Chapter 9
The Response of Plants to Simultaneous Biotic and Abiotic Stress

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9.1 Introduction

Plants have developed specific mechanisms that allow them to detect precise environmental changes and respond to complex stress conditions, minimising damage whilst conserving valuable resources for growth and reproduction. Plants activate a specific and unique stress response when subjected to a combination of multiple stresses (Atkinson et al. 2013; Suzuki et al. 2014), and consequently the imposition of single stresses individually may be suboptimal for developing and testing stress-tolerant plants (Mittler and Blumwald 2010). This is particularly true for signalling pathways that can act antagonistically such as the combinations of biotic and abiotic stresses (Anderson et al. 2004; Asselbergh et al. 2008a). There is an urgent need to understand the nature of multiple stress responses in plants and to create avenues for developing plants that are resistant to multiple stresses yet maintain high yields. In this chapter, we consider the effects of biotic and abiotic stresses acting simultaneously on plants, with an emphasis on elucidating the molecular mechanisms involved.

Evidence in the literature from field, laboratory and molecular studies suggests that plants respond to a specific combination of stresses in a manner distinctly different from the additive response to the individual stresses (Atkinson et al. 2013; Prasch and Sonnewald 2013; Rasmussen et al. 2013; Rizhsky et al. 2004; Suzuki et al. 2014; Iyer et al. 2013). Plants must produce an appropriate response to specific multiple stress conditions, as often the individual stresses may elicit opposing reactions. For example, heat stress often causes plants to open their stomata in order to cool the leaves, but under drought conditions this would be disadvantageous as

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more water would be lost (Rizhsky et al. 2004). Further, increased transpiration caused by heat stress could enhance the uptake of salt or heavy metals, heightening the damage from these factors (Mittler and Blumwald 2010). The cost of plant defence is likely to be reduced if specific genes have more general roles in different stress responses, thus explaining the overlap between stress response pathways (Asselbergh et al. 2008a; Bergelson and Purrington 1996; Herms and Mattson 1992). This hypothesis is supported by studies showing that certain molecular signalling pathways (AbuQamar et al. 2009; Dubos et al. 2010; Mengiste et al. 2003; Narusaka et al. 2004; Vannini et al. 2006; Zhang et al. 2006).

Plants exposed to a pest or pathogen often show increased susceptibility to an abiotic stress such as water deficit (Audebert et al. 2000; Cockfield and Potter 1986; English-Loeb et al. 1997; English-Loeb 1990; Khan and Khan 1996; Smit and Vamerali 1998). Conversely, the long-term abiotic stress can weaken defences and cause enhanced susceptibility to pathogen attack (Amtmann et al. 2008; Goel et al. 2008; Mittler and Blumwald 2010). The number of reports in the literature that have focussed on the interaction between biotic and abiotic stresses is growing, but is still limited: this chapter reviews that literature, with additional in-depth analysis of rice, an increasingly important crop plant in the study of stress tolerance.

