-independent.⁴⁸

Arabidopsis thaliana plants under drought stress showed increased tolerance to bacterial pathogen *P. syringae* pv. tomato DC3000. Likewise, it was reported that simulated drought slowed down the disease development of powdery mildew (caused by *Erysiphe cruciferarum*) in *Alliaria petiolata* (garlic mustard).⁴⁹

In plants, salinity is known to exert two kinds of effects, osmotic effect and ionic effect.⁵⁰ Wiese et al. (2004) have shown that salinity stress can increase resistance of barley (*Hordeum vulgare*) plants to powdery mildew caused by *Blumeria graminis* f. sp. *hordei* race A6. This resistance has been suggested to be not because of ion toxicity affecting the fungal growth directly, as the induction of resistance by ions and the time course of salt accumulation in the leaves were independent.⁴⁶ Similarly, hyperaccumulation of metals provided resistance against pathogens. In *Thlaspi caerulescens*, a hyperaccumulator of heavy metals, hyperaccumulation of zinc (Zn), nickel (Ni), and cadmium (Cd) inhibited the growth of bacterial pathogen *P. syringae* pv. *maculicola* (*Psm*)⁵¹ through direct ionic effect. In potato (*Solanum tuberosum*) and wheat (*Triticum aestivum*), pretreatment of plants with aluminum (Al) resulted in enhanced tolerance of plants against *Phytophthora infestans* and *Fusarium oxysporum*, respectively, via enhanced ROS homeostasis and salicylic acid (SA) signaling.^{52,53}

Ozone treatment or UV-irradiation, can elicit responses similar to biotic stresses, thereby increasing plants' resistance to pathogens.^{14,54–56} Sublethal exposure of plants to oxidative stress through ozone treatment has rendered plant tolerance to *P. syringae* through induction of SA signaling and *PR*-gene expression in *Arabidopsis* plants.⁵⁵ Similarly, ozone exposure induced resistance to *Tobacco mosaic virus* (TMV) in tobacco and *B. graminis* f. sp. *tritici* (*Bgt*) in wheat through activation of SA/jasmonic acid (JA) signaling.^{56,57}

Rising temperatures due to climate change is predicted to expand the host range and increase the severity of diseases.⁵⁸ On the contrary, at elevated temperatures, *Tomato bushy stunt virus* (TBSV) showed reduced symptoms in protoplasts.⁵⁹ Recently, it has been shown that Xa7-mediated resistance of rice plants to the bacterial blight pathogen, *Xanthomonas oryzae*, might be better under high temperature due to inhibition of ABA signaling and not by the activation of SA signaling.⁶⁰ In spring wheat, warm air temperatures provided durable resistance to stripe rust (*Puccinia striiformis*).⁶¹ Similarly, pretreatment of tomato genotypes to high temperature caused a slight suppression of the pathogen *Pseudoidium neolyopersici* development through activation of defense signaling pathways involving JA, ABA, and peroxidase activity.⁶² Apart from high temperatures, cold acclimation has also been suggested to impart cross-tolerance. Long-term exposure of wheat and barley plants to low nonfreezing temperatures provided partial protection to paraquat and H₂O₂ treatments. Same plants also showed resistance against the net blotch disease caused by fungus *Pyrenophora teres* f. *teres* through ROS homeostasis.⁶³ Similarly, in *Arabidopsis*, acclimation of plants to cold stress resulted in enhanced tolerance to bacterial pathogen *P. syringae* pv. *syringae* strain DC3000 through *NAC with Transmembrane Motif 1 Like 6* (*NTL6*)-mediated cold induction of the *PR*-genes.⁶⁴ These studies indicate

that abiotic stress induced biotic stress resistance depends on the severity of the stress, plant species, and the stressors. For example, increased resistance of drought and salt stressed plants to pathogen could be due to osmotic effect on the pathogens. Some pathogens require more water in the apoplastic space for disease progression and hence osmotic effect might restrict the spread of those pathogens.^{47,49} On the other hand, intrinsic ability of abiotic stress exposed plants to trigger defense responses common to both stresses might also contribute to cross-tolerance. This is very evident in ozone inducing the biotic stress responses in plants¹⁴ and low/high temperatures activating the ROS homeostasis.

17.2.2 Effect of biotic stresses on plant tolerance to abiotic stresses

Similar to abiotic stresses, inducing tolerance to biotic stresses, biotic factors also influence abiotic stress responses of plants. This has been well studied with beneficial microorganisms, which are mostly endophytes. Endophyte mediated abiotic and biotic stress tolerance is an emerging area and has been considered an ecofriendly approach for better crop growth and yield. Inoculation of Arabidopsis plants with the plant-growth-promoting rhizobacteria (PGPR), *Paenibacillus polymyxa*, and subsequent challenging with either the pathogen *Erwinia carotovora* or drought stress resulted in improved tolerance to both pathogen and drought stress.⁶⁵ This improved tolerance was associated with enhanced expression of the *Early Response to Dehydration 15 (ERD15)* gene. Such an improved tolerance to abiotic stresses in plants pretreated with many beneficial rhizobacteria and arbuscular mycorrhizal fungi has been shown in many crop species. The mechanisms associated with enhanced tolerance was production of antioxidants, osmolytes, ABA, suppression of ethylene (ET), improved soil characteristics, sustained water, and source-sink relations.⁶⁶⁻⁷² As this chapter mainly focuses on plant pathogens, we suggest readers refer to Lata et al. (2018) for information on the role of beneficial microbes on cross-tolerance to abiotic and biotic stresses.⁷³

Besides beneficial microbes, some pathogenic microbes are also known to exert positive effects on plant responses to abiotic stresses. Plants infected with pathogens close stomata to prevent pathogen entry, which might result in reduced water loss from infected tissues, thus having a positive effect on plant tolerance to drought stress.⁷⁴ Virus infection has been shown to improve tolerance to abiotic stresses in many plant species.⁷⁵ In tobacco, beet, and rice plants inoculated with four different RNA viruses, *Brome mosaic virus (BMV)*, *Cucumber mosaic virus (CMV)*, TMV, and *Tobacco rattle virus (TRV)*, there was delayed appearance of drought symptoms with leaves maintaining higher relative water content for longer. There was improved tolerance of beet plants to freezing stress when infected with CMV. The increase in tolerance of these virus treated plants to abiotic stresses was shown to be due to accumulation of osmoprotectants and antioxidants, which play a key role in abiotic stress tolerance.⁷⁵ Arabidopsis plants infected with soil

borne fungal plant pathogen *Verticillium longisporum* showed improved tolerance to drought stress due to de novo xylem formation, which helps in water flow. This observed xylem formation is associated with induced expression of Vascular-related NAC Domain (VND) TF VND7.⁷⁶

Further evidence of biotic stresses positively regulating abiotic stress responses came from exogenous application of chemicals, which induce biotic stress response in plants. Application of β -aminobutyric acid (BABA), a nonprotein amino acid, resulted in enhanced resistance of *Arabidopsis* plants to several abiotic stresses including heat, drought, and salinity.⁷⁷ BABA is a known inducer of plant resistance against numerous pathogens.⁷⁸ Jakab et al. (2005) demonstrated that BABA-induced drought tolerance was due to enhanced accumulation of ABA, resulting in accelerated stress gene expression and stomatal closure. Similarly, exogenous application of SA and JA, inducers of biotic stress response, has been shown to improve tolerance of plants to many abiotic stresses.^{79,80} Capiati et al. (2006) have shown that mechanical wounding increases salt stress tolerance in tomato plants through a mechanism that involves the signaling peptide systemin and JA. Possible involvement of LeCDPK1, a Ca^{2+} -dependent protein kinase, as a signaling intermediate in this cross-tolerance has been suggested.¹⁵ In wheat, *Barley yellow dwarf virus-Padi-avenae virus* (BYDV) infection did not harm plants at moderate water deficit; however, under severe drought stress, infection improved plant tolerance to drought stress.⁸¹ It is not yet clear why and how pathogenic microbes switch their role as beneficial microbes to plants under abiotic stresses. In addition to activating common signals, improved soil and water-relations of pathogen treated plants might also be contributing to enhanced abiotic stress tolerance.⁷⁶

