

Chapter 10

Impact of Concurrent Drought Stress and Pathogen Infection on Plants

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10.1 Introduction

In the field conditions, plants are constantly exposed to concurrent abiotic and biotic stresses that affect their overall growth and development (Mittler 2006; Atkinson and Urwin 2012). Plant responses to individual biotic and abiotic stresses have been well explored and a number of genes conferring tolerance to the individual stresses have been identified. Some of the genes have also been reported to impart tolerance to multiple independent abiotic and biotic stress conditions (Wang et al. 2010, 2013; Senthil-Kumar et al. 2013; Tamirisa et al. 2014). A few recent studies suggest that the combined effect of two or more abiotic stresses cause greater reduction in crop yield when compared with the losses incurred by individual stresses (Rizhsky et al. 2002, 2004; Mittler 2006; Suzuki et al. 2014). Environmental factors like drought, extreme temperature, and salinity potentially alter the occurrence and intensity of a particular disease by modulating the plant responses to pathogen (Szittyá et al. 2003; Wiese et al. 2004; Achuo et al. 2006; Amtmann et al. 2008; Goel et al. 2008; Madgwick et al. 2011; Atkinson and Urwin 2012). The importance of different

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predisposing abiotic stress factors on plant–pathogen interactions has also been recently reviewed (Bostock et al. 2014).

The data from a number of individual stress studies have been analyzed using bioinformatics tools to find the common genes altered under biotic and abiotic stress conditions. For example, the response of thale cress (*Arabidopsis thaliana*, hereafter referred to as *Arabidopsis*) to a variety of abiotic and biotic stresses was studied by the comparison and cluster analysis of differentially expressed genes from publicly available microarray datasets (Ma and Bohnert 2007). Similarly, the gene expression profiles of chickpea plant under different abiotic (drought, cold, and high salinity) and biotic stress (*Ascochyta rabiei*; causal agent of blight in chickpea) conditions were compared (Mantri et al. 2010). Meta-analysis of transcriptomic data from rice (*Oryza sativa*) and *Arabidopsis* plants each exposed to independent drought and bacterial stresses revealed the commonality of 38.5 and 28.7% differentially expressed genes between two stress conditions in the respective plants (Shaik and Ramakrishna 2013, 2014). Yet, in another study, the molecular response of rice plants to multiple biotic and abiotic stress conditions was compared and genes responsive to both the stresses and to exclusively biotic stresses were identified (Narsai et al. 2013). Several other studies also support the existence of cross talk between the abiotic and biotic stress pathways (Narusaka et al. 2004; Fujita et al. 2006; Fraire-Velázquez et al. 2011). However, in all these studies, the plants were not concurrently exposed to biotic and abiotic stresses, but only the data from independently stressed plants were compared. Although the biotic and abiotic stress response pathways have common elements, plant-“tailored” responses to the actual concurrent abiotic and biotic stress cannot be predicted using the data from individual stress studies (Mittler 2006).

The physiological and molecular responses against concurrent abiotic and biotic stresses are beginning to be studied (Atkinson et al. 2013; Rasmussen et al. 2013; Bostock et al. 2014; Kissoudis et al. 2014; Prash and Sonnewald 2014). The available literature provides evidence that plants perceive concurrent stresses as a “new stress” leading to reprogramming of their responses. Gene expression studies in *Arabidopsis* plants exposed to concurrent stress conditions like cold and high light, salt and heat, salt and high light, heat and high light, heat and flagellin, and cold and flagellin also revealed that on an average 61% of the transcripts expressed during concurrent dual stresses were not observed in the single stress treatments (Rasmussen et al. 2013). Likewise, drought and concurrent nematode infection in *Arabidopsis* plants led to the induction of 50 unique genes (Atkinson et al. 2013).

Drought is one of the most important and frequently occurring abiotic factors and can potentially alter the end result of plant–pathogen interaction. Hence, this chapter is focused on the impact of drought stress on plant–pathogen relations and the different ways through which drought modulates the plant–pathogen (fungi, oomycete, bacteria, and virus) relations. We also speculate various aspects involved in the concurrent stress-responsive signaling network of plants by reviewing recent studies.