9.2 The Challenge of Simultaneous Biotic and Abiotic Stresses in Agriculture

Crops in field environments experience a wide range of environmental perturbations during development that could limit their productivity. When plants are grown under suboptimal environmental conditions, a yield gap is observed and thus the actual average yield obtained is much lower than the maximum yield potential of the particular crop (Lobell et al. 2009). The yield gaps for three major cereal crops—wheat, rice and maize—are 40, 75 and 30 % respectively, in major growing areas of the world (Fischer et al. 2009). The major factors responsible for the yield gap in crop species can be classed as: (i) abiotic factors, such as temperature extremes, insufficient water or minerals or (ii) biotic factors, such as bacterial, viral, fungal or insect attack (Gaspar et al. 2002). These environmental stresses are responsible for large-scale crop loss each year and with the predicted climate change, such losses are expected to increase. Nearly 50 % of crop yield losses each year are comprised of abiotic stresses (Wang et al. 2003). The predicted climate change, characterised by an increase in temperature, an increase in concentration of greenhouse gases, an intensified hydrological cycle and an increase in troposhperic ozone levels, will have a multifaceted effect on crop growth and productivity. The results from free-air carbon dioxide (CO_2) experiments (FACE) have established that an increase in CO_2 levels in the atmosphere will lead to photosynthetic carbon gain, increased nitrogen-use efficiency and decreased water use in the leaves, but the yield gain in crop species will be much smaller than anticipated (Leakey et al. 2009). Also, the change in hydrological cycle will cause frequent extreme events of floods and storms in coastal areas accompanied by drought and reduced soil moisture in the drier regions, resulting in reduced productivity (Schmidhuber and Tubiello 2007). The anticipated rise in temperature will lead to a shorter life cycle and increased biomass in plants. Temperature changes outside the typical range during the major growth stages of crop plants will highly affect the productivity (Moriondo et al. 2011). Currently, pests and pathogens account for 15 % of the annual crop loss across the globe (Maxmen 2013). The increase in temperature and precipitation will alter the geographic distribution and host range of various pests and pathogens (Newton et al. 2011). The predicted changes will leave crop plants vulnerable to a large number of biotic and abiotic environmental stresses, acting upon them simultaneously.

Traditional molecular studies designed to explore plant stress responses have been driven by systems that artificially impose one particular stress or exogenous application of hormones on model plant species grown in laboratory conditions. The results of such studies have enhanced our understanding of the signalling cascades and hormonal pathways that mediate plant responses towards various stresses and have been used in achieving tolerance to biotic and abiotic stresses. However, the plants engineered for tolerance to a single biotic or abiotic stress in the laboratory have repeatedly failed to attain similar results in the fields (Atkinson and Urwin 2012; Mittler 2006). This is because the crops in the field encounter more than one type of stress at any given point in time, and with the prophesied climate change model the incidences of simultaneous biotic and abiotic stresses on plants are bound to increase.

The effect of climate change on plant–pest interactions has been widely reviewed in recent years (Chakraborty 2005; Garrett et al. 2006; Gregory et al. 2009; Luck et al. 2011; Newton et al. 2011; Scherm 2004). The response of plants to a combination of biotic and abiotic stresses is tailored to the exact nature of the stresses and there can be additive, negative or interactive effects of each of the individual responses (Atkinson and Urwin 2012). Evidence suggests that increased CO_2 levels in the atmosphere will lead to suppression of plant defence responses by the manipulation of the hormonal signalling pathways. Soybean plants show the down-regulation of jasmonic acid (JA) and ethylene (ET) pathways resulting in the reduction of cysteine protease inhibitors under increased CO_2 levels that in turn reduce the plants' defence against coleopteran pathogens (Zavala et al. 2008). At the same time, the increased CO_2 levels also result in the increased global expression of salicylic acid (SA) in soybean plants (Casteel et al. 2012). The increased CO_2 levels are likely to provide legumes with a photosynthetic advantage and protection against drought-induced loss in N_2 (Rogers et al. 2009). In tomato plants, elevated CO_2 levels have resulted in decreased resistance to the root-knot nematode (RKN) *Meloidogyne incognita* (Sun et al. 2010). Apart from elevated levels of CO_2, temperature plays an important role in plant–pathogen interactions (Fu et al. 2009; Zhu et al. 2010). Temperature-dependent resistance is seen towards blast disease in rice, broomrape in sunflower and clover, downy mildew in musk melon and stripe rust in wheat (Balass et al. 1993; Eizenberg et al. 2004; Eizenberg et al. 2009; Fu et al. 2009; Webb et al. 2010). An increase in temperature will also lead to more rapid development, increased reproductive potential and more generations of pests and pathogens in a season. These changes in pest life cycle and productivity could cause unprecedented damage to the crops in one season (Scherm 2004).

