

# Chapter 1

## RETRACTED CHAPTER: Impact of Biotic and Abiotic Stresses on Plants, and Their Responses



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### 1.1 Introduction

In the present era of drastic climate changes such as global warming, erratic rainfall and depletion of arable land and water resources, plants encounter a diverse range of climate-induced biotic and abiotic stresses (Atkinson et al. 2013; Narsai et al. 2013; Prasad and Sonnewald 2013; Suzuki et al. 2014; Mahalingam 2015; Pandey et al. 2015; Ramegowda and Senthil-Kumar 2015). Stress may be defined as an adverse condition for plant growth and development, caused by either environmental or biological factors, or both. Under natural conditions, concurrent occurrence of two or more different types of stresses—such as drought and salinity, drought and heat are more detrimental to global crop production. Concurrent abiotic stresses are more destructive in disrupting plant metabolism and reducing yield than the same stresses occurring separately at different growth stages. Co-occurrence of drought and heat stress or drought and salinity stress during summer are examples of combined abiotic stresses. Biotic stresses also play a central role in regulating outbreaks of pests, pathogens, insects and weeds (Coakley et al. 1999; Scherm and Coakley 2003; McDonald et al. 2009; Ziska et al. 2010; Peters et al. 2014). These

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stresses also influence plant–pest interactions by altering the physiological and adaptive responses of plants (Schermer and Coakley 2003). Because of their enhanced water use efficiency, weeds outcompete crops under abiotic stress (Patterson 1995; Ziska et al. 2010; Valerio et al. 2013). Abiotic stress has a massive impact on plant growth; consequently, it is responsible for huge losses in yield. The consequential growth reductions can reach up to 50% in most plant species (Wang et al. 2003). Daryanto et al. (2016) reported that the yield of maize is reduced by up to 40% and 21% reduction in the yield of wheat is also noted with a 40% water reduction. The cowpea yield is also decreased, and the extent of the reduction varies between 34% and 68%, depending on the developmental stage and drought stress (Farooq et al. 2017). In case of cowpea, which is an important crop in Africa, and source of food to the millions of farmers, the yield reduction can vary to a great extent depending on the developmental stage and the severity of drought stress. In 2002 it was estimated that soil salinity alone caused losses of more than US\$11 billion annually and affected about 10% of the world's arable land, greatly influencing global food production and is considered as the main stress to influence the global crop productivity (Tanji 2002; Ahmad et al. 2019).

In addition to several combinations of abiotic stresses, plants also encounter multiple biotic stresses, commonly through pathogen or herbivore attack simultaneously or sequentially. Biotic stress is an additional threat and puts a great pressure on plant productivity (Mordecai 2011; Maron and Crone 2006; Maron and Kauffman 2006; Strauss and Zangerl 2002; Brown and Hovmoller 2002). A common case of combined biotic stresses is simultaneous attacks by bacterial and fungal pathogens on plants. For example, combined attacks by the bacterium *Xanthomonas arboricola* and fungal pathogens such as *Fusicarium* spp., *Alternaria* spp., *Cladosporium* spp., *Colletotrichum* spp., or *Phytophthora* spp. cause brown apical necrosis of *Juglans regia* (Belisario et al. 2002). Plants are severely damaged by concurrent fungal, bacterial and viral infections, which lead to more severe disease symptoms than separate infections with these pathogens.

The impact of concurrent stresses on plants is determined by the types of interactions between various kinds of stress factors (Prasch and Sonnewald 2013; Choudhary et al. 2016). Therefore, the impact of concurrent stresses can be evaluated by understanding the underlying mechanisms of such interactions between various stress factors. Mittler (2006) and Suzuki et al. (2014) showed that the interactions between various stress factors can have either positive or negative effects on plant growth. Plants act in response to concurrent stresses by inducing the expression of diverse set of genes whose products such as secondary metabolites (phenolics) play critical roles in alleviating a broad range of stresses (Niakoo et al. 2019). Plants alter their responses to concurrent stress factors and reveal numerous distinctive responses, along with other general responses. Improved plant tolerance to concurrent stresses involves recognition of physiomorphological traits that are affected by these concurrent stresses. Bearing in mind the global occurrence and the influence of concurrent stresses on agricultural productivity, this chapter attempts to provide

insights into the current understanding of stress combinations and improvement of physiomorphological traits to mitigate the effects of concurrent stresses. The significance of studies assessing the impact of concurrent stresses on plant growth is documented and additionally, some important and common examples of different, naturally occurring combinations of stresses are described.