Table 10.1 A few examples of drought-mediated modulation of plant–pathogen interaction in plants

S. No.	Pathogen	Name of the disease	Host plant	Effect on plant–pathogen interaction	References
<i>Fungi</i>					
	<i>Thielaviopsis basicola</i>	Black root rot	Tobacco	Susceptibility decreased	Bateman 1961
	<i>Cephalosporium gramineum</i>	Stripe	Wheat		Bruehl 1968
	<i>Sclerotinia sclerotiorum</i>	White mold	<i>Nicotiana benthamiana</i>		Ramegowda et al. 2013
	<i>Sclerotinia</i> sp.	White mold	Soybean, sunflower, canola, peanut		Markell et al. 2008
	<i>Fusarium solani</i> f. sp. <i>pisi</i>	Root and stem rot	Sweet pea	Susceptibility increased	Krafs and Roberts 1969
	<i>Macrophomina phaseoli</i>	Charcoal rot	Soybean, sorghum, cotton		Mayek-Perez et al. 2002
	<i>Ucinula necator</i>	Powdery mildew	Grapes	Susceptibility increased	Hartman and Beale 1998
	<i>Penicillium</i> sp. and <i>Aspergillus</i> sp.	Seed decay	Wheat		Griffin 1966
	<i>Rhizoctonia</i> sp.	Stem canker	Potato	Susceptibility increased	Lootsma and Scholte 1997
	<i>Verticillium</i> sp.	Early dying	Potato		Markell et al. 2008
	<i>Drechslera tritici-repentis</i>	Tan spot	Wheat	Susceptibility increased	Janda et al. 2008 ^a
	<i>Ascochyta</i> sp.	<i>Ascochyta</i> blight	Pea, lentil, chickpea		Markell et al. 2008
<i>Oomycetes</i>					
	<i>Pythium</i> sp.	Root rot	Pea	Susceptibility decreased	Kerr 1964
	<i>Aphanomyces</i> sp.	Root rot	Sunflower		Markell et al. 2008
	<i>Plasmopara</i> sp.	Downy mildew	Sunflower	Susceptibility increased	Markell et al. 2008
	<i>Phytophthora</i> sp.	Root rots	Soybean, safflower, rhododendron, tomato		McDonald and Cahill 1999; Dumway 1977; Blaker and MacDonald 1981; Ristaino and Dumway 1989

Table 10.1 (continued)

S. No.	Pathogen	Name of the disease	Host plant	Effect on plant–pathogen interaction	References
<i>Virus</i>					
	<i>Pineapple mealybug wilt-associated virus-1</i>	Pineapple Mealybug Wilt	Pineapple	Susceptibility increased	Sether and Hu 2001
	<i>Maize dwarf mosaic virus</i>	Mosaic	Sweet corn		Olson et al. 1990
	<i>Turnip mosaic virus</i>	Growth retardation	<i>Arabidopsis</i>		Prasch and Sonnewald 2013
<i>Bacteria</i>					
	<i>Xylella fastidiosa</i>	Pierce's disease	Vine	Susceptibility increased	McElhone et al. 2001
	<i>Pseudomonas syringae pv. tomato</i> 1065	Bacterial speck disease	<i>Arabidopsis</i>		Mohr and Cahill 2003
	<i>Streptomyces scabies</i>	Common scab	Potato	Susceptibility decreased	Cook and Papendick 1972
	<i>Pseudomonas syringae pv. Tabaci</i>	Bacterial speck disease	<i>Nicotiana benthamiana</i>		Ramegowda et al. 2013

^a PEG-mediated osmotic stress

PEG Polyethylene glycol

10.2 Drought Modulates Plant–Pathogen Interaction

The net effect of concurrent drought and pathogen infection on plants depends on duration and intensity of the two stresses. Based on these factors, the combination of drought and pathogen infection can have two outcomes. In the first scenario, both the stresses when occurring concurrently can act in unison to hamper plant growth and development. For example, drought stress has been shown to aggravate many fungal (Mayek-Perez et al. 2002), bacterial (McElrone et al. 2001; Mohr and Cahill 2003), and viral (Olson et al. 1990; Prasch and Sonnewald 2013) infections in plants. On the contrary, in the second case, the drought stress has been shown to enhance the tolerance of the plants toward pathogens (Ramegowda et al. 2013; Achuo et al. 2006). The nature and outcome of plant–pathogen interaction under drought stress differs with the type of pathogens (fungi, oomycete, bacteria, and viruses) as they employ different strategies for infection. The different ways by which drought modulates plant’s interactions with these pathogens are discussed. Apart from the above-mentioned two scenarios, pathogens can enhance the resistance of plants to drought (Reusche et al. 2012; Xu et al. 2008). However, this aspect is not discussed in this chapter.

10.2.1 Plant–Fungal/Oomycete Pathogen Interactions During Drought Stress

The availability of moisture is crucial for the establishment of fungal/oomycete infections on plants (Agrios 2005). The effect of concurrent drought and fungal/oomycete pathogen infection on plant growth has been fairly investigated in the past (Table 10.1). Drought stress can affect the plant–pathogen interaction by increasing or decreasing plant’s propensity for infection. For soil-borne pathogens, the outcome of drought and fungal/oomycete pathogen interaction also depends on the effect of drought on the pathogen per se. So, under drought conditions, the degree of infection caused by a soil-borne fungi/oomycete on plants varies depending on whether the pathogen is favored by wet or dry soils (Cook and Papendick 1972). Drought can also influence the plant–pathogen interactions by inducing changes in the host physiology. The drought-induced changes in host physiology can be direct or indirect. The direct effects include the modulation of plant defense mechanisms against the pathogen. The indirect effects consist of changes in the nutritional status of plants brought about by drought stress.