17.3 Convergence of abiotic and biotic stress signals during cross-tolerance

Interactions between abiotic and biotic stresses induce complex responses depending on the stresses involved. Several components of signaling pathways are common to both abiotic and biotic stresses; these include Ca^{2+} , ROS, phytohormones, and other downstream genes.⁴ These signaling cascades allow plants to adjust their responses to stresses depending on the stressors involved. Here, we discuss ROS and phytohormones, especially ABA, ET, and other growth regulators, SA, and JA in abiotic and biotic stress interactions leading to cross-tolerance of plants.

17.3.1 Reactive oxygen species

Generation of ROS, such as superoxide ($\text{O}_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\bullet\text{OH}$), is the most important and common signaling event in the early responses of plants to many abiotic and biotic stresses.⁸² ROS are beneficial or harmful to plants depending on their levels of production. Lower levels serve as signaling molecules

(second messengers) and regulate plant stress responses, while high levels are destructive and harmful to the plants.⁸³ Therefore, production of ROS is finely modulated. Under abiotic stress, ROS are produced due to disequilibrium in the electron transfer reactions, especially in oxygenic organisms such as higher plants, leading to oxidative stress.⁸⁴ Under biotic stress, plasma membrane bound NADPH oxidases or peroxidases deliberately generate ROS to kill or restrict the pathogen spread through a phenomenon called hypersensitive response (HR).⁸⁵ So far, no specific receptors that can bind to ROS have been identified and hence it is not clear how plant cells sense ROS. The possibility is that ROS can directly modify the redox-sensitive proteins.⁸²

ROS play a pivotal role in cross-tolerance of plants to abiotic and biotic stresses through regulation of both ABA signaling and disease resistance.^{86,87} H_2O_2 was suggested to be the likely intermediate for the ABA response leading to the activation of *Catalase 1 (CAT1)* gene.⁸⁷ Further, in *Arabidopsis*, guard cell-expressed NADPH oxidase catalytic subunit genes, *AtrbohD* and *AtrbohF*, have been shown to be required for ROS generation, leading to ABA-induced stomatal closure and HR to pathogen attack.^{88,89} Mutations in these genes impaired ABA-induced stomatal closure, ROS production, cytosolic Ca^{2+} increase, and activation of plasma membrane Ca^{2+} permeable channels in guard cells. Exogenous application of H_2O_2 reversed these effects, suggesting a role for ROS in ABA signaling.⁸⁹ Similarly, mutations in these genes increased cell death when infected with *Peronospora parasitica*, suggesting the role of NADPH oxidase in regulating plant tolerance to both abiotic and biotic stresses through ROS dependent ABA signaling.

ROS scavengers such as superoxide dismutase (SOD), glutathione peroxidase (GPX), glutathione reductase (GR), ascorbate peroxidase (APX), and catalase (CAT), which detoxify the cytotoxic effects of ROS under various stresses, have been the major targets of improving plant tolerance to both abiotic and biotic stresses. The role of these enzymes in improving plant tolerance to abiotic stresses is well documented.⁸⁴ Under biotic stress, ROS is required to defend against pathogens. During pathogen infection, ROS reinforces the cell wall by cross-linking proteins and induces programmed cell death at the site of infection, thereby restricting the pathogen spread. Upon recognition of a pathogen, there is activation of NADPH oxidases and peroxidases on the plasma membrane, leading to accumulation of $O_2^{\bullet-}$. Here, SOD is required to convert $O_2^{\bullet-}$ into H_2O_2 , which can diffuse into cells and activate defense responses⁹⁰ and hence, SOD plays a positive role in plant responses to both abiotic and biotic stresses. Similarly, it has been noted that the activity of CAT1 enzyme was always higher in smut (*Sporisorium scitamineum*) resistant variety of sugarcane than in susceptible variety, suggesting the positive role of CAT1 in smut resistance.⁹¹ But this is not true under all situations and with all the detoxifying enzymes. Since ROS is required in higher concentration for activation of defense responses, detoxification of ROS is detrimental to plants. Therefore, the role of ROS in cross-tolerance between abiotic and biotic stresses can be explained from the context of capacity to detoxify the excess ROS which is beyond signaling.

In cucumber, Xia et al. (2009) have shown that brassinosteroid (BR) treatment enhanced NADPH oxidase activity and elevated the levels of H_2O_2 in the apoplast.⁹² BR treated plants showed increased tolerance to photo-oxidative stress, cold stress, and resistance to CMV. Inhibition of NADPH oxidase activity and scavenging of H_2O_2 resulted in reduced stress response with reduced expression of defense and antioxidant-responsive genes *Respiratory Burst Oxidase Homologs (RBOH)*, *Mitogen-Activated Protein Kinase 1 (MAPK1)*, and *MAPK3*, suggesting the role of ROS in cross-tolerance of cucumber plants. HSFA1b, a heat shock TF, is known to regulate heat and cold tolerance in many plant species.^{93,94} In Arabidopsis, overexpression of *AtHSFA1b* resulted in increased tolerance to drought as well as bacterial pathogen *Pst*DC3000. Interestingly, this response was dependent on H_2O_2 signaling.⁹⁵ A C_2/H_2 -type TF, Zinc finger of *A. thaliana* 6 (ZAT6), has been shown to positively regulate resistance to salt, drought, and chilling stress, as well as resistance to bacterial infection (*Pst*) through activation of *PR*-genes such as *Enhanced Disease Susceptibility 1 (EDS1)*, *Phytoalexin Deficient 4 (PAD4)*, *PR1*, *PR2*, and *PR5*, and abiotic stress-responsive genes *C-repeat-Binding Factor 1 (CBF1)*, *CBF2*, and *CBF3*. These responses were due to modulation of ROS (H_2O_2 and $O_2^{\bullet -}$) and SA levels.⁹⁶ Similarly, a WRKY family TF, WRKY30, has been shown to be involved in abiotic-biotic stress cross-tolerance mediated by ROS. *WRKY30* was induced by inoculation with several Pathogen-Associated Molecular Patterns (PAMPs) and methyl viologen and its overexpression improved tolerance to oxidative as well as salt stress.⁹⁷

In Arabidopsis, suppression of SIZ-type small ubiquitin-related modifier (SUMO) E3 ligase led to reduced stomatal aperture and enhanced drought tolerance through regulation of SA-induced accumulation of ROS.⁹⁸ In wheat, increased resistance of plants to rust pathogen, *P. striiformis*, was shown to be regulated by the *Yr36* gene, which was associated with higher accumulation of ROS and activated HR under high temperature.⁹⁹ In tomato, involvement of ROS in heat tolerance and resistance against fungal pathogen *O. neolycopersici* has been shown through regulation of HSP70 accumulation.¹⁰⁰ Mitochondrial Uncoupling Protein (LeUCP) has been shown to play a key role in the regulation of heat tolerance and pathogen (*B. cinerea*) defense in tomato by lower accumulation of ROS.¹⁰¹ In Arabidopsis, Mitogen-Activated Kinase Kinase 1 (*AtMKK1*) and *AtMKK6* coupled signaling has been shown to mediate ABA-induced *CAT1* expression and H_2O_2 production, suggesting the possible existence of fine modulation between ROS production and scavenging.¹⁰² Therefore, ROS mediated cross-tolerance of plants to abiotic and biotic stresses might be regulated by fine modulation of balance between scavenging to prevent the damage and production, which is necessary for plant defense responses.