### 1.1.1 Stress Combinations Occurring in Nature

Stresses are categorized as single, multiple individual, concurrent, and repetitive stresses, depending on the number of interacting factors. A single stress involves only one stress factor, whereas multiple individual stresses represent two or more stresses occurring without any overlap and concurrent stresses represent two or more stresses occurring simultaneously with a little overlap. In repetitive stresses, plants face a single stress or multiple stresses followed by recovery periods, which may be of shorter or longer duration. Several spells of hot days, or multiple events of drought and heat stress may occur at different developmental stages of plants. The interactions between various stress factors may either enhance the tolerance capacity or predispose the plant toward a wide range of stresses. For example, drought facilitates the growth of *Macrophomina phaseolina* in the roots of *Sorghum bicolor* and results in a severe reduction in its productivity (Goudarzi et al. 2011). Likewise, the productivity of *Vitis vinifera* is reduced by the occurrence of concurrent drought and cold stress in North China (Su et al. 2015). Plants growing in hot and dry regions such as arid and semi-arid areas are often challenged by the onset of concurrent salinity and heat stress. In the Mediterranean region cold and light stresses are most prevalent and affect the growth and development of plants (Loreto and Bonghi 1989). The frost durability of *Triticum aestivum* and the production of *Cicer arietinum* are significantly reduced by concurrent cold and ozone stresses and by concurrent salinity and ozone stresses, respectively (Barnes and Davison 1988; Welfare et al. 2002). Likewise, the combination of salinity and ozone stress plays a critical role in decreasing yield of chickpea and rice cultivars. As in the case of diverse concurrent abiotic stresses, plants are faced with the challenge of concurrent biotic stresses and are damaged more severely by the combinations of fungal and bacterial infections than by infections with these pathogens individually. Parashah and Venturi (2015) have documented the incidence of different concurrent biotic stresses and their impacts on plant growth and yield. Plants have evolved a perception network that enables them to perceive both biotic and abiotic stressors simultaneously and help them to mitigate the devastating impact of stresses. The effects of abiotic stresses such as drought or salinity may lead to either susceptibility or resistance of plants to biotic stresses such as powdery mildew, rust, and wilt depending on the timing and severity drought and/or salinity stress.

### 1.1.2 Impact of Stress Combinations on Plant Physiology and Development

The nature of the interactions between the stressors and the duration of stress exposure can lead to a series of effects on the plant growth, development overall yield. The nature of the interactions between stressors also determines the extent of the influence on crop productivity. For instance, abiotic–abiotic stresses such as concurrent drought and heat stress can lead to a greater reduction in the crop yield due to increased soil water evaporation. Mittler (2006) noted that the synergistic effects of drought and heat stress on the physiological aspects of plant growth lead to substantial reduction in crop yield and Stuart et al. (1984) reported that weeds outcompete crops because of their efficient water use ability during concurrent drought and heat stress. These concurrent stresses cause substantial drop in the leaf water potential and transpiration rate, which eventually result in increased leaf and canopy temperature particularly in tropical and subtropical environments (Turner et al. 2001; Simoes-Araujo et al. 2003). Several workers have reported that concurrent stress induced increase in the transpiration rate affects vital physiological processes in plants. Drought and heat stress greatly impact nutrient relations, consequently retarding growth by limiting the nutrient mobility through diffusion, and also lead to reductions in the mass, number and growth of roots (Barber 1995; Wahid et al. 2007; Huang et al. 2012). Drought and heat stress alter photopigments and damage thylakoid membranes, usually leading to either reduced chlorophyll biosynthesis and increased chlorophyll degradation or combined effects of both processes (Anjum et al. 2011; Dutta et al. 2009). The damage due to these concurrent stresses affects light reactions occurring in the thylakoid lumen and light-dependent chemical reactions taking place in the stroma. Camejo et al. (2005) reported that photosystem II is very sensitive to concurrent stresses, and its activity is significantly altered or even reduced to zero under severe heat stress. In the event of concurrent abiotic–biotic stresses such as heat and pathogen stress, heat stress promotes the growth of pathogens and leads to occurrence of a wide range of bacterial and fungal diseases such as wilt in tomato (caused by *Ralstonia solanacearum*), seedling blight and bacterial fruit blotch of cucurbits (caused by *Acidovorax avenae*), and panicle blight in rice (caused by *Burkholderia glumae*) (Kudela 2009). Ladanyi and Horvath (2010) reported that heat stress negatively influences the growth and development of plants but promotes pathogen growth and reproduction. In addition to the promotive effects on pathogen growth, heat stress favors the growth of various vectors, thereby facilitating the occurrence of vector borne diseases. Another example of concurrent biotic–abiotic stresses is salinity and pathogen stress. Salinity influences the virulence of pathogens, the physiology of plants and the activity of microbes in the soil (Triky-Dotan et al. 2005). Daami-Remadi et al. (2009) reported that salinity causes more sporulation in fungi and leads to severe *Fusarium* wilt in tomato.