10.2.1.1 Negative Effect of Concurrent Drought Stress and Fungal/Oomycete Infection on Plants

Fungal pathogens like *Sclerotium cepivorum* (causal agent of root rot in onions), *Streptomyces scabies* (causal agent of common scab in potato), *Fusarium* sp. (causal agent

of wilt in crop plants), and *Urocystis agropyri* (causal agent of smut on cereals), whose infections are known to be favored in dry soils, show more aggressive pathogenesis under drought conditions (Colhoun 1973). Edmunds (1964) observed that *Macrophomina phaseoli* (causal agent of charcoal stalk rot in sorghum) infection on sorghum plants under drought conditions caused more damage compared to nonstressed conditions. Drought conditions also enhanced the susceptibility of safflower and rhododendron to oomycete pathogen *Phytophthora* sp. (causal agent of root rot; Duniway 1977; Blaker and MacDonald 1981). Similarly, disease-resistant wheat plants were shown to become susceptible to *Fusarium roseum* f. sp. *cerealis* under drought stress (Papendick and Cook 1974). In all the above cases, the semidry conditions in soil apparently favored the fungal infection. The successful infection by fungal pathogens in dry soils can be possibly due to the fact that infection by these fungi depends on volatile root exudates that diffuse more rapidly through dry soil (Kerr 1964).

The altered physiology of plants due to drought stress can also favor the pathogen infection. For example, drought stress leads to nutrition deficiency in some plants and this secondary effect along with drought-induced physiological changes can aggravate the pathogen infection (Lawlor and Cornic 2002; Lawlor 2002). Drought stress-induced changes like the accumulation of osmolytes and nutrient leakage have been reported to lead to enriched nutrient supply for the pathogen. Drought stress-mediated exacerbation of infection under this category is best exemplified by pathogenesis of *Macrophomina phaseolina* (causal agent of charcoal rot in common bean) in common bean (Mayek-Perez et al. 2002). The stress-related amino acids like proline and asparagine have recently been shown to be utilized efficiently by *M. phaseolina* (Ijaz et al. 2013). The impact of drought was found to be more severe on a number of wilt and root-rot diseases. The wilt- and root-rot-causing fungi are known to interfere with the water relations of plants by colonizing the xylem vessels (Yadeta and Thomma 2013). Thus, the drought along with the pathogen imposes additional stress on plants and causes severe impact on plant growth.

10.2.1.2 Positive Effects of Concurrent Drought Stress and Fungal/Oomycete Pathogen Infection on Plants

The root-infecting oomycetes like *Pythium* sp. (causal agent of root rot in crops), *Aphanomyces* sp. (causal agent of root rot in sunflower and sugar beets), and *Plasmopara* sp. (causal agent of downy mildew) need adequate soil moisture for their survival in soil and for plant infection. Hence, the occurrence of downy mildew of sunflower and *Aphanomyces* root rot of sugar beets was less severe under drought stress conditions (Markell et al. 2008). Similar to soil-borne oomycete pathogens, less moisture in the atmosphere during drought is also shown to affect the pathogenesis of foliar fungal and oomycete pathogens. Many foliar pathogens such as those causing leaf spots are able to infect plants only when leaves are moist. Additionally, many foliar fungal pathogens produce spores that are dispersed by rain splash and germinated under high-humidity conditions. Pathogens that need rain to spread are unlikely to cause epidemics under drought conditions (Markell et al. 2008). The above-mentioned reports exemplify the effect of atmospheric water on the pathogen infection.

Drought acclimation in plants is known to combat some fungal pathogen infection during the combined stress. Ramegowda et al. (2013) showed that upon infection with *Sclerotinia sclerotiorum* (causal agent of white mold in beans), the well-watered *Nicotiana benthamiana* plants showed severe cell death, whereas the drought-acclimated plants exhibited reduced cell death. Thus, moderate drought was found to enhance plant's defense against pathogens by inducing expression of defense-related genes. The drought-mediated suppression of infection can also be attributed to the accumulation of abscisic acid (ABA). For example, drought-stressed tomato plants which showed the accumulation of ABA exhibited enhanced resistance against *Botrytis cinerea* (causal agent of grey mould in tomato; Achuo et al. 2006).

Taken together, drought can be favorable to either the pathogen or the host defense response. However, the consequences of concurrent drought on pathogen infection depend on the host, type of pathogen as well as the severity of drought stress. The ability of some fungi to interfere with the water relations of the plants and utilize the stress-induced molecules as nutrient source gives them an advantage under water stress conditions. On the other hand, plants can also fine-tune their defense responses under drought conditions to combat the pathogen infection. Thus, the modulation of plant–fungal/oomycete pathogen interaction during drought stress involves many facets, which can be interpreted by more systematic studies in this direction.