17.3.2 Phytohormones and growth regulators

Plant hormones are known to regulate all phases of plant growth and development, in addition to regulating plant responses to both abiotic and biotic stresses.¹⁰³ They form

the baseline pathway that trigger signal transduction cascade by perception of abiotic and biotic stresses.¹⁰⁴ ABA, SA, JA, and ET have been shown to be associated with abiotic and biotic stress responses. In plants, hormones are found in trace quantities and their synthesis and accumulation are tightly regulated. Depending on their responses to different cues they are majorly grouped into two categories: the ones that mainly regulate abiotic stresses (ABA) and the ones that regulate biotic stresses (SA, JA, and ET). ABA is the well-studied hormone regulating plant responses to abiotic stresses.¹⁰⁵ SA is the central regulator in coordinating plant defense responses against biotrophic and hemibiotrophic pathogens, besides establishment of systemic acquired resistance (SAR), while JA and ET are involved in regulating the defense responses against necrotrophic pathogens and insect herbivores.¹⁰⁶ Besides specific signaling pathways regulated by each hormone or growth regulator, they are known to interact and regulate several stress responses through crosstalk. Plant hormones are suggested to act both synergistically and antagonistically, forming a multifaceted network of pathways with crosstalk at different levels.⁴

17.3.2.1 Role of ABA, an abiotic stress hormone, in plant defense responses

ABA has major roles in abiotic stress responses of plants and genes for the core ABA signaling pathway consisting of *pyrabactin resistance 1/PYR1-like* regulatory component of ABA receptor (*PYR/PYL/RCAR*), *phosphatase 2Cs (PP2Cs)*, and *Snf1-related kinases 2 (SnRK2s)*, etc., are well studied.¹⁰⁷ Besides its role in abiotic stress responses, ABA also mediates plant defense responses.¹⁰⁸ Recent findings suggest that ABA acts both synergistically and antagonistically, with crosstalk at different levels regulating both abiotic and biotic stress responses.⁴ Increased ABA content, either due to endogenous accumulation under abiotic stresses or due to exogenous application, is known to affect defense responses of plants when they are faced with pathogens.¹⁰⁹ The role of ABA as a negative regulator of pathogen response is through antagonistic interactions with SA and JA/ET signaling pathways.³⁰

Cross-tolerance of plants through ABA-mediated signaling is predominantly in pre-invasive defense against pathogens by increasing the penetration resistance through rapid closure of stomata.^{108,110,111} A mechanistic connection between PAMP-induced stomatal closure and ABA signaling in the guard cells has been shown using components of ABA signaling. For example, ABA-deficient mutant, *aba3-1*, plants compromised in their ability to respond to either *Pst* DC3000 or *Pst* DC3000/*avrRpt2* bacteria compared to wild-type plants, suggesting the involvement of ABA biosynthesis in stomatal closure in response to the bacteria.¹⁰⁸ In some plants, stomatal movement determines the pathogen entry, which is triggered by recognition of Microbe-Associated Molecular Patterns (MAMPs) such as flagellin and chitin.¹¹² In Arabidopsis, MAMP-triggered stomatal closure is regulated by both ABA and SA¹¹³ and in tomato and moss (*Physcomitrella patens*) ABA triggers stomatal closure.¹¹⁴

In addition to preinvasive resistance, ABA has also been shown to exert postinvasive defense. In barley, resistance against powdery mildew (*B. graminis*) was induced by ABA application to the root medium due to papilla-mediated resistance.⁴⁶ In Arabidopsis, ABA has been shown to be essential for plant resistance against *Pythium irregulare* and *Alternaria brassicicola* through regulation of JA biosynthesis and activation of defense genes.¹¹⁵ The enhanced resistance observed in these studies was due to reduced pathogen spread achieved by ABA-mediated callose biosynthesis or inhibition of its degradation. ABA mediated cross-tolerance of plants has also been observed in BABA treated plants. BABA enhances plant resistance through potentiation of defense responses by enhancing callose deposition. Callose deposition due to BABA priming was absent in ABA-insensitive mutants *abi4-1* and *aba1-5*, suggesting that ABA regulates BABA primed callose deposition.¹¹⁶ An activation-tagged allele of *Activated Disease Resistance 1 (ADR1)*, a resistance (*R*)-gene, involved in broad spectrum disease resistance mediated by SA showed cross-tolerance to drought that was dependent on *ABA1*.¹¹⁷ Involvement of endogenous ABA in methyl jasmonate (MeJA)-induced stomatal closure has been shown using fluridon, an ABA biosynthesis inhibitor, and *aba2-2*, an ABA-deficient mutant. Both fluridon treatment and *aba2-2* mutation inhibited MeJA-induced stomatal closure, but not ABA-induced stomatal closure, through inhibition of MeJA-induced Ca²⁺ release. MeJA stimulated the expression of *NCED3*, suggesting the role of endogenous ABA in MeJA signal transduction and stomatal closure in Arabidopsis guard cells.¹¹⁸

Synergistic interaction between ABA and JA in plant herbivore defense responses has also been suggested.^{119–121} In Arabidopsis, this interaction has been shown to be mediated by *MYC2* and its homologs, *MYC3* and *MYC4*. ABA induces the expression of these *MYC* genes in a Coronatine Insensitive (COI)-dependent manner, leading to the expression of wound/herbivore-responsive genes, and hence, insect resistance.^{122–124} However, the mechanistic understanding of ABA and JA interaction in synergistic response of plants to wounding/herbivores is limited. Jasmonate ZIM-domain (JAZ) proteins are suggested to be the link between ABA-JA interaction that work downstream of JA biosynthesis.¹²⁵ For example, Arabidopsis plants expressing the maize (*Zea mays*) gene, *ZmJAZ14*, showed enhanced tolerance to JA, ABA, PEG, and GA treatments through induced expression of several JA, ABA, and GA signaling pathway genes.¹²⁶ Taken together, being a key component of abiotic stress signaling, the role of ABA in cross-tolerance against pathogens is very limited and is mainly toward increasing the penetrative resistance through interaction with SA and JA.