Concurrent abiotic–abiotic or abiotic–biotic stresses do not necessarily affect plant growth and development negatively, as one stress may enhance plant tolerance to the other stress. Some concurrent stresses counteract the effects of one

another and eventually result in a net neutral or positive effect on plant growth; therefore, the yield is not always reduced. The yield of *Medicago truncatula* (alfalfa) was improved under concurrent drought and ozone stress as compared with individual drought and ozone stress (Puckette et al. 2007). The improved yield was attributed to enhanced tolerance of the alfalfa plants towards this stress combination. Similarly, concurrent salt and heat stresses led to an improved yield of *Solanum lycopersicum* in comparison with individual salt and heat stresses, and attributed this increase in yield to the improved tolerance of tomato plants towards concurrent salt and heat stresses (Rivero et al. 2014).

### 1.1.3 Complex Interactions in Stress Combinations

Unlike simple interactions in the aforementioned stress combinations, some stress combinations interact in a complex manner and have variable effects on plants. Examples are the effects of concurrent heat–pathogen and concurrent drought–pathogen stress combinations on *T. aestivum* and *Avena sativa* (oats). Coakley et al. (1999) reported that exposure of *T. aestivum* and *A. sativa* to heat stress facilitates growth and reproduction of *Puccinia* spp., thereby increasing their susceptibility to more severe infection. However, in *Cynodon dactylon* (Bermuda grass) the same stress enhances tolerance to a wide range of rust diseases. Heat–pathogen and drought–pathogen interactions are considered agroeconomically important stress combinations. Pautasso et al. (2012) and Garrett et al. (2006) reviewed the influences of concurrent heat and pathogen interactions on plants. Plant interactions with concurrent drought and pathogen stress have been well investigated in cases of abiotic and biotic stress combinations (Carter et al. 2009; Király et al. 2008; Mayek-Perez et al. 2002; McElroy et al. 2003; Ramegowda et al. 2013; Sharma et al. 2007; Wang et al. 2009; Xu et al. 2008). Here we emphasize the effects of abiotic and biotic stress combinations on plants, with special reference to drought and pathogen stress combinations.

## 1.2 Potential Traits for Genotype Screening for Combined Drought and Pathogen Stress Tolerance

### 1.2.1 Root System Architecture

The spatial configuration of the root system is referred to as the root system architecture (RSA). The genetic control of the RSA and its relationship to increased productivity under stress is well documented in a wide range of crops, especially cereals. Roots play vital roles in crop production by facilitating water and nutrient uptake, forming symbiotic associations with fungi and bacteria, providing