10.2.2 Plant–Bacterial Interaction During Drought Stress

Like fungi/oomycete, bacterial pathogens also depend on water for infection. The majority of the bacterial diseases are favored by the conditions of high humidity. A high water content in the apoplast facilitates bacterial growth. Incubation of plants at high relative humidity was shown to promote the growth of avirulent bacteria on plants (Freeman and Beattie 2009). Water-soaked lesions are typical characteristics of many bacterial leaf spot diseases and are known to be important for bacterial multiplication (Rudolph 1984). This reflects the importance of water in bacterial infections on plants. Thus, water scarcity should reduce bacterial infection on plants. This is true for the majority of cases. However, drought in few cases enhances plant's susceptibility to bacterial infections. Thus, drought can modulate plant–pathogen interactions for either the benefit of the host plant or the bacterium. A detailed discussion of both the scenarios is provided below.

10.2.2.1 Negative Effect of Concurrent Drought Stress and Bacterial Infection on Plants

Drought stress was found to enhance the susceptibility of grapevines to *Xylella fastidiosa* (causal agent of Pierce's disease; Thorne et al. 2006). *X. fastidiosa* has been reported to spread in plants by causing damage to intra-vessel pit membranes (Newman et al. 2003). The exposure of plants to drought conditions has also been

shown to lead to the disruption of pit membranes (Stiller and Sperry 2002). Drought stress, thus, facilitates the spread of *X. fastidiosa* in the plant. Drought-stressed *Arabidopsis* plants were found to be susceptible to an avirulent bacterial pathogen, *Pseudomonas syringae* pv. *tomato 1065* (Mohr and Cahill 2003). In this study, the susceptibility induced by drought was attributed to ABA. The exogenous ABA treatment is shown to render *Arabidopsis* plants susceptible to *P. syringae* infection by probably suppressing the salicylic acid (SA)-mediated defense responses (Mohr and Cahill 2003). Bacteria also modulate ABA-mediated responses for their infection and survival inside the plants. HopAM1, a type III effector of *P. syringae*, increases the virulence of a weak pathogen (*P. syringae* pv. *maculicola* M6 CE) under drought stress condition by enhancing the ABA-mediated suppression of basal defense responses in plants (Goel et al. 2008).

Drought stress has also been found to contribute to enhanced susceptibility of plants to vascular wilt causing bacteria. In combination with drought stress, *X. fastidiosa* (causal agent of Pierce's disease) increases the severity and progression of leaf scorch in *Parthenocissus quinquefolia* vine, reducing the total leaf area and number of nodes (McElrone et al. 2001). The dual stress caused increased reduction in stomatal conductance, leaf water potential, hydraulic conductivity, and xylem vessel length (McElrone et al. 2003) compared to individual stresses.

Another factor responsible for severe occurrence of disease under drought condition is reduction in the population of antagonistic bacteria in dry soils. For example, drought conditions are known to increase infection caused by *S. scabies* (causal agent of common scab in potatoes) in potatoes (Lapwood 1966). The decreased abundance of antagonistic bacteria in dry soil which otherwise limit lenticels infection by *S. scabies* leads to enhanced infection under drought conditions (Lewis 1970).

10.2.2.2 Positive Effect of Concurrent Drought Stress and Bacterial Infection on Plants

Moderate drought stress can enhance the tolerance of plants to bacterial infection by activating the stress response machinery. The acclimation of *N. benthamiana* plants to moderate drought stress (40–60% field capacity [FC] of soil) increased its tolerance to bacterial pathogen *P. syringae* pv. *tabaci* (causal agent of wildfire disease in tobacco) (Ramegowda et al. 2013). The degree of disease tolerance in drought-stressed plants was correlated to the extent of reactive oxygen species (ROS) accumulation (Ramegowda et al. 2013). The relation of increased ROS content to defense against bacterial infection was further substantiated by the application of methyl viologen (MV), a compound that provokes ROS production by disrupting electron transport chain in chloroplast. The MV-treated plants had high ROS and showed decreased bacterial growth (Ramegowda et al. 2013).

Drought stress can also help prevent pathogen multiplication and spread. At cellular level, water-deficit conditions help the plant to prevent bacterial survival and progression. In fact, *Arabidopsis* plants are known to promote effector-mediated signaling for localized desiccation of site of pathogen infection (Freeman and

Beattie 2009). Plants employ this effector-mediated localized desiccation possibly by one of the three ways, namely programmed cell death (PCD) of the vascular tissues, pectin-mediated occlusion of vessels, and reduction in aquaporin-mediated water exchange from xylem to surrounding tissues (Beattie 2011).