17.3.2.2 Role of SA, JA, and ET in abiotic stress responses

SA, JA, and ET are mainly known to regulate plant defense responses against various biotic factors.¹¹¹ SA generally activates defense responses of plants against biotrophic and hemibiotrophic pathogens.¹²⁷ SA signaling is mediated by its receptor and regulator NPR1 (Nonexpressor of PR-genes 1), and NPR3 and NPR4, which are also receptors

but mediate SA dependent NPR1 degradation.^{128,129} JA and ET regulate plant defenses against necrotrophic pathogens and herbivorous insects.^{130,131} Once synthesized in response to pathogens, SA can trigger the defense responses in distant plant parts to protect undamaged tissues from pathogen attack; this long lasting and broad-spectrum induced resistance is known as SAR.¹⁰⁶ Besides its role in plant defense responses, SA has been shown to protect plants against abiotic stresses such as heavy metals, temperature (high/low), salinity, osmotic stress, drought stress, ozone, and UV-irradiation.^{132–137} Exogenous application of SA can impart abiotic stress tolerance. SA supplementation has enhanced drought tolerance of several plant species such as barley,¹³⁸ *Brassica juncea* (mustard),¹³⁹ maize,¹⁴⁰ and wheat.¹⁴¹ This SA mediated drought tolerance is associated with secondary metabolite and antioxidant production, enhanced chaperonin activity and plant defense gene expression. In support of this, SA-accumulating mutants *constitutive expresser of PR-genes 5 (cpr5)* and *acd6* of Arabidopsis showed improved drought tolerance through induction of PR-genes.⁹⁸ Similarly, in Arabidopsis, SIZ1-mediated endogenous accumulation of SA resulted in drought tolerance.⁹⁸

Exogenous application of SA has improved tolerance of *Cucumis melo* (muskmelon), mustard, *Glycine max* (soybean), *Poa pratensis* (Kentucky bluegrass), maize, rice, and *Linum usitatissimum* (flax) to Cd stress.^{132, 142–147} Similarly, SA improved growth of rice under lead (Pb),¹⁴⁸ common bean under copper (Cu),¹⁴⁹ and *Catharanthus roseus* under Ni treatments.¹⁵⁰ In heavy metal hyperaccumulator *Thlaspi goesingense*, there was constitutive elevation of SA signals compared to other nonaccumulators such as Arabidopsis and *Thlaspi arvense*.¹⁵¹ In most of these cases the enhanced tolerance was associated with mineral nutrient homeostasis and antioxidant production. SA induced salt stress tolerance has also been shown in many plant species, such as *Vicia faba* (broad bean),¹⁵² mustard,¹³⁴ *Medicago sativa*,¹⁵³ and *Vigna radiata* (mung bean).¹³³ SA-mediated salinity tolerance has been suggested to be due to alleviation of oxidative stress through activation of antioxidant enzymes. In line with this, SA-deficient *Salicylate hydroxylase* gene (*NahG*) Arabidopsis plants showed reduced activity of antioxidant enzymes.¹⁵⁴ Similarly, SA-mediated tolerance of plants to temperature (low/high) stress, ozone, and UV-irradiation has also been shown to be through enhanced antioxidant capacity.¹⁵⁵ Under ozone and heat stress, SA is also involved in crosstalk with other phytohormones such as JA and/or ET.^{137,156} Taken together, potentially, SA-mediated cross-tolerance mechanisms involve modulation of osmolytes synthesis, activation of antioxidant system, production of secondary metabolites, and mineral nutrient homeostasis.

The role of JA in pathogen defense responses has been clearly demonstrated.¹⁵⁷ Besides, JA also plays a predominant role in plant defense against herbivore attack.¹⁵⁸ An F-box protein, COI1, the receptor of JA,¹⁵⁹ and co-ordination of several TFs has been suggested to regulate JA signaling. Mainly, Jasmonate Insensitive 1 (JIN1)/MYC2 and members of APETALA2/ethylene response factor (AP2/ERF) family TFs such as ERF1, ERF2, ERF5, and ERF6 have been suggested to regulate JA signaling through

regulation of *Plant Defensin 1.2*, a JA-responsive marker gene.¹⁶⁰ This pathway has been well characterized under JA response against necrotrophic pathogens. Repression of JA signaling is controlled by Jasmonate-JIM-Domain (JAZ) proteins through their interaction with JIN1/MYC2 and inhibition of JA-responsive genes.¹⁶¹

In addition to plant disease and insect resistance, there is growing evidence to suggest the key role of JA in regulating abiotic stress responses. JA has been shown to regulate abiotic stress response and help in plant adaptation to salinity, drought, high or low temperature, heavy metals, ozone, and UV-irradiation.¹⁶² Treatment of Arabidopsis plants with the JA precursor 12-Oxo-Phytodienoic Acid (OPDA) conferred drought tolerance through enhanced stomatal closure, regulated by elevated OPDA levels.¹⁶³ In *Agropyron cristatum*, JA protected the plants against drought stress through regulation of antioxidants.¹⁶⁴ Similar observations were made in JA treated wheat seedlings, wherein enhanced salt tolerance was due to ROS scavenging by antioxidants.¹⁶⁵ In barley, JA treatment resulted in low Na⁺ accumulation in shoot tissue with overlapping expression of genes regulated by both JA and salt stress.⁸⁰ Under low temperatures, JA is known to modulate CBF/DREB1 cascade and impart freezing tolerance in Arabidopsis and tomato.^{166,167} In *Wolffia arrhiza*, JA application prevented the accumulation of Pb through increased antioxidant capacity.¹⁶⁸ Similar observations were also made in rice and *Avicennia marina*, resulting in reduced Cd accumulation.^{169,170} JA pretreatment also alleviated the damaging effects of UV-B in barley and wheat through increasing the activities of antioxidant enzymes.^{171,172} It seems that, similar to SA, the potential mechanisms of JA-mediated abiotic stress cross-tolerance are through activation of antioxidants, regulation of plant water relations through stomata, production of osmolytes, and metal homeostasis.

Ethylene (ET), a gaseous hormone, is known to play diverse roles in plant growth and development, and in stress response, besides its crucial role in ripening and senescence. The core of ET signaling consists of receptors (Ethylene Receptor 1 (ETR1), ETR2, Ethylene Response Sensor 1 (ERS1) and ERS2) in endoplasmic reticulum, which activate Ethylene Insensitive 2 (EIN2), leading to activation of TF EIN3 and Ethylene Insensitive 3-Like 1 (EIL1) in the nucleus.¹⁷³ ET response is negatively regulated by Constitutive Triple Response 1 (CTR1) through phosphorylation of EIN2, leading to degradation of EIN2 by F-box proteins EIN2 Targeting Protein 1/2 (EPT1/2)¹⁷⁴ and further degradation of EIN3/EIL1 in the nucleus through ubiquitin-proteasome, mediated again by F-box proteins EPT1/2.¹⁷⁵ The role of ET in resistance against necrotrophic, biotrophic, and hemibiotrophic pathogens is well known in many plant species. ET acts in coordination with other hormones such as SA, JA, and ABA in regulating these defense responses against pathogens. The diverse role of ET in abiotic stress tolerance such as cold and freezing, salinity, drought, heat, and flooding has been reviewed in detail.¹⁷⁶ The classic role of ET in submergence tolerance through regulation of morphological and anatomical traits that improve aeration has been studied fairly well in rice.¹⁷⁷

This phenomenon has also been proven with ET primed plants resulting in improved survival under anoxia.¹⁷⁸ In rice, Submergence 1 (SUB1) locus, which encodes SUB1A, SUB1B, or SUB1C TFs, has been clearly demonstrated to impart submergence tolerance.¹⁷⁹ Submergence promotes ET accumulation, which in turn antagonizes ABA response in GA-mediated stem elongation. Further, SUB1 has feedback regulation on ET biosynthesis and negatively regulates GA-responsiveness by antagonizing ABA and hence blocking the GA-mediated growth.¹⁸⁰ Therefore, ET and SUB1A-mediated submergence tolerance through reduced plant growth has been suggested to conserve energy during anoxia.