anchorage and serving as storage organs. Additionally, they serve as the main interface for interactions between the plants and various stress factors, and they play a vital role in mitigating the devastating impacts of stress on plant growth and development. The types of interactions that occur between roots and stress factors are determined by the organization and structure of the roots such as their length and density. Resistance to drought stress in rice varieties is linked to increased root length density (RLD) and a wide root diameter. Allah et al. (2010) reported that drought-resistant rice varieties had a greater RLD, which promoted access to the moisture available in the deeper layers of the soil. Under drought stress, maize with a greater RLD and fewer lateral roots showed a higher photosynthetic rate, a more favorable plant water status and greater stomatal conduction than maize with a lesser RLD and more lateral roots. Zhan et al. (2015) reported that the presence of fewer but longer lateral roots led to good use of water available in the deeper layers of the soil by virtue of enhanced rooting, thereby helping the plant to perform better under drought stress (Lynch et al. 2014). The RSA also plays a critical role in reducing pathogen infection in plants. Higginbotham et al. (2004) reported that *T. aestivum* lines with increased root length were less vulnerable to fungal infection with *Pythium debaryanum* and *Pythium ultimum*. Berta et al. (2005) reported that the fungal pathogen *Rhizoctonia solani* decreased root length, root branching and root tips which eventually impaired water absorption from deeper layers of the soil. Hence, it can be concluded that pathogen infection could be reduced to a great extent by increasing the RLD. The RSA plays a key role in crop plant's responses to drought stress and pathogen attack; however, drought and pathogen stress often occur concurrently in field conditions, which leads to greater damage to plants due to complete disruption of the RSA. For instance, in a study of chickpea plants exposed to concurrent drought and infection with the pathogen *Ralstonia solanacearum*, plants that faced progressive drought with 2 and 4 days of *R. solanacearum* infection were categorized as experiencing short-duration (SD) and long-duration (LD) stress stresses, respectively. The study revealed that SD combined stress reduced the growth and reproduction of the pathogen, but there was no significant change in LD combined stress (Sinha et al. 2017). Dryden and Van Alfen (1984) reported stunted growth of *Phaseolus vulgaris* under concurrent stresses caused by drought and the pathogen *Fusarium solani*. The reduced growth was attributed to root rot caused by the pathogen, thereby limiting acquisition of water from deeper layers of the soil. Concurrent drought and pathogen stress are often reported to decrease plant size, leaf area, hydraulic conductance and photosynthetic and transpiration rates (Pennypacker et al. 1991; Abd El-Rahim et al. 1998; Choi et al. 2013).

The timing of pathogen attacks and the onset of drought affect plant growth in different ways, as seen in *S. lycopersicum* infected with *Phytophthora parasitica*. A pathogen attack during drought stress resulted in greater damage as evidenced by decreased root numbers and root mass, with a greater proportion of brown roots and lower fresh weight than those seen with a pathogen attack followed by drought stress. Schroth and Hildebrand (1964) and Duniway (1977) also reported that root rot disease is more severe in plants exposed to concurrent drought and pathogen

stress. They attributed the severity of infection to drought-induced increased release of root exudates such as alanine, proline, pentose, and glucose, which serve as nutrients for the growth of soilborne pathogens. Apart from increased exudate release, pathogens also induce changes in the composition of root exudates, and this has been reported in tomato roots infected with *Fusarium oxysporum*. The pathogen attack induced greater release of succinic acid and restricted the release of citric acid, whereas in uninfected plants, such a trend in the release of exudates was not found (Kamilova et al. 2006).

Several researchers have reported contradictory findings of no correlation between drought and the severity of pathogen infection. Balota et al. (2005) found that *Gaeumannomyces graminis* infection in *Triticum* had similar effects under low and severe drought stresses. Likewise, infection of *T. aestivum* cultivars with *Pythium irregulare* and *R. solani* did not result in any change in root lesions under drought stress versus well-watered conditions (Aldahadha 2012). The RLD gets affected and that impairs water acquisition under combined drought and pathogen stress. The RLD is high in plants that show tolerance to concurrent drought and pathogen stress. Taking the vital role of the RLD into consideration, these traits offer a basis for screening for varieties with tolerance to combined drought and pathogen stress.

Modern genetic tools have identified quantitative trait loci (QTLs) linked to the RSA under drought stress (Comas et al. 2013). For instance, one QTL known as root-abscisic acid 1 (ABA1) is linked to root branching and root mass (Giuliani et al. 2005). While working on *Arabidopsis thaliana*, Fitz Gerald et al. (2006) and Xiong et al. (2006) reported another QTL that was associated with abscisic acid-stimulated inhibition of lateral root growth. Therefore, to accomplish the development of drought-resistant and pathogen-resistant plants, a broader study is needed to screen QTLs linked to effective and efficient RSA.