10.2.3 Plant–Viral Interaction During Drought Stress

The majority of the available reports on the effect of concurrent drought on viral infection suggest the negative impact of the concurrent stresses on plants (Olson et al. 1990; Clover et al. 1999; Sether and Hu 2001; Prasch and Sonnewald 2013). Drought stress has been shown to affect susceptibility of plants to viral infection. Moderate drought (0–15%) increases the susceptibility of bean plants to *tobacco mosaic virus* (TMV) by fourfold (Yarwood et al. 1955). Furthermore, the simultaneous infection of *Pineapple mealybug wilt-associated virus-1* (PMWaV-1) and drought stress in pineapple has been reported to cause more loss in fruit production than that caused by the individual stresses (Sether and Hu 2001). Similarly, the concurrent drought stress and *Maize dwarf mosaic virus* (MDMV) infection in sweet corn during vegetative and reproductive stages were found to additively reduce the growth and yield of plants (Olson et al. 1990). This may be due to the fact that viral infections under drought stress can subvert plants' metabolic machinery toward viral multiplication and stress responses. Recently, Prasch and Sonnewald (2013) studied the molecular responses of *Arabidopsis* plant subjected to concurrent *turnip mosaic virus* (TuMV) infection, heat, and drought stress. The concurrent drought and viral infection led to greater reduction in biomass. However, the TuMV level was not altered in the dually stressed plant (Prasch and Sonnewald 2013). The combined stress was found to alter the circadian rhythm of plant by increasing the expression of circadian clock-associated 1 (*CCA1*) gene that is known to regulate a wide array of genes including genes involved in photosynthesis. The combination of viral infection and drought stresses down-regulated the genes involved in photosynthesis, adenosine triphosphate (ATP) synthesis, glycolysis, and tricarboxylic acid (TCA) cycle. In contrast, the expression of genes involved in photorespiration, such as glycolate oxidase and glucose–glyoxylate aminotransferase, was up-regulated. This possibly resulted in reduction in biomass (Prasch and Sonnewald 2013). Thus, the concurrent drought and viral infection possibly force plant machinery to divert its energy toward defense responses, thereby leading to the down-regulation of photosynthesis and other primary metabolic pathway genes.

Drought has also been shown to negatively affect virus translocation in plants (Liu et al. 2009). For example, drought inhibits the systemic spread of *tomato spotted wilt virus* in tomato (Cordoba et al. 1991). Moreover, in the study of Yarwood et al. (1955), increased drought intensity was found to decrease the viral infection in bean leaves. This signifies that the intensity of drought has a role to play in deciding the outcome of plant–viral interactions. Unlike bacteria, fungus, and oomycete, virus does not require nutrients for its growth, so drought-driven alleviation of viral infection apparently occurs by some other mechanisms that are not yet known.

10.3 Plant–Pathogen Interactions During Drought Stress: Current Understanding of the Underlying Molecular Mechanisms

The signaling mechanisms involved in plant responses to biotic and abiotic stress conditions have been well elucidated. Various studies in this direction have led to the identification of a number of genes that are co-regulated under abiotic and biotic stress conditions. The occurrence of cross talk between signaling pathways of abiotic and biotic stresses is well known (Fujita et al. 2006; Tippmann et al. 2006; Fraire-Velázquez et al. 2011). A couple of reports on the molecular mechanisms of plant's resistance against concurrent drought–nematode and drought–viral infection (Atkinson et al. 2013; Prasch and Sonnewald 2013) revealed the occurrence of “shared” and “tailored” responses in plants exposed to the concurrent stresses. The shared response consists of genes commonly expressed in abiotic and biotic stress conditions. The tailored response, on the other hand, implies the genes activated/repressed exclusively in response to the concurrent stress conditions. The “shared response” can be largely understood from the molecular mechanisms of plant response under independent and concurrent stress conditions. However, the inferences drawn from the individual stress studies cannot be extrapolated to explain the tailored response of plants under concurrent stresses. In this section, we describe the molecular basis of plant responses to concurrent drought and pathogen stresses based on our understanding from independent and the combined stress studies (Fig. 10.1).

10.3.1 Clues from Studies on Independent Stresses

As already stated, the abiotic and biotic stress response machinery of plants shares some common elements (Fig. 10.1a). The various elements of abiotic and biotic stress signaling are known to interact with each other leading to a cross talk between the signaling components of the two stress response pathways. Among the common elements, the most important are ROS and Ca^{2+} . Independent exposure of plants to drought and pathogen stress leads to a rapid increase in the levels of Ca^{2+} and ROS in the cells (Takahashi et al. 2011; Miller et al. 2010). The further downstream components of the signaling cascades, namely calcium-dependent protein kinases (CDPKs) and mitogen-activated protein kinases (MAPKs), are also known to play a synergistic role in drought and pathogen stress response of plants. For example, SA-induced MAPK (SIPK) is known to be activated by both SA and osmotic stress (Mikolajczyk et al. 2000; Hoyos and Zhang 2000). However, the modulation of MAPK expression also confers antagonistic effects on different stress responses (Xiong and Yang 2003; Shi et al. 2011). Also, silencing of OsMAPK5 in rice leads to constitutive up-regulation of pathogenesis-related (PR) proteins and enhanced pathogen resistance. However, these plants were sensitive to salt, cold, and drought stress (Xiong and Yang 2003).