Species dependent association of enhanced ET levels or exogenous application of ET/1-aminocyclopropane-1-carboxylic acid (ACC) resulting in cold and freezing tolerance were observed.^{181,182} ET signaling positively regulating salt tolerance has been shown using ET receptor mutants such as *etr1* and *ein4*, which showed increased salt sensitivity.^{183,184} Under salt stress, *ETR1* and *EIN4* stimulate ABA biosynthesis to inhibit germination. Further, *EIN2*, a key gene in ET signaling, has been shown to enhance salt tolerance by positively regulating ABA biosynthesis.¹⁸⁵ *EIN3*, TF acting downstream of the *EIN2*, also positively regulates salt stress tolerance. Mutation of *EIN3* reduced seed germination under salt stress, probably due to degradation of *EIN3* Binding F-box 1 (*EBF1*) and *EBF2*, negative regulators of *EIN3*.^{186,187} In Arabidopsis, this salt induced stabilization of *EIN3* leading to salt tolerance has been suggested to be due to reduced accumulation of ROS.¹⁸⁷ Further, *EIN3* mediated salt tolerance is at least partly due to induced expression of stress-responsive genes and ROS detoxification by AP2/ERF TF Ethylene and Salt Inducible 1 (*ESE1*), *ERF1* and Salt-Induced and *EIN3*/*EIL1*-Dependent 1 (*SIED1*) acting downstream of *EIN3*.^{188,189} In rice, a mutation in Ethylene Overproducer 1-Like (*OsETOL1*) protein resulted in elevated levels of ET, which is associated with increased drought tolerance. The wild-type *OsETOL1* was shown to interact with ACC synthase 2 (*OsACS2*) and reduces its activity, thereby reducing ET accumulation.¹⁹⁰ These studies suggest that ET and abiotic stress signaling share several pathways, mainly in crosstalk with ABA.

17.4 Genetic control of cross-tolerance to abiotic and biotic stresses

17.4.1 Kinases

Protein phosphorylation and dephosphorylation plays a significant role in plant tolerance to abiotic and biotic stresses. In eukaryotes, Receptor Like Kinases (RLKs) and Mitogen-Activated Protein Kinases (MAPKs/MPKs) are the two signaling cascades that are widely activated and central regulators of diverse cellular processes including cell differentiation, proliferation, growth, and stress responses.¹⁹¹ RLKs, one of the largest superfamily of genes in plants, are classified into several subfamilies. Among them, leucine-rich repeat (LRR) subfamily is the largest and plays essential roles in different plant processes,

including plant adaptation to abiotic and biotic stresses.¹⁹² RLKs are known to play positive as well as negative regulatory roles in plant abiotic and biotic stress responses.¹⁹³ An RLK gene, *GbRLK*, from cotton (*Gossypium barbadense*) was shown to be involved in both abiotic and biotic stress tolerance. In Arabidopsis, *GbRLK* enhanced tolerance to salinity and drought through regulation of stress-responsive genes to reduce water loss.¹⁹⁴ In cotton as well as Arabidopsis, *GbRLK* improved resistance of plants to wilt caused by *Verticillium dahliae* both under greenhouse and field conditions through regulation of several abiotic and biotic stress-responsive genes and reduced water loss.¹⁹³ Therefore, *GbRLK* could be a key regulator of cross-tolerance to abiotic and biotic stresses in plants.

MAPKs are another group of kinases acting downstream to RLKs in the signaling events and are central for the transduction of cellular signals by activation and repression of downstream target proteins through phosphorylation. The mechanism of MAPK signaling is usually threefold, wherein MAP Kinase Kinase Kinase (MAPKKK) are activated by the stress stimuli first which in turn phosphorylates Kinase Kinases (MAPKK). MAPKK further activates MAPK, which is involved in activation of downstream cellular proteins. MAP kinases are critical players in crosstalk between abiotic and biotic stresses. Several MAP kinases that are induced under and impart tolerance to both abiotic and biotic stress have been identified (Table 17.1). For example, the activation of Salicylic acid-Induced Protein Kinase (SIPK) by both SA and osmotic stress suggests the converging abiotic and biotic stress.²²⁵ OsMPK5 (also known as OsMAPK2, OsMAPK5, OsBIMK1, OsMSRMK2, or OsMAP1), the most extensively studied MAPKs in rice, has been shown to positively regulate ABA-mediated resistance against necrotrophic brown spot pathogen *Cochliobolus miyabeanus* and abiotic stress tolerance.²²⁶ However, it has also been shown to negatively regulate ET-mediated defense against the hemibiotrophic fungus *Magnaporthe oryzae*.^{227,228} A pentatricopeptide repeat protein (PPRP) for Germination on NaCl (PGN), a potential Botrytis-Induced Kinase 1 (BIK1), from Arabidopsis showed tolerance to necrotrophic fungal pathogens *B. cinerea* and salinity. PGN has been suggested to function in regulation of ROS homeostasis in mitochondria during abiotic and biotic stress through ABA signaling.²²⁹ These studies emphasize the involvement of complex MAPK-mediated signaling with diverse as well as overlapping functions. Together, the function of MAPKs in cross-tolerance might be through ABA-ROS signaling.

17.4.2 Transcription factors

Manipulation of upstream signaling molecules such as phytohormones, second messengers (ROS and Ca²⁺), and kinases will usually have pleiotropic effects, as they modulate several downstream signaling components, including TFs and other functional genes. Therefore, upstream regulatory components such as second messengers, kinases, etc. are not often the targets to improve cross-tolerance of plants to abiotic and biotic stresses. On the other hand, TFs, regulate very specific downstream signaling components and

Table 17.1 Genes associated with cross-tolerance of plants to abiotic and biotic stresses

Gene name	Gene family	Modified plant species	Abiotic stress	Biotic stress	Possible mechanism of action	References
a. Signaling						
<i>VaRGA1</i>	TIR-NB-LRR	<i>Nicotiana benthamiana</i>	Drought and salt	Downy mildew caused by <i>Phytophthora parasitica</i>	SA signaling and Phenylpropanoid pathway	195
<i>OsCPK10</i>	Kinase	Rice	Drought and oxidative stress	Blast disease caused by <i>Magnaporthe oryzae</i>	ROS detoxification through catalase	196
<i>ZmSIMK1</i>	Kinase	Tobacco	Drought	Bacterial speck caused by <i>Pseudomonas syringae</i>	ROS scavenging and SA mediated signaling	197
<i>mik2-1</i>	Kinase	Arabidopsis	Salt	Wilt caused by <i>Fusarium oxysporum</i>	JA/SA mediated signaling and cellulose biosynthesis pathways	198
b. Transcription factors						
<i>bos1</i>	MYB	Arabidopsis	Water deficit, salinity, and oxidative stress	Gray mold caused by <i>Botrytis cinerea</i> and black spot caused by <i>Alternaria brassicicola</i>	JA signaling	199
<i>OsMYB4</i>	MYB	Arabidopsis	Drought, salt, UV, and ozone	Gray mold caused by <i>B. cinerea</i> , bacterial speck caused by <i>P. syringae</i> , and mosaic disease caused by <i>Tobacco necrosis virus</i>	Osmolyte and phenylalanine ammonia-lyase (PAL) involved SA signaling	200