Drought can aid pest and pathogen outbreaks in fields, at the same time pathogens can severely influence plant water relations and lead to low water potential in plant cells (Mattson and Haack 1987). The bacterium *Xylella fastidiosa* causes pathogen-induced drought in grape by severe reduction of water potential (Choi et al. 2013). In the case of foliar pathogens, stomatal closure is the first physiological barrier in the defence response. Stomatal closure is also a drought avoidance strategy, thus drought-induced stomatal closure reduces pathogen entry into the plant tissue. Similarly, pathogen-induced stomatal closure helps the plant in efficient use of water (Sawinski et al. 2013). Drought enhances the symptoms of fungal charcoal rot disease in common bean (Mayek-Perez et al. 2002), and leads to reduction in plant water status and in turn increasing concentration of metabolites in the plant tissue. Increased concentration of defence compounds in drought-stressed tomato plants results in reduced susceptibility towards the herbivore *Spodoptera exigua* (English-Loeb et al. 1997). However, the change in herbivore's feeding behaviour also depends on the nature of the pest and its specificity towards the plant species (Gutbrodt et al. 2011). Drought stress can influence the interaction between two pathogens acting on the same plant and vice versa. Root-feeding herbivores can also enhance resistance against foliar herbivores by abscisic acid (ABA)-mediated hydraulic changes (Erb et al. 2011). The plant response towards simultaneous infestation by a foliar herbivore (aphids), their parasitoids and a root herbivore is also altered by drought stress (Tariq et al. 2013).

Drought-induced changes in roots can interact or counteract root-specific pathogens. In water-dependent agricultural ecosystems, drought can increase the incidence of soil-borne disease, especially plant-parasitic nematodes (PPNs). Drought and PPN infection are the two biotic and abiotic stresses that are often encountered simultaneously by rice plants in the fields. Drought can increase susceptibility of rice to root-knot nematode infection in all ecosystems, especially in aerobic rice cultivation. Cyst nematodes (CNs) can contribute to the drought-related losses in rice by causing reduced stomatal conductance and reduced leaf water potential (Audebert et al. 2000). A study on simultaneous drought and CN infection on *Arabidopsis* has revealed that under simultaneous biotic and abiotic stress, the plant responses are dominated by abiotic stress-responsive changes (Atkinson et al. 2013).

An integrated approach should be used to test resistance traits under a range of stress treatments (Mittler and Blumwald 2010). It is crucial to impose the stresses simultaneously and treat each set of environmental conditions as an entirely new stress to truly characterise the response of plants to multiple stresses (Mittler 2006).

9.3 Transcriptomic Studies of Simultaneous Biotic and Abiotic Stresses

Traditionally, plant molecular responses to multiple stresses have been predicted by comparing the results from two or more individual transcriptomic studies conducted independently by exposing plants to a singular stress. The results obtained by these comparisons identify the genes that might be involved in general stress responses of a plant, but fail to highlight the genes that might play an important role when plants are simultaneously exposed to a combination of biotic and abiotic stresses. Evidence suggests that the response towards a pair of simultaneous biotic and abiotic stress is not always additive of the responses seen towards these stresses individually. Plants treat each set of simultaneous stresses as a different environmental condition and tailor their response specifically to it (Atkinson and Urwin 2012). This may involve differential regulation of a new set of genes that were not induced or repressed by any of the stresses individually and vice versa (Mittler 2006). A systematic study performed in *Arabidopsis* exploring transcriptomic response to simultaneous application of flagellin and change in temperature determines that nearly 49.3 % of the changes seen as a response to combinatorial stress could not have been predicted by just studying the response to each of these stresses singly. The number of differentially expressed genes increases with severity and complexity of the combination of stresses (Rasmussen et al. 2013). When *Arabidopsis* plants are subjected to virus infection in combination with drought and/or heat, the transcriptomic responses are much more severe in the triple stress, followed by simultaneous virus and heat and then simultaneous virus and drought stress treatment (Prasch and Sonnewald 2013). By comparing the response of *Arabidopsis* plants under single, double and triple stress, down-regulation of primary carbon metabolism was seen as plant's general response to stress. The abiotic stresses can significantly influence R-gene-mediated defence in plants by significantly reducing the expression of defence-related genes and in turn making plants highly susceptible to pathogen attack (Prasch and Sonnewald 2013). The study identified 11 genes that were differentially regulated in all stress combinations and 23 genes that were specifically regulated when plants were subjected to simultaneous heat, drought and virus infestation. When virus-infected plants were subjected to drought or heat stress, 175 and 309 genes were differentially regulated, respectively. In some cases, the transcriptomic response to combinatorial stress can be dominated by one of the stresses. Transcriptomic investigations of the combined effect of a biotic stress, *Aspergillus parasiticus*, and an abiotic stress, drought, in peanut, showed that the response to the combinatorial stress was more similar to the drought response alone with a very small proportion of multiple stress-specific responses (Luo et al. 2005). Similar results were seen in *Arabidopsis* plants simultaneously exposed to dehydration and infection with the CN *Heterodera schachtii*. Ninety-seven percent of the genes differentially expressed in leaves and roots under multiple stress treatment were also differentially expressed in drought-only treatment. Only 50 genes were expressed specifically in response to simultaneous drought and nematode infection (Atkinson et al. 2013).