The response of plants to drought and pathogen infection is known to be largely regulated by phytohormones. The exogenous application of drought-responsive hormone, ABA, has been shown to increase the disease susceptibility in a number of studies (Thaler and Bostock 2004; Mohr and Cahill 2003; Audenaert et al. 2002; de Torres-Zabala et al. 2007). The ABA-deficient tomato (*sitiens* mutant) plants have been found to exhibit enhanced resistance to *B. cinerea* infection due to enhanced PR proteins and repression of SA response (Thaler and Bostock 2004; Audenaert et al. 2002). The enhanced resistance to pathogen infection in ABA-deficient mutants can be attributed to reduced cuticle thickness and enhanced H₂O₂ production in response to *B. cinerea* in tomato (Asselbergh et al. 2007) and altered cell wall composition in *Arabidopsis* (Sanchez-Vallet et al. 2012). Contrastingly, the role of ABA as a positive regulator of defense has also been reported (Mauch-Mani and Mauch 2005; Melotto et al. 2006; Ton et al. 2009). ABA is shown to regulate plant defense responses against pathogens through a number of ways like modifying callose deposition, promoting stomatal closure, and regulating the expression of defense genes. For example, ABA is necessary for β -aminobutyric acid (BABA)-induced callose deposition during defense against fungal pathogens (Ton and Mauch-Mani 2008). However, it blocks the callose deposition induced by bacterial infection (de Torres-Zabala et al. 2007). ABA activates stomatal closure that acts as a barrier against bacterial infection (Melotto et al. 2006). Moreover, transcriptome and meta-analyses of gene expression profiles of *Arabidopsis* plants infected with *Pythium irregulare* led to the identification of ABA-responsive element (ABRE) in the promoters of many of the defense genes (Adie et al. 2007; Wasilewska et al. 2008). Thus, ABA acts as a global switch regulating response toward biotic and abiotic stresses (Asselbergh 2008). However, the mechanism of action of ABA is still not completely deciphered. The identification of the molecular mechanisms involved in phytohormone-mediated cross talk between biotic and abiotic stress signaling needs to be done in order to elucidate the exact molecular mechanism by which different phytohormones modulate plant defense responses against different pathogens under drought conditions.

Together with the phytohormones, transcription factors (TF) like ABA-responsive element-binding protein (AREB), MYC, NAM//ATAF1/CUC2 (NAC), ethylene-responsive element-binding protein (EREB), WRKY, and coronatine insensitive 1 (COI1) are activated by pathogen challenge and drought stress (Atkinson et al. 2013). MYC2 has been found to be important in the interaction between the abiotic and biotic stress pathways. It is activated by ABA (Abe et al. 2003) and positively regulates jasmonic acid (JA)-induced defense genes, but represses the combined JA- and SA-mediated gene expression (Laurie-Berry et al. 2006; Pieterse et al. 2009). NAC and AP2/ERF TFs have also been associated with both abiotic and biotic stress signaling. NAC TFs like OsNAC6 (*O. sativa* NAC), tobacco stress-induced1 (TSI1), RD26, and botrytis-susceptible1 (BOS1) induce tolerance to both abiotic and biotic stresses, others like *A. thaliana* activating factor 1 (ATAF1) impart tolerance to either of the stresses (Mengiste et al. 2003). Apart from these, ribosome production factor 1 (RPF1), WRKY82, and WRKY85 have been shown to play roles in conferring stress tolerance to both biotic and abiotic stresses (Asselbergh et al. 2008;