## 1.2.2 Leaf Pubescence

Under drought or normal conditions the transpiration rate plays a central role in the plant response to a stress stimulus. The traits that affect the rate of transpiration include leaf characteristics such as the leaf area, root-to-leaf ratio, leaf orientation, leaf shape, leaf thickness, and distribution of stomata. Among these, the important factors are the leaf surface characteristics (pubescence/glabrousness). The presence and pattern of hairs (trichomes) on the leaf surface and their density are controlled by both the genotype and the habitat of the plants. Trichomes are modified epidermal cells, which may be branched or unbranched, and glandular or nonglandular, depending on the plant species. Plants show wide variations in the density and pattern of trichomes as a response to mitigate the impacts of combined drought and pathogen stress (Ehleringer et al. 1976; Wagner 1991; Wagner et al. 2004). The trichomes facilitate foliar absorption of water and play a vital role in maintaining leaf hydration in plants found in semiarid climates. In *Arabidopsis* a drought tolerance

mutant named cap binding protein 20 (*cbp20*) revealed more trichomes and lower stomatal conductance than control plants (Papp et al. 2004; Jäger et al. 2011). Research on *Phlomis fruticosa* (Jerusalem sage) and *Hedera helix* (ivy) exposed to drought stress revealed that they maintain a low water potential by absorbing dew droplets via their trichomes, unlike plants without trichomes (Grammatikopoulos and Manetas 1994). Additionally, the photosynthetic rate of pubescent leaves was greater than that of glabrous leaves under drought conditions (Grammatikopoulos and Manetas 1994). Roy et al. (1999) reported that *Sinapis arvensis* (wild mustard) subjected to drought stress produced more trichomes than unstressed plants.

Lai et al. (2000) reported that glandular trichomes also resist the spread of bacterial infection by releasing oxidative enzymes, as is evident in *Solanum tuberosum* infected with *Phytophthora infestans*. Furthermore, trichomes reduce the relative humidity of the leaf surface, thereby making the conditions unfavorable for fungal spore germination (Lai et al. 2000). Secretion of T-phyllolpanins from the glandular trichomes of tobacco inhibited the growth and reproduction of *Peronospora tabacina* (the causal agent of blue mold disease) in comparison with mock-inoculated plants (Kroumova et al. 2007; Nguyen et al. 2016). It was concluded that trichomes can also prevent the spread of infection by release of antifungal components. Armstrong-Cho and Gossen (2005) reported that trichome exudates in chickpea are capable of preventing the spread of infection with *Ascochyta rabiei* (the causal agent of ascochyta blight). The inhibition of the growth and reproduction of *A. rabiei* was found to be exudate concentration dependent, as a lower concentration promoted the infection. The number of nonglandular trichomes was found to be increased in *Hordeum vulgare* exposed to concurrent drought and pathogen stress, in comparison with control plants (Liu and Liu 2016). Furthermore, it can be concluded that concurrent drought and pathogen stress tolerance is directly correlated with the number and kind of trichomes present all over the leaf surface. Ehleringer et al. (1976) stated that both glandular and nonglandular trichomes release antimicrobial components, which thereby serve as the first line of defense against pathogens. Monier and Lindow (2003) reported contradictory findings and reported that trichomes promoted the growth and reproduction of *Pseudomonas syringae*. They attributed this to the retention of water by the trichomes and suggested that exudates released from the broken cuticle at the base of the trichomes might favor microbial growth. Calo et al. (2006) reported that in *A. thaliana*, a mutant designated as *gll* (*GLABROUS1*) had lower trichome density and increased resistance to *Botrytis cinerea*, whereas another mutant designated as *try* (*TRYPTYCHON*) had higher trichome density and decreased resistance.

Further studies need to be undertaken to fully understand the role of trichomes in pathogen infection. Under concurrent drought and pathogen stress, the roles of glandular trichomes and their exudates in cases where trichomes enhance pathogen growth need to be studied. Gene-mapping studies have screened and isolated leaf pubescence-linked QTLs in many plants, including *Gossypium hirsutum* and *A. thaliana* (Lacape and Nguyen 2005; Bloomer et al. 2014). It can be assumed that increased numbers of trichomes play a critical role in enhancing the tolerance to concurrent drought and pathogen stress, and trichomes can be considered a



potential morphophysiological trait conferring tolerance to this stress combination. Isolation of QTLs that govern the number, density, and antimicrobial exudates of trichomes can enable plant breeders to create varieties with better tolerance to concurrent abiotic–biotic stresses. Moreover, it is useful to explore the genes and biochemical pathways that regulate the density and secretions of trichomes, which can be suitably modified to confer tolerance to combined stresses.