9.3.1 Case Study: Rice Transcriptomic Responses to Simultaneous Biotic and Abiotic Stresses

A comprehensive investigation of systemic and local transcriptomic responses of rice towards drought and nematode stress, in isolation as well as in combination, was conducted using Affymetrix Rice GeneChip® arrays that provide maximum coverage of the rice genome, representing 57,381 transcripts from both japonica- and indica-type cultivars (Jain et al. unpublished). The replicate arrays for drought and simultaneous drought and nematode stresses cluster in one group, whereas the control and nematode stress arrays form the other group. The experimental model was designed to mimic realistic stress conditions encountered by rice plants in the fields.

The transcriptome response to the application of simultaneous stresses was dominated by changes also observed in response to drought stress alone (95 %), with some additional unique transcript changes (5 %). Nearly 10 % (4480) of the genes on the chip had a twofold expression change at a significant level ($p \leq 0.05$) in the roots, and a similar level was observed for drought stress. The transcriptomic changes were tissue specific with only 5 % overlap between the roots and the leaves. A total of 297 genes showed multiple stress-specific regulation. Of these, 75 % were up-regulated genes whilst 25 % were repressed. The changes unique to simultaneous stress included novel members of gene families such as lipid-transfer protein genes (LTPLs) and cytochrome P450s, known to be involved in crosstalk between abiotic and biotic stresses. One of the genes highly induced specifically under multiple stresses was LTPL 11, a previously uncharacterised member of this stress-responsive protein family was known to be involved in pathogenesis as well as abiotic stress response in rice (Atkinson et al. 2013; Vignols et al. 1997). In *Arabidopsis*, LTPLs impart SA-mediated response and signal transduction during fungal and bacterial pathogen attack (Maldonado et al. 2002; Molina and García-Olmedo 1997). Four cytochrome P450 genes were differentially regulated in response to simultaneous stress, two in leaves and two in roots (Jain et al. unpublished). Cytochrome P450s in *Arabidopsis* mediate crosstalk between the abiotic and biotic stress-responsive hormone pathways. They are involved in catabolism of ABA, the major abiotic stress-responsive hormone, deactivation of gibberellic acid and negative regulation of jasmonate pathway (Koo et al. 2011). The up-regulation of the α-amylase responsible for the degradation of sucrose and the down-regulation of starch synthase in multiple stressed plants indicate that multiple stresses significantly modulate carbohydrate metabolism. Drought stress affects α-amylase in leaves and thus modulates sugar metabolism (Jacobsen et al. 1986). Sucrose is required for plant growth, and it also acts as a signalling molecule by modulating a proton–sucrose symporter (Gupta and Kaur 2005).

The simultaneous stress response in rice is characterised by a unique set of genes that is not differentially regulated when any of the two stresses act individually on the plant, emphasising that the response to a combination of stresses is not additive but is interactive of the responses seen under the influence of any of the stresses singly.

9.4 Hormone Signalling and Master Regulators in Stress Interaction

Due to the complex interacting nature of plant stress responses, research aimed at developing stress-tolerant crops is increasingly focusing on the points of crosstalk between pathways, or master regulators (Denancé et al. 2013; Miller et al. 2010).