<i>MYB96</i>	MYB	Arabidopsis	Drought	Bacterial speck caused by <i>P. syringae</i>	ABA-SA crosstalk	201, 202
<i>SLAIM1</i>	MYB	Tomato	Salt and oxidative stress	Gray mold disease caused by <i>B. cinerea</i>	ABA signaling	203
<i>TaPIMP1</i>	MYB	Tobacco and wheat	Drought and salt	Wilt caused by <i>Ralstonia solanacearum</i> , root rot caused by <i>Bipolaris sorokiniana</i>	ROS scavenging, SA and ABA signaling	204, 205
<i>PacMYBA</i>	MYB	Arabidopsis	Salt	Bacterial speck caused by <i>P. syringae</i>	Osmolytes, SA, and/or JA signaling	206
<i>AaNAC1</i>	NAC	<i>Artemisia annua</i> or Arabidopsis	Drought	Gray mold caused by <i>B. cinerea</i>	Artemisinin, dihydroartemisinic acid synthesis, and SA/JA signaling	207
<i>NTL6</i>	NAC	Arabidopsis	Cold	Bacterial speck caused by <i>P. syringae</i>	Inducing PR gene expression	64
<i>CaERFLP1</i>	AP2/ERF	Tobacco	Salt	Bacterial speck caused by <i>P. syringae</i>	Regulation of defense (<i>PR</i>) and drought (<i>ERD10</i>) gene expression	208
<i>ERF1-V</i>	AP2/ERF	Wheat	Salt and drought	Powdery mildew caused by fungal pathogen <i>Blumeria graminis</i>	ROS and salt signaling	209
<i>GmERF3</i>	AP2/ERF	Tobacco	Salinity and drought	Wilt caused by <i>R. solanacearum</i> , leaf spot caused by <i>Alternaria alternate</i> , and Tobacco mosaic virus (TMV)	Osmolyte synthesis	210

Table 17.1 Genes associated with cross-tolerance of plants to abiotic and biotic stresses—cont'd

Gene name	Gene family	Modified plant species	Abiotic stress	Biotic stress	Possible mechanism of action	References
<i>Tsi1</i>	AP2/ERF	Tobacco	Salt	Bacterial speck caused by <i>P. syringae</i>	Induction of <i>PR</i> genes	211
<i>OPBP1</i>	AP2/ERF	Tobacco	Salt	Bacterial speck caused by <i>P. syringae</i> and downy mildew caused by <i>P. parasitica</i>	<i>PR</i> gene expression	212
<i>CBF/DREB1s</i>	AP2/ERF	Arabidopsis	Drought, salt and cold	Bacterial speck caused by <i>P. syringe</i>	Stress gene expression (<i>COR15A</i> , <i>RD22</i> , and <i>KIN1</i>) and sugar accumulation	213
<i>AtZAT6</i>	Zn finger	Arabidopsis	Salt, drought and freezing	Bacterial speck caused by <i>P. syringae</i>	SA and ROS signaling	214
<i>SpWRKY1</i>	WRKY	Tobacco	Salt and drought	Late blight caused by <i>Phytophthora nicotianae</i>	Stress gene expression (<i>NtPOD</i> , <i>NtSOD</i> , <i>NtLEA5</i> , <i>NtP5CS</i> , and <i>NtNCED1</i>)	215
<i>SpWRKY1</i>	WRKY	Tomato	Salt and drought	Black shank caused by <i>Phytophthora infestans</i>	SA/JA and ABA signaling	216
<i>SIDRW1</i>	WRKY	Tomato	Oxidative stress	Gray mold caused by <i>B. cinerea</i>	JA/ET signaling	217
<i>FvWRKY42</i>	WRKY	Arabidopsis	Drought and salt	Powdery mildew caused by <i>Golovinomyces cichoracearum</i>	ABA signaling	218

c. Functional genes

<i>GmCYP82A3</i>	CYP82	<i>N. benthamiana</i>	Salinity and drought	Gray mold caused by <i>B. cinerea</i> and root and stem rot caused by <i>P. parasitica</i>	JA/ET signaling	219
<i>ZmLEA3</i>	LEA	Tobacco	Osmotic and oxidative stress	Holcus spot caused by <i>P. syringae</i>	Enhanced expression of <i>PR</i> genes (<i>PR1a</i> , <i>PR2</i> , and <i>PR4</i>)	220
<i>AnnBj1</i>	Annexin	Tobacco	Dehydration, salt, heavy metal, and oxidative	Black shank caused by <i>P. parasitica</i>	Peroxidase activity and <i>PR</i> gene expression	221
<i>BOI</i>	Ring E3 ligase	Arabidopsis	Salt	Gray mold caused by <i>B. cinerea</i>	<i>BOI</i> degradation and <i>PR</i> gene expression	222
<i>MoHrip1</i> and <i>MoHrip2</i>	Protein elicitors	Rice	Drought	Rice blast caused by <i>M. oryzae</i>	ABA and SA signaling	223
<i>CABPR1</i>	PR	Arabidopsis	Oxidative stress	Leaf speck caused by <i>P. syringae</i>	<i>PR</i> -genes expression (<i>PR-4</i> , <i>PR-5</i> , and <i>PDF1.2</i>)	224

hence have been extensively studied for their role in cross-tolerance. Several genes belonging to the MYB, NAC, HSF, AP2/ERF, WRKY, and Zinc Finger TF superfamilies have been reported to impart cross-tolerance of plants to abiotic and biotic stresses (Table 17.1). Among the MYB family of TFs, increasing evidence suggests that the R2R3-MYB subfamily is involved in diverse abiotic and biotic stress responses. For example, heterologous expression of *PacMYB* in *Arabidopsis* enhanced tolerance of plants to salt stress and resistance against *Pst* DC3000 infection through decreased osmotic potential, increased proline and peroxidase content in addition to altered levels of expression of salt stress and pathogen-responsive genes.²⁰⁶ Similarly, overexpression of R2R3-MYB TF, *TaPIMP1*, in wheat resulted in enhanced resistance to the fungal pathogen *Bipolaris sorokiniana* and drought tolerance through the induction of ABA and SA signaling associated genes such as Dehydration-Responsive 22 (RD22), *Thaumatococcus*-Like Protein 4 (TLP4), and *PR1a*.²⁰⁵ The same gene has been shown to impart tolerance to pathogen, *Ralstonia solanacearum*, and to abiotic stresses (drought and salt) in transgenic tobacco with enhanced activity of phenylalanine ammonia-lyase (PAL) and SOD.²⁰⁴ *Botrytis Susceptible 1 (BOS1)* is another classic R2R3-MYB TF conferring resistance to pathogens and tolerance to salt and drought stresses through a JA-mediated defense signaling pathway. *bos1* mutants were susceptible to necrotrophic fungi *B. cinerea* and *A. brassicicola*, and biotrophic bacterial pathogen *P. syringae* and sensitive to abiotic stresses salinity, drought, and oxidative stress.¹⁹⁹ These findings indicate the essential role of MYB family TFs in cross-tolerance through mediation of ABA-SA signaling.