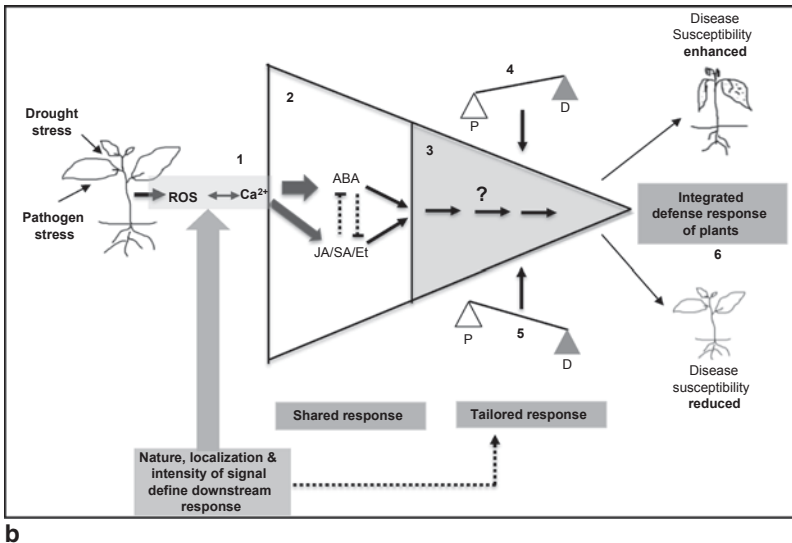
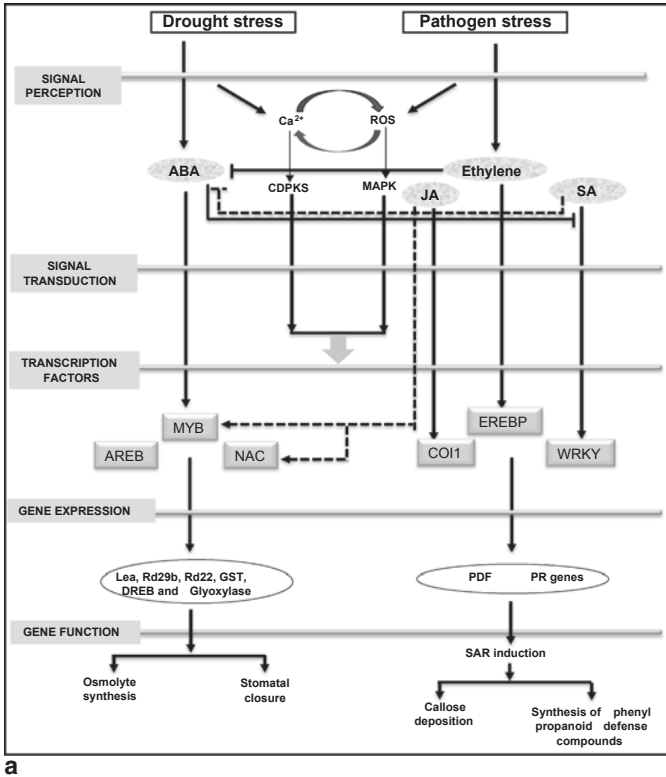


Fig. 10.1 Molecular understanding of the effect of concurrent drought on plant–pathogen interactions. **a** Schematic representation of cross talk between key players of plant defense response against concurrent drought and pathogen infection. The figure shows the signaling cascades and

Qiu and Yu 2009; Peng et al. 2011). Genes that confer tolerance to both biotic and abiotic stress can form a part of the shared response exhibited by plants under concurrent drought and pathogen infection. However, their function under concurrent stress conditions needs to be validated. The above-described independent single stress studies are not useful for understanding the tailored response. Clear understanding can be obtained only from combined stress studies.

10.3.2 Clues from Combined Stress Studies

A recent study by Atkinson et al. (2013) on concurrent drought and nematode infection revealed that in addition to the overlapping transcript changes, the combined stress treatment induced a set of genes that were not differentially regulated by either of the single stresses. This study thus points toward the activation of a tailored response which consists of unique program of gene expression in response to the combined stresses. The genes differentially expressed under combined stress included those involved in cell wall modification, carbohydrate metabolism, redox regulation, and transcriptional regulation. A characteristic down-regulation of disease-resistance genes (e.g., azelaic acid induced 1; *AZII*) was also observed under concurrent stress treatment. This may be due the suppression of SA-mediated signaling by ABA. In order to understand the effect of concurrent stress on plants, Prasch and Sonnewald (2013) subjected *Arabidopsis* plants to concurrent drought, heat stress, and viral infection. The analyses of the microarray profiles of the stressed plants revealed the expression of 11 genes under all the stress (single, double, and triple stress combinations) conditions. These common genes are the ones encoding transcription factors like Rap2.9 and G-box binding factor 3 (GBF3), a transmembrane receptor and a lipase. The transcript analysis also showed 23 stress-specific genes that were differentially expressed in the triple stress condition. This consisted

a few representative proteins. The *dotted arrows* indicate the induction or suppression of abiotic stress response elements by the biotic stress response elements, whereas the *bold arrows* indicate the modulation by the ABA on biotic stress response elements. **b** Schematic representation of the hypothetical response of plants to concurrent stress conditions. The first line of defense in plants exposed to concurrent drought and pathogen infection presumably consists of Ca²⁺-dependent ROS production (1). The nature, localization, and intensity of ROS and Ca signals can define the downstream events. The overall response of plants to concurrent stress is a combination of shared (2) and tailored responses (3) and this defines increased or decreased plant susceptibility to pathogen infections under drought stress. The question mark signifies the unexplored events of the tailored mechanism. The response (6) of the plants to the concurrent stress conditions depends on the intensity of the two stresses (4/5) as well as the nature of host and plant. The *small triangles* represent the intensity of drought stress (*D*) and the pathogen load (*P*). *ROS* reactive oxygen species, *ABA* abscisic acid, *JA* jasmonic acid, *SA* salicylic acid, *Et* ethylene, *SAR* systemic acquired resistance, *PR* genes pathogen-related genes, *CDPKs* calcium-dependent protein kinases, *MAPK* mitogen-activated protein kinase, *AREB*, ABA-responsive element-binding protein, *NAC NAM//ATAF1/CUC2*, *COI1* coronatine insensitive 1, *MYB myeloblastosis*, *EREBP ethylene responsive element binding protein*, *WRKY* stands for the first four amino acids (tryptophan [W], arginine [R], lysine [K] and tyrosine [Y]) of the heptapeptide WRKYGQK, which is the hall mark of WRKY proteins, transcription factors