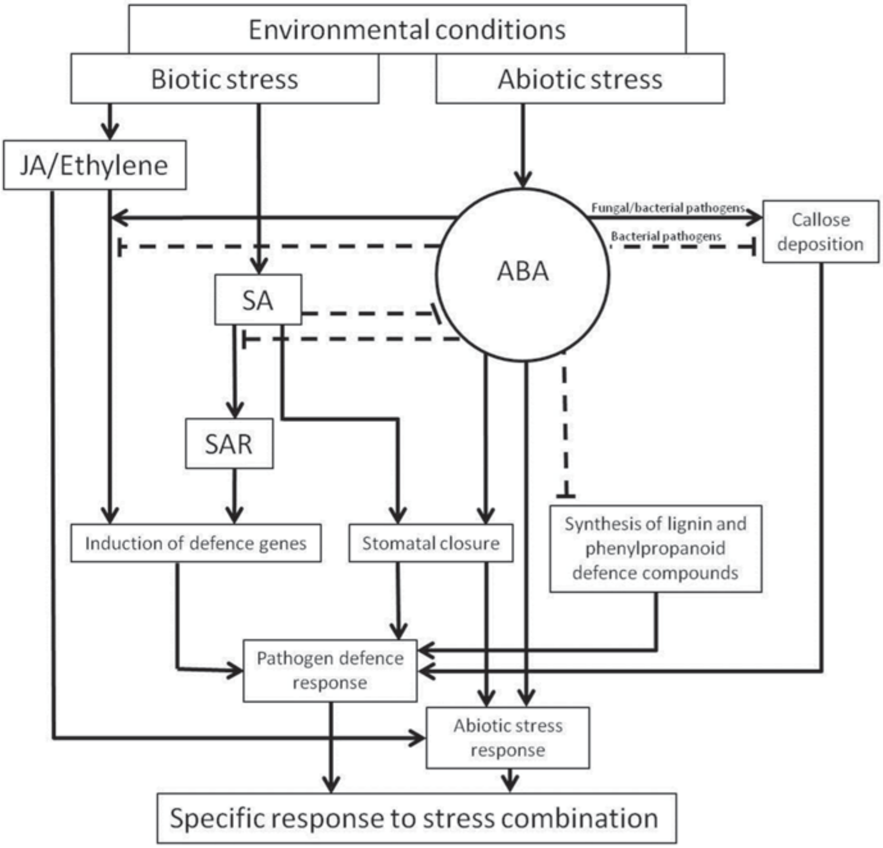

Fig. 9.1 The multifaceted role of abscisic acid (*ABA*) in plant biotic and abiotic stress responses. This figure summarises the main interactions of *ABA* with components of the pathogen defence pathway. ABA has both a positive and negative effect on various hormones and events involved in the response to biotic stress, as well as orchestrating the abiotic stress response. Positive regulation is shown by *solid arrows*, whilst negative regulation or inhibition is shown by *dashed bars*. *JA* jasmonic acid, *SA* salicylic acid, *SAR* systemic acquired resistance

Plant hormones are at the hub of this interaction, in particular ABA (Atkinson and Urwin 2012; Ton et al. 2009). ABA is central in the fine-tuning of stress responses and is now considered a global regulator that can control the switch in priority between the response to biotic or abiotic stress, allowing plants to respond to the most severe threat (Fig. 9.1; Anderson et al. 2004; Asselbergh et al. 2008a; Mauch-Mani and Mauch 2005; Ton et al. 2009). This dominant role of ABA may arise from its involvement in both the biotic and abiotic stress-regulatory networks.