### 1.2.3 Leaf Water Potential and Leaf Turgidity

Under concurrent drought and pathogen stress, plants reveal wide variation in their leaf water potential and leaf turgidity which could be attributable to increases in hydraulic resistance and cell turgor loss (Paul and Ayres 1984; Yan et al. 2017). An alteration in the leaf water potential is directly correlated with soil moisture and is also influenced by pathogen stress, which can disrupt or even degenerate the plant's vascular system. Concurrent drought and pathogen stress negatively affect the traits that play a role in maintenance of the leaf water potential and leaf turgidity—for instance, stomatal closure in response to drought stress reported by several workers. Some pathogens may decrease the plant water content even under sufficient soil moisture conditions, as seen in *P. vulgaris* infected with *Uromyces phaseoli* (the causal agent of leaf rust), which releases toxins that inhibit stomatal closure and lead to increased water loss. This further reduces the leaf water potential and leaf turgidity of plants under drought stress (Laniway and Durbin 1971), which indicates that pathogen attack can influence drought tolerance. McElrone et al. (2003) reported that the leaf water potential and leaf turgidity can be considered a physiological parameter for evaluation of the plant water status under concurrent stresses. They investigated the influences of separate and concurrent stresses caused by drought and the pathogen *Xylella fastidiosa* (the causal agent of bacterial leaf scorch) on the leaf water potential of Virginia creeper (*Parthenocissus quinquefolia*). A low water potential and less leaf turgidity was found in plants exposed to these stresses concurrently, causing more severe scorch symptoms than those seen in plants that faced separate drought and pathogen stress. The decreased hydraulic conductance and increased embolism in response to infection could be attributable to a low water potential less leaf turgidity. Likewise, Burman and Lodha (1996), while studying the impacts of concurrent drought and *M. phaseolina* stress in cowpea (*Vigna unguiculata*), found drastic decreases in the leaf water potential, leaf turgidity, and transpiration rate under combined stress. Similarly, Paul and Ayres (1984) reported a decreased leaf water potential in *Senecio vulgaris* (groundsel) subjected to concurrent drought and infection with *Puccinia lagenophorae* (the causal agent of rust). They attributed the reduced leaf water potential to cuticle breakdown stimulated by the infection and its subsequent sporulation. Similarly, Mayek-Perez et al. (2002) reported a high transpiration rate, reduced water potential and low stomatal resistance in *P. vulgaris* subjected to simultaneous drought and *M. phaseolina* stress. Drought stress caused the plants to synthesize carbohydrates,

which promoted the growth and reproduction of *M. phaseolina*. Moreover, it was found that resistant varieties maintained a higher leaf water potential than susceptible varieties. Contradictory results were reported by Pennypacker et al. (1991) in alfalfa exposed to concurrent drought and *Verticillium albo-atrum* (the causal agent of wilt stress), revealing a high leaf water potential than that seen in drought-stressed plants. Hence, it can be concluded that the impacts of concurrent drought and pathogen stress may have different influences on the leaf water potential and leaf turgidity depending on the type of plant and the type of pathogen.

The QTLs that govern the regulation of the leaf water potential have been identified in several plants. Bernier et al. (2009) and Shamsudin et al. (2016) identified a QTL in rice plants, designated as *qDTY12.1*, that regulates the leaf water potential under drought stress. Identification of QTLs associated with the xylem diameter and xylem pit anatomy can be used to explore molecular pathways and provide greater understanding of the mechanisms that confer tolerance to concurrent drought and pathogen infection. Pouzoulet et al. (2014) reported that xylem vessel dimensions play a vital role in conferring tolerance to vascular pathogen infection. *V. vinifera* genotypes with a smaller xylem diameter were found to be less affected by fungal vascular wilt pathogens. Hence, the plant water potential can be used as a potential morphophysiological trait to screen plants for resistance to concurrent drought and pathogen infection.

#### 1.2.4 Cuticular Wax and Composition of Cuticular Layer

Cuticular wax and composition of cuticular layer is of paramount importance in conferring tolerance to concurrent drought stress and pathogen invasion. Kim et al. (2007) reported that *Sesamum indicum* (sesame) exposed to drought stress produced higher-density cuticular wax than unstressed plants. In response to these combined stresses, plants show wide variations in cuticular wax composition (Marcell and Beattie 2002; Foster et al. 2009). The cuticular layer serves as a physical barrier to pathogen infection, as it is hydrophobic in nature and lacks any moisture content (Martin 1964). Several workers have documented the vital role of the cuticular layer in conferring resistance to drought and pathogen stress. Kosma et al. (2009) reported that exposure of *Arabidopsis* plants to drought stress induced an increase in the concentration of the cuticular wax components, resulting in increased wax deposition in stressed plants. Hameed et al. (2002) reported that the thickness of the cuticular layer is determined by drought stress, and it can also determine the resistance to drought stress, as observed in drought-resistant *T. aestivum* plants, which possessed a thicker cuticle than susceptible plants. Marcell and Beattie (2002) subjected control and glossy mutants of *Zea mays* (*gl4*) to *Clavibacter michiganensis* (the causal agent of leaf blight and Goss's wilt in maize). They found that control plants were less affected, with fewer bacterial colonies present on their leaf surfaces than on those of the *gl4* mutants, which exhibited a thin cuticular layer due to a modified wax biosynthetic pathway. The greater sporulation of the pathogen may