of three transcription factors including DREB2A, and two zinc finger proteins together with other stress-responsive proteins like cold-regulated 47, ABI5 binding protein (AFP1), a pentatricopeptide repeat-containing protein, and a universal stress protein family protein. The gene list also shows the presence of positive and negative regulators of a particular pathway. For example, AFP1 is a negative regulator of ABA, whereas *Arabidopsis Toxicos en Levadura* (ATL4) is a positive regulator. Major factors that can decide responses under concurrent stress conditions include the severity and complexity of the stresses imposed. For example, in the above study, the number of significantly regulated genes corresponding to drought alone, virus alone, and stress combinations varied and corresponded to 518, 682, and 1744 respectively (Prasch and Sonnewald 2013).

On the basis of both the cross talk and concurrent stress studies, we hypothesize a mechanism of plants response to concurrent stress conditions (Fig. 10.1b). Like the individual stress conditions, under concurrent stress conditions, the Ca^{2+} -dependent ROS production forms the first line of defense. We hypothesize a preferential role for ABA in governing the concurrent stress responses than the other hormones. However, this certainly needs to be validated and there may be exceptions. The regulation mediated by JA, SA, and ET, however, also seems to be important and this can be a key feature in the differentiation of response of plants against various pathogens (necrotrophic/birotrophic).

10.4 Conclusions and Future Perspectives

The global climate change is leading to the emergence of new and complex stress combinations and the impact of these stress combinations on crop productivity is evolving as a major concern. Considering the impact of abiotic and biotic stress conditions on crop yield, enormous efforts have been made over the past three decades, to understand the independent effect of these stress conditions on plants. The concurrent drought and pathogen infection can either increase the susceptibility of plants to the pathogen or it can suppress the pathogen infection depending on various factors like type of the pathogen, host species, and severity of drought stress. For example, drought aggravates the diseases caused by wilt/rot-causing pathogens. On the other hand, drought acclimation has been shown to confer resistance to pathogen infection in some cases. Drought environment can also affect the pathogen per se. Although a number of reports reflect on the physiological effect of concurrent drought stress on plant–pathogen interactions (Table 10.1), the understanding of molecular mechanism imparting combined stress tolerance in plants is in its infancy. As is evident from the two reports on molecular responses of plants to concurrent stresses, the combat mechanisms of plants to concurrent abiotic and biotic stresses are characterized by a combination of shared and tailored responses. Whereas the shared responses are nearly well deciphered, the molecular events leading to and explaining the tailored responses are yet to be understood. The detailed analysis of the plant responses under concurrent drought and pathogen infection is needed to

unravel the intricate regulatory network involved in plant–pathogen interactions under such conditions. The candidate genes differentially expressed under the concurrent stress conditions can be the potential targets for the manipulation in order to develop plants with improved resistance under concurrent drought–pathogen infection. These genes can also serve as important markers for selecting the concurrent stress-resistant crops.

However, the experimental evaluation of the effects of the combined drought and pathogen stress on plants is a challenging task owing to the difficulties in accurate concurrent stress imposition on plants. For example, compared to imposition of heat stress, coinciding drought stress conditions that occur gradually in soil-drying experiments with pathogen infection is difficult. The other hurdle of combined stress studies is the optimization of inoculum concentration and drought intensity that would not be lethal to the plant when imposed concurrently. These two factors are important deciding factors of the outcome of combined stresses. Owing to these complexities, physiological, molecular, and biochemical changes in plants exclusively exposed to concurrent stress conditions are yet to be identified. We need to develop standardized protocols for the imposition of drought stress and concurrent pathogen infection in order to assess the impact of drought on plant–pathogen interaction.

Effective categorization of the pathogens on the basis of their dependence on water for infection needs to be done. The pathogen which is more infective under drought conditions can be a possible threat to crops in the areas prone to drought stresses. Thus, understanding the effect of drought on pathogen can help in the prediction of emerging diseases under drought condition. This would be particularly helpful in case of predicting the effect of pathogens causing wilts and rot on plants under drought conditions. Overall, unraveling of physiological and molecular basis of plant responses to concurrent drought and pathogen infection will be a crucial step forward for the development of stress-resistant crops that can survive under the field conditions.

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