Members of NAC, a plant specific, TF family have also been shown to impart cross-tolerance of plants to abiotic and biotic stresses. OsNAC6 is a positive regulator of plant responses to both abiotic and biotic stresses. Overexpression of *OsNAC6* enhanced tolerance of plants to drought, salinity and resistance against hemibiotrophic fungal pathogen *M. oryzae* in rice through activation of several stress-responsive genes especially peroxidase.²³⁰ In *Artemisia annua*, *AaNAC1* overexpression enhanced tolerance of plants to drought and resistance to *B. cinerea* by increasing Artemisinin biosynthesis.²⁰⁷ Artemisinin is an efficient antimalarial drug and has been shown to work against multidrug-resistant strains of the malaria parasite *Plasmodium falciparum* in addition its role against multiple stresses in plants.²³¹ Similarly, expression of a cold activated and plasma membrane-tethered NAC TF, NTL6, enhanced tolerance of plants to drought as well as resistance against bacterial pathogen *P. syringae* pv. *syringae* strain DC3000 through induction of the *PR*-genes.⁶⁴

AP2/ERF family TFs have long been known for their role in both abiotic and biotic stress signaling in addition to plant growth and development. Several studies suggest their role in cross-tolerance of plants to abiotic and biotic stresses. For example, Tsi1, OPBP1, CaERFLP1, GmERF3, CaPF1, BIERF1-4, and ERF1-V have been shown to enhance abiotic and abiotic tolerance in different plant species.^{208-212,232,233} The mechanisms associated with AP2/ERF TFs-mediated cross-tolerance are osmolyte accumulation

and increased antioxidant activity, mediated through SA/JA signaling. Dehydration Responsive Element Binding's (DREBs), members of the AP2/ERF super family of TFs, are key regulators of abiotic stress signaling, especially drought and cold. However, they have been shown to play additional signaling functions under biotic stresses. AtDREB2 was shown to work through an ABA-independent and SA-dependent pathway in imparting pathogen resistance in crosstalk with ADR1 activated signaling pathways.¹¹⁷ In ADR1 overexpression plants, DREB2A has been shown to be activated by SA-dependent ROS signaling. Similarly, melatonin induced DREB1/CBF TFs, AtCBF1, AtCBF2, and AtCBF3, enhanced tolerance of plants to drought, cold, salinity, and *Pst* DC3000.²¹³ These plants accumulated more stress-responsive genes (*Cold-Responsive 15A*, *RD22*, and *Cold-Induced KIN1*) and sugars. Taken together, these studies suggest that most of AP2/ERF TFs work in an ABA-independent pathway to regulate cross-tolerance through activation of genes common to both abiotic and biotic stresses.

The HSF family TFs primarily regulate abiotic stress responses especially heat stress through activation heat shock proteins. However, recent evidence suggests a role for these factors in biotic stress response also. In support of this, overexpression of AtHSFA1b enhanced tolerance of plants to drought, resistance against the bacterial pathogen *Pst* DC3000, and the oomycete pathogen *Hyaloperonospora arabidopsidis*, strain WAC09 (Hpa).⁹⁵ This HSFA1b-induced drought and pathogen tolerance was mediated by H₂O₂ signaling.

WRKY, another family of TFs, are key regulatory components of plant responses to abiotic and biotic stresses. A pathogen (*P. infestans*) induced *SpWRKY1* from the wild tomato, *Solanum pimpinellifolium* L3708, has been shown to impart resistance to *Phytophthora nicotianae* in tobacco and to *P. infestans* in tomato. In both species, *SpWRKY1* increased tolerance of plants to drought and salt stress (*Solanum lycopersicum*) through enhanced expression of SA/JA- and ABA-responsive genes and ROS scavenging enzymes.^{215,216} Expression of a rice stress inducible *OsWRKY45* gene in Arabidopsis enhanced resistance to the bacterial pathogen *Pst* DC3000 and tolerance to salt and drought stresses, via an ABA-dependent pathway.²³⁴ However, Shimono et al. (2012) have shown a role for *OsWRKY45* in benzothiadiazole-induced and SA-mediated defense signaling in rice, suggesting that WRKY45 might be involved in ABA and SA signaling crosstalk.²³⁵ Similarly, the *B. cinerea*-responsive WRKY gene *SIDRW1* (*S. lycopersicum* Defense-Related *WRKY1*) from tomato was shown to be required for tomato resistance against *B. cinerea* and tolerance to oxidative stress.²¹⁷ These studies indicate that WRKY TF mediated cross-tolerance of plants might be through both ABA and SA/JA signaling.

17.5 Achieving cross-tolerance of plants to abiotic and biotic stresses

A number of evidences suggest the simultaneous occurrence of several abiotic and biotic stresses. Therefore, it is crucial to work toward improving tolerance of plants to different

types of abiotic and biotic stresses.³⁰ Understanding the regulatory pathways specific or common to a stress combination is critical for developing stress-tolerant crops. Recently, researchers have been treating multiple abiotic and biotic stresses that occur together as a different type of stress and trying to understand the effects of these stresses on a specific plant species under a specific growing environment.^{29,31,236,237} It is evident from these studies and from the above-described interactions that several abiotic and biotic stresses share common pathways. These pathways, mechanisms, or genes can be exploited to improve the cross-tolerance of plants to specific abiotic and biotic stress combinations.^{54,238} Potential strategies that can be deployed in understanding and improve cross-tolerance of plants to abiotic and biotic stresses are illustrated in Fig. 17.1.

17.5.1 Targeted breeding

In nature, plants will be exposed to different intensities of multiple stresses throughout the growing cycle and have evolved to endure these stresses, suggesting that plants have acquired multistress tolerance traits. This inherent capacity to withstand multiple stresses might be due to overlapping/shared pathways as plants have to balance their energy distribution between growth and reproduction, and survival under these conditions. Through domestication, we have lost many traits associated with multiple stress tolerance and hence the narrow genetic base in today's elite cultivars is a major bottleneck for improving plants cross-tolerance to abiotic and biotic stresses. The rich genetic diversity that exists in the wild relatives of crop species should be exploited to enhance crop

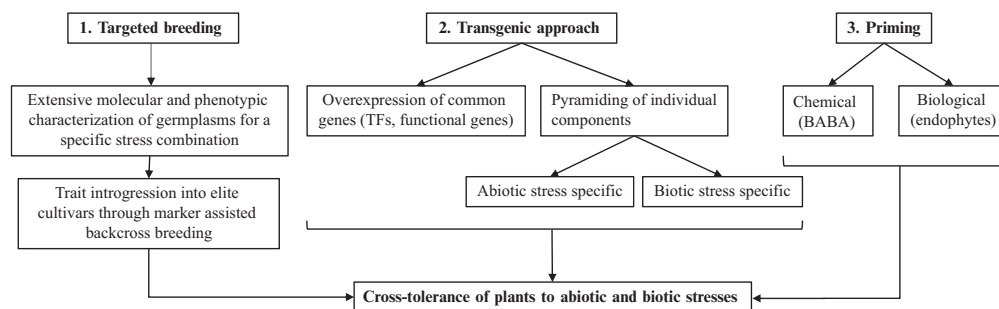


Fig. 17.1 Potential approaches to improve cross-tolerance of plants to abiotic and biotic stresses. Three strategies are proposed. 1. Targeted trait-based breeding though is a long drawn process, it helps bringing in large genetic diversity from the wild relatives into cultivated varieties. 2. Transgenic approach either through genetic manipulation of components common to both abiotic and biotic stresses identified in stress combination studies or bringing together individual stress specific components through gene stacking. Selection of genes in transgenic approach depends on the pathogen, abiotic stress and the plant species. 3. Priming for cross-tolerance using chemical or biological agents. The selection of priming agents depends on stresses and crop species.

adaptation to multiple stresses.²³⁹ Though breeding for cross-tolerance to abiotic and biotic stresses can be challenging, the emergence of modern molecular and genomic tools will help accelerate the identification of traits underlying cross-tolerance and also enable rapid transfer of these traits into elite cultivars.²⁴⁰

Marker assisted breeding has been extensively used for the genetic improvement of crops.²⁴¹ Similarly, success has been achieved in improving the cross-tolerance of plants to abiotic and biotic stresses through molecular breeding. For example, in rice, quantitative trait loci (QTLs) were identified for high grain yields and drought tolerance in a mapping population tolerant to rice blast disease.²⁴² In addition, through marker assisted selection, Das and Rao (2015) successfully stacked genes/QTLs for disease resistance (blast disease (Pi2, Pi9)), insect resistance (gall Midge (Gm1, Gm4)), and tolerance to abiotic stresses such as submergence (SUB1), and salinity (Saltol) in the rice variety Lalat, which already contained the bacterial blight resistance genes *Xa5*, *Xa13*, *Xa21*, and *Xa4*.²⁴³ The same genes/QTLs have been successfully pyramided in another elite rice cultivar, and Tapaswini²⁴⁴ suggested the possibility of improving cross-tolerance of plants to both abiotic and biotic stresses through breeding. Recent advances in genomic selection strategy combined with speed breeding approaches can effectively accelerate the crop improvement process to achieve a comprehensive improvement in plant performance under combinatorial stress conditions.