Traditionally, ABA has been connected primarily with the response to abiotic stress, whilst defence against pathogens and other biotic stresses is determined by the mutual antagonism between SA, JA and ethylene signalling. New evidence suggests that ABA acts both synergistically and antagonistically with these defence pathways, with crosstalk at different levels (Asselbergh et al. 2008a; Atkinson and

Urwin 2012; Fujita et al. 2006; Yasuda et al. 2008). Its influence depends on the timescale of infection and the nature of the pathogen (Ton et al. 2009). In the early stages of defence against microbial invasion, ABA acts through the SA signalling pathway as a key strategy to induce stomatal closure and thus reduce infection (Melotto et al. 2006). After penetration, ABA is necessary for β-amino-butyric acid (BABA)-induced callose deposition as a defence against fungal pathogens (Ton and Mauch-Mani 2004), whilst during bacterial infection ABA can block callose production or indeed has a positive effect, a balance that depends on the external environmental factors such as light and glucose levels (De Torres-Zabala et al. 2007; Luna et al. 2011). Induced protection against the bacteria *Ralstonia solanacearum* in *Arabidopsis* is unexpectedly independent of SA, JA and ethylene and is instead dependent on ABA signalling and synthesis (Feng et al. 2012).

In the later stages of a pathogen infection, the hormones SA, JA and ethylene are induced by pathogen-associated molecular patterns (PAMPs) to regulate a broad spectrum of defensive compounds, processes that are generally inhibited by ABA (Asselbergh et al. 2008b; Ton et al. 2009). Treatment with ABA actually increases susceptibility to fungal and bacterial pathogens, a phenomenon demonstrated in *Arabidopsis*, tomato and potato (Asselbergh et al. 2008b; Audenaert et al. 2002; Henfling et al. 1980; Mohr and Cahill 2003) and in rice, where ABA treatment has been shown to cause a reduction in plant defence against the blast fungus Magnaporthe *grisea* (Koga et al. 2004). Furthermore, disruption of the ABA signalling pathway can improve defence against pathogens (Anderson et al. 2004; Asselbergh et al. 2007; Audenaert et al. 2002; Mohr and Cahill 2003). For example, *Arabidopsis* mutants with impaired ABA biosynthesis or signalling are more resistant to the necrotrophic fungi *Plectosphaerella cucumerina* (Sánchez-Vallet et al. 2012). On the analysis of transcription patterns in these mutants compared to wild-type plants, it was found that defence genes regulated by SA, JA and ethylene were specifically down-regulated by the ABA pathway. ABA treatment can repress the SA-mediated systemic acquired resistance (SAR) pathway in *Arabidopsis* and tobacco, and inhibits the accumulation of important defence compounds such as lignins and phenylpropanoids (Kusajima et al. 2010; Mohr and Cahill 2007; Yasuda et al. 2008). In contrast, SA is known to obstruct abiotic stress signalling, leading to drought susceptibility in maize when applied exogenously (Németh et al. 2002). In rice, resistance to the rice blast fungus *M. grisea* is mediated by the balance between ABA and SA (Jiang et al. 2010). ABA also antagonises JA and ethylene defence signalling through the repression of defence genes such as *PDF1.2* (Anderson et al. 2004), although JA production can contribute positively to tolerance against certain abiotic stresses such as chilling, salt, drought and osmotic stress (Santino et al. 2013).

This close association of ABA with defence signalling pathways may allow a subtle shift in environmental conditions to cause a dramatic difference in stress response, as any increase in ABA due to abiotic stress could repress the SA, JA and ethylene defence responses. As abiotic stress conditions such as drought tend to be a much greater threat to survival than biotic stresses, this would then allow plants to prioritise the response to the more urgent stress.

The fine-tuning in the regulation of stress responses by ABA may be partially controlled by the diversity amongst downstream signalling elements (Lee and Luan 2012). There are 14 members of the PYR/PYL/RCAR ABA receptor family, which in turn activate 6–9 members of the A-type PP2C phosphatases and at least 3 members of the SnRK2 kinases, known to carry out downstream protein phosphorylation and dephosphorylation events (Lee and Luan 2012; Ma et al. 2009; Wasilewska et al. 2008). Between them, these provide more than 200 signalling combinations that may activate similar or different downstream targets. These molecular components of the ABA signalling pathway may additionally provide opportunities for genetic engineering of stress tolerance in crop plants.