have been attributable to increased nutrient and water exudation through the weak cuticular layer, eventually favoring greater pathogen growth in the *gl4* mutants. Jenks et al. (1994), while working on mutants of *S. bicolor*, reported that bloomless (*bm*) mutants exhibited a thin cuticular layer and were more susceptible to infection with *Setosphaeria turcica* (the causal agent of leaf blight) than control plants. Furthermore, the transpiration rate was higher in the *bm* mutant plants than in the control plants. This apparently reflects the fact that the cuticular wax thickness can be employed to identify plants tolerant to *Exserohilum turcicum*. However, the importance of cuticular wax under concurrent stresses is yet to be studied. A detailed study of the pathways that alter the structure and composition of the cuticle layer may be useful in exploring targets that can be manipulated to provide plants with enhanced resistance to concurrent drought and pathogen stress. In rice plants, Srinivasan et al. (2008) have identified a QTL on chromosome 8 for epicuticular wax, the leaf transpiration rate, and the harvest index, collocated with QTLs associated with shoot- and root-related drought tolerance traits. Considering the significance of cuticular wax and composition of cuticular layer in conferring tolerance to pathogen invasion, isolation of QTLs associated with wax content and disease tolerance need to pay a wider attention. Therefore, cuticular wax and composition of cuticular layer may be considered a potential trait that can be used to screen plants for tolerance to concurrent drought and pathogen infection.

### 1.2.5 Canopy Temperature

Tolerance to drought and pathogen stress can be evaluated by measuring the canopy temperature (Gonzalez-Dugo et al. 2005). In response to concurrent drought and pathogen infection, plants alter their transpiration rate, thereby changing their canopy temperature to sustain growth. Under drought and pathogen stress the canopy temperature varies between leaves, as stress-induced drooping and curling of leaves cause differences in reflection of radiation (Jackson 1986). The canopy temperature plays a major role in plant growth under drought stress, as it has been observed that wheat plants under drought stress have a higher canopy temperature and a lower yield than well-watered plants (Blum et al. 1989). Moreover, it was reported that plants that had a lower canopy temperature were drought resistant, whereas plants with a higher canopy temperature were susceptible to drought stress (Blum et al. 1989). Plants that maintain a high canopy temperature under drought stress conditions have a lower plant water status and thus are less adapted to drought stress (Blum 2009). The significance of the canopy temperature in preventing pathogen infection was also reported by Eyal and Blum (1989). In comparison with control plants, the canopy temperature of wheat plants infected with *Mycosphaerella graminicola* (the causal agent of *Septoria tritici* blotch) was high, and the increase in canopy temperature was directly linked to the severity of the disease. The canopy temperature of *T. aestivum* plants infected with *M. graminicola* could be positively correlated with the occurrence of the disease, as infected plants had a higher

canopy temperature. The rise in canopy temperature could be attributable to cuticular layer damage caused by pathogen invasion. Therefore, assessment of the canopy temperature could be helpful in identifying infected and uninfected plants (Eyal and Blum 1989). Pinter et al. (1979) and Dow et al. (1988) studied alterations in the canopy temperature in *Beta vulgaris* (sugar beet) subjected to concurrent drought and pathogen infection. They reported that sugar beet has a high canopy temperature under concurrent drought and infection with *Pythium aphanidermatum* (the causal agent of root rot). The sudden rise in the canopy temperature could be attributable to pathogen-induced root damage, hampering water uptake and causing a reduction in the plant water potential. Likewise, *Cucumis sativus* (cucumber) infected with the pathogen *Pseudoperonospora cubensis* (the causal agent of downy mildew) showed a higher canopy temperature than control plants (Corle et al. 2006). Pinter et al. (1979) reported a raised canopy temperature in *Cossypium* spp. infected with *Phymatotrichum omnivorum* (the causal agent of *Phymatotrichum* root rot) under drought stress. Similarly, under concurrent drought and infection with *M. phaseolina* (the causal agent of charcoal rot infection), a raised leaf temperature and reduced stomatal resistance were noted in *B. vulgaris* (Mayek-Perez et al. 2002). Hence, as the canopy temperature shows significant variations under concurrent drought and pathogen infection, it can be considered a potential trait for evaluation of the concurrent drought and pathogen tolerance of plants. Infrared thermometers can be employed for measurement of the canopy temperature; thereby, screening for plant tolerance to concurrent drought and pathogen infection can be done.