17.5.2 Gene pyramiding through transgenic approach

Enhancing cross-tolerance of plants to different type of stresses is a complex trait as majority of abiotic and biotic interactions result in antagonism, with one stress predisposing the other. However, as discussed above, there are interactions that are synergistic, with one stress sharing the signaling/stress response pathway with another. In the recent past, the role of several genes in cross-tolerance to different abiotic and biotic stresses has been shown (Table 17.1). It is possible to engineer these genes/pathways in a stress combination and plant species dependent manner to improve cross-tolerance of plants. It is also evident from recent transcriptomic studies that under a combination of abiotic and biotic stresses there are specific signaling pathways/genes upregulated in addition to shared pathways and genes.^{236,245,246} These shared or stress combination specific responses can be engineered to improve plant cross-tolerance. However, such an approach requires extensive phenotyping and functional analysis of these genes under stress combinations. For example, Atkinson et al. (2013) identified 50 multiple-stress-regulated genes through transcriptomic analysis under combination of drought and the plant-parasitic nematode *Heterodera schachtii*. The potential roles of a few candidate genes in controlling drought and nematode tolerance have been assessed. *Rapid Alkalinization Factor-Like 8* (*AtRALFL8*) was identified as negative regulator as it conferred susceptibility to both drought stress and nematode infection. However, two more genes, *Methionine Gamma*

Lyase (AtMGL) and *Azelaic Acid Induced 1 (AZI1)*, though induced by both the stresses, did not impart tolerance to both the stresses when overexpressed.²³⁶ Therefore, mere induction of these genes under stress combination may not lead to major conclusion unless they are functionally validated under stress combination. An alternative approach for developing cross-tolerant plants to both abiotic and biotic stresses is pyramiding of genes to individual stresses that do not interfere with each other. In this direction, pyramiding of two or more transgenes against a single abiotic or biotic stress has proven successful in conferring tolerance to that particular stress.^{247–250} However, attempts towards gene pyramiding through transgenic approach for improved tolerance to both abiotic and biotic stresses are limited but a possibility.

17.5.3 Chemical or biological priming

Priming is a phenomenon wherein exposure of plants to mild stresses or chemical/biological inducers prepares plants to deploy a more rapid and stronger defense response to a more severe stress in the future. In an unpredictable environment, as seen today, priming plants against abiotic and biotic stresses has gained a lot of interest as an adaptive trait. Priming has been induced through chemical compounds (BABA, GABA, phosphite, laminarin, 2,6-dichloroisonicotinic acid, SA, JA, H₂O₂, NO), biological agents (pathogens, beneficial microbes, insect herbivores), or environmental factors.^{251,252} Different priming agents induce different mechanisms of defense in plants, but the majority of them work through ABA, SA, JA, and ROS signaling.²⁵³ The majority of the priming mediated stress tolerance has been achieved under individual stresses or closely related stresses. However, there are reports suggesting the usefulness of priming in understanding and achieving cross-tolerance of plants to abiotic and biotic stresses. For example, application of BABA enhanced plant resistance to fungal pathogens, as well as tolerance to abiotic stresses such as heat, drought, and salinity.⁷⁸ Similarly, application of biotic stress inducers, SA, JA, H₂O₂, and NO has rendered plants tolerance to abiotic stresses in addition to triggering biotic stress response.^{79,80,254}

Besides chemical compounds, biological agents, especially beneficial microbes, have primed plants against abiotic or biotic stresses.^{73,255} Though these microbes have stimulated growth of plants by improving soil fertility and suppressing the individual abiotic and biotic stresses, their role in cross-tolerance is also gaining importance.²⁵⁵ The role of endophytes in this direction is being actively explored. Besides improving soil fertility, some endophytic bacteria have been shown to possess biocontrol activity through the production of antifungal metabolites and antibiotics, which in turn induce plant defense responses against pathogens.^{256,257} In corroboration with this, treatment of plants with endophytes from the family Clavicipitaceae resulted in enhanced tolerance to drought and resistance to pests and fungal diseases.²⁵⁸ Similarly, tomato seeds treated with *Trichoderma harzianum* enhanced plant resistance to damping off and root rot diseases caused by

Pythium ultimum and tolerance to abiotic stresses such as osmotic stress, salinity, chilling, and heat.²⁵⁹ In cucumber, *Pseudomonas aeruginosa*, a wheat endophytic bacterium, enhanced resistance to fungal blight pathogen *Sclerotium rolfsii* and tolerance to salinity stress.²⁶⁰ Recent findings have also suggested that enhanced defense response of plants due to priming can be inherited epi-genetically from primed plants to the next generation.²⁶¹ Therefore, use of priming through chemicals or biological agents is a promising field to explore and improve cross-tolerance of plants to abiotic and biotic stresses avoiding manipulation of the genome.

17.6 Conclusions

Recent research has radically changed the notion that abiotic and biotic stress responses of plants are controlled by different pathways/genes. It seems that several signaling events/genes are directly or indirectly associated with multiple stress responses. Though the majority of these associations have been suggested to be antagonistic, there are also synergistic interactions resulting in cross-tolerance. The phenomenon of cross-tolerance to abiotic and biotic stresses has been known for a while, but only recently has it gained a lot of importance, with researchers treating combined abiotic and biotic stresses as a different state of stress and understanding their responses. So far, the progress made toward plant cross-tolerance is coming from model plants grown under controlled laboratory conditions. However, under field conditions, plants are exposed to complex environmental conditions with multiple stresses occurring together with constant change in light intensity, temperature, humidity, and a plethora of pathogens. This requires a concerted effort toward studying the plant responses under field conditions and translating the knowledge into crop plants for agricultural use.

Several approaches have been followed toward improving cross-tolerance of plants to abiotic and biotic stresses with fairly good success. It seems that tolerance of plants to multiple stresses depends on several factors, including plant species, growth stage, first occurring stress, stress intensity, and duration. All these factors will determine the first few signaling events upon exposure of plants to multiple stresses. Therefore, modification of early signaling events such as phytohormones, second messengers (ROS, Ca²⁺), kinases, etc., may not be feasible as their interactions are complex and might not work under all conditions, resulting in undesirable effects on plants. On the contrary, several TFs have been shown to confer cross-tolerance to a combination of multiple abiotic and biotic stresses without any adverse effect on plants (Table 17.1). Therefore, downstream genes such as TFs and functional effector genes are the best targets for genetic improvement of plants to abiotic-biotic stresses. We believe that with the tremendous progress made in phenotyping and genomics, the task of understanding and subsequently introgressing cross-tolerance can be effectively achieved in important crop species.

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