Points of crossover between hormone signalling pathways include several influential TFs, such as MYC2. This is activated by ABA (Abe et al. 2003), is a positive regulator of JA-responsive defence genes (Anderson et al. 2004; Pieterse et al. 2009), and in addition represses the SA pathway (Laurie-Berry et al. 2006). Members of the MYB and NAC TF family are also crucial controlling factors in multiple stress responses, and have been fully reviewed recently (Atkinson and Urwin 2012).

Large multi-protein mediator complexes may function to integrate downstream stress response signals from multiple sources (Balderas-Hernández et al. 2013). These are central components of transcription complexes in eukaryotes, which interact with ribonucleic acid (RNA) PolII and promote the assembly of TFs on promoter sequences (Bourbon 2008). In *Arabidopsis*, mediator is made up of at least 27 subunits, one of which is Med25, encoded by the *phytochrome and flowering time 1* (*PTF1*) gene. It regulates a multitude of signalling pathways by interacting with TFs central to the ABA and JA/ethylene cascades, such as MYC2 and ABA insensitive 5 (ABI5) which transcriptionally activates ABA-responsive genes (Balderas-Hernández et al. 2013).

Heat shock factors (HSFs) have also been identified as potential master regulators of the response to multiple stresses (Atkinson and Urwin 2012). These are TFs that act as molecular sensors of cellular stress-responsive reactive oxygen species (ROS) and induce the expression of heat shock proteins (Miller and Mittler 2006). As different stresses elicit different combinations of HSFs, they may contribute to the fine-tuning of stress response outcomes (Rizhsky et al. 2004; von Koskull-Döring et al. 2007; Yoshida et al. 2011). Recently, HSFA1b has attracted attention as a target for engineering stress tolerance in crops. Post-transcriptionally regulated during stress conditions, HSFA1b itself regulates 509 genes. When over-expressed in *Arabidopsis* it confers dehydration tolerance, resistance to bacterial pathogens and oomycetes, and improved seed yield under water-limited conditions. (Bechtold et al. 2013). In oilseed rape, its over-expression led to improved productivity characterised by an increased harvest index and seed yield. This is of particular interest given that many stress-tolerant *Arabidopsis* mutants over-expressing the ABA or SA signalling pathways show a diminished fecundity (Bechtold et al. 2013; van Hulten et al. 2006). Clearly to attain impact in the development of broad-spectrum stress-tolerant crop plants, improved disease and abiotic stress responses must go hand in hand with the maintenance of growth and yield characteristics.

9.5 Interaction of Volatile Compounds in Simultaneous Biotic and Abiotic Stresses

Plants interact with each other by emitting a unique blend of volatile organic compounds (VOCs). The intensity and chemical composition of VOCs emitted by a plant can define the physiological state of a plant and is an indication of the nature of the stress acting upon them. The ratio of various compounds in the volatile blend can hint to herbivorous insects or parasitic plants about the location of their potential host (Runyon et al. 2006; Tumlinson 2014). Some of the VOCs are specific to certain plant species. For example isothoicynates, volatile catabolites of the glucosinolates, are characteristic of the brassicaceous plants. Specialist brassica pests like the cabbage aphid *Brevicoryne brassicae* and the cabbage seed weevil *Ceutorhynchus assimilis* use isothiocyanates for host location (Bruce et al. 2005). However, as plants in nature may suffer from more than one stress at a time, it can be hypothesised that the multiple stresses will have a VOC signature different to any of the stresses acting individually on the plants (Blande et al. 2014). Abiotic stresses like heat, water stress, high-intensity light, ozone and salt stress lead to increased emission of volatile compounds including isoprene, monoterpenes and sesquiterpenes (Holopainen and Gershenzon 2010; Loreto and Schnitzler 2010). The emission under a biotic stress is dominated by terpenes and green leaf volatiles (GLVs), C_6 aldehydes, alcohols and esters of lipoxygenase cleavage of fatty acids (Holopainen and Gershenzon 2010). Two different stresses, two biotic or two abiotic stresses, are capable of initiating emissions of similar types of compounds that might suggest an underlying common signature for the biotic and abiotic stresses. In lima beans, exposure to ozone and spider mite infestation triggered the emission of (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and (*E, E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT; Vuorinen et al. 2004).

Similar to the molecular and physiological effects, simultaneous application of a biotic and an abiotic stress can have additive or opposing effects on the VOCs emission. Additive effects can result in an increase in emitted VOCs and also can increase susceptibility towards other stresses. Simultaneous exposure to ozone and infection with spider mites in lima beans gave a 31 % increase in the emission of VOCs compared to plants exposed to single stress and also made plants more susceptible to secondary herbivore attack by predatory mites. In behavioural assays, the predatory mites preferred plants under dual stress over the plants that were just exposed to high levels of ozone. This preference was a result of increased ratio of (*E*)-β-ocimene in the emission blend of dual stressed plants (Vuorinen et al. 2004). An additive effect on emitted VOCs was also observed in the deciduous tree *Alnus glutinosa* during drought stress and simultaneous infection with the larvae of green alder sawflies. Concurrent application of the two stresses increased the emission of GLVs, monoterpenes and the markers of herbivory, (*E*)-β-ocimene and methyl jasmonate (Copolovici et al. 2014). The mild drought stress before larval attack in this case showed a priming effect and made plants less susceptible to herbivory, in contrast to the effect seen in lima beans under simultaneous ozone exposure and spider mite attack. Perhaps the ozone dose used was insufficient to initiate a priming effect similar to drought stress. *Brassica napus* (oilseed rape) plants subjected to herbivory under elevated levels of ozone or CO_2 show contrasting interactions between the biotic and the two abiotic stresses. Terpenoid emission was increased in plants under elevated CO_2 and subjected to herbivory, but reduced in the elevated ozone and herbivory group. However, under both stress combinations plants became susceptible to herbivory as determined by olfactory tube assays (Himanen et al. 2009).

A detailed study to elucidate the effect of simultaneous biotic and abiotic stresses in maize plants was conducted using inoculation of caterpillar regurgitant in combination with changes in soil humidity, air humidity, temperature, light and mineral dosage. The amount and the composition of the VOCs emitted by the maize plants did not change with the abiotic conditions, but on simultaneous induction of biotic stress there was an increase in the VOCs emission under all stresses except the change in soil humidity. The composition of the emission blend also changed with simultaneous application of biotic and abiotic stresses. Table 9.1 gives a detailed overview of changes in VOCs under pairs of simultaneous biotic and abiotic stresses in different species. In most cases, simultaneous stresses change the composition and increase the amount of VOCs emitted by a plant, depending on the nature of the stresses applied. The VOCs emitted by stressed plants play a vital role in plant–pathogen interaction. A better understanding of VOCs emission under multiple stresses may be valuable for managing insect pests of crop species.

9.6 Points of Convergence Between Biotic and Abiotic Stress Signalling Pathways

Biotic and abiotic stress signal transduction is characterised by a complex arrangement of interacting factors. Certain gene products are now known to be central to both biotic and abiotic stress signalling, and may therefore control the specificity of the response to multiple stresses (Fujita et al. 2006; Mauch-Mani and Mauch 2005). Transcriptomic and genetic analyses have highlighted a number of putative candidates that might act as points of convergence, including TFs, map kinases, HSFs, ROS and small RNAs, and these discoveries have been fully reviewed recently (Atkinson and Urwin 2012).

9.6.1 Rice as a Case Study

As one of the most important crop plants worldwide and a model monocotyledon, rice is increasingly becoming a focus for applied plant stress research in the field and laboratory. Discoveries of key stress response genes in rice will provide direct opportunities for translational work to improve stress tolerance in cereal crops. Key

Table 9.1 Impact of simultaneous biotic and abiotic stresses on the emission of volatile compounds

Plant species	Biotic stress	Abiotic stress	Total VOCs in dual stress	(*Z*)-3-hexen-1-yl acetate	β-myrcene	(*E*, *E*)-α-farnesene	(*E*)-β-farnesene	linalool	DMNT	Indole	