### 1.3 Role of Genomics in Developing Crops with Combined Drought and Pathogen Stress Tolerance

A few important molecular studies have recently been employed to elucidate the molecular responses of plants to combined drought and pathogen stress. These studies have not only shed light on plant defense mechanisms against combined stresses but also revealed some potential candidates for improvement of plant tolerance to combined stresses. Some of the important candidate genes identified so far are methionine gamma lyase (*AtMGL*, a methionine homeostasis gene), rapid alkalization factor-like 8 (*AtRALFL8*, involved in cell wall remodeling), and azelaic acid induced 1 (*AZ11*, which functions in systemic plant immunity) (Atkinson et al. 2013). Tolerance to combined drought and pathogen stress is also contributed by genes involved in cross talk between the drought-associated and pathogen infection-associated signaling pathways. The roles of proline and polyamine metabolism in combined drought and pathogen stress tolerance in *A. thaliana* and *V. vinifera* have also been indicated by some studies (Hatmi et al. 2015; Gupta et al. 2016). The identified candidate genes can be suitably modulated to confer enhanced tolerance to these combined stresses. The modification can be done by genome editing using tools such as the CRISPR/Cas9 [clustered regularly interspaced short palindromic

repeats and CRISPR-associated protein 9] system. CRISPR/Cas9 can also be used to modulate the transcription of the genes of interest by guiding catalytically inactive dead Cas9 (dCas9) or dCas9 fused with transcriptional repressors/activators to the promoter of a gene. Further research in this direction using the different functional genomic approaches can thus help to reveal the responses of plants to combined drought and pathogen stress.

## 1.4 Conclusion and Future Perspectives

Plants grown under field conditions face a combination of different abiotic and biotic stresses and to mitigate the effects plants have evolved complex signalling pathways. The interactions between these stresses and their impacts on plants have been discussed here. The interactions between the two different types of stress conditions may either negatively or positively affect plant growth. For example, a co-existing drought can modulate the interaction of different pathogens and plants differently, leading to either suppression of pathogen growth or an increase in it. Therefore, it becomes very important to study the interaction between the two different types of stresses in order to better understand the net impact of stress combinations on plants. Several important diseases such as dry root rot, powdery mildew, and charcoal rot are significantly affected by concurrent drought conditions, and identification and development of superior cultivars can be done if a mechanistic understanding of the interactions between pathogen and drought stress is attained. Strategies for improving crop performance under combined drought and pathogen stress require deeper understanding. Attempts to understand the interactions have already commenced in the form of transcriptomic studies. Well-designed experiments involving simultaneous drought and pathogen stress on plants have also been undertaken, revealing some aspects of drought–pathogen interactions (Gupta et al. 2016; Sinha et al. 2016). Plant genotypes can be screened for traits such as their root system architecture, leaf water potential, leaf turgidity, leaf pubescence, and leaf cuticular waxes for identification of superior germplasm lines. To vividly assess the effects of different stress combinations on plants, it is imperative to design experiments that can reveal different aspects of interactions between the two different types of stresses. A well-considered stress imposition protocol that is not very different from stresses occurring under field conditions, complemented by relevant physiological assays and the recently evolved genomic tools, can help uncover the responses of plants to stress combinations. Understanding obtained from studies on plant responses to combined drought and pathogen stresses can be utilized by breeders and field pathologists to better analyze the performance of tolerant genotypes. Further development of crop simulation models involving a combination of drought and pathogen stress can help in disease forecasting in places where concurrence of the two stresses is prevalent. Thus, integrative efforts made by crop modeling experts, agronomists, field pathologists, breeders, physiologists, and molecular biologists can efficiently lead to development of combined-stress-tolerant crops that can perform well under field conditions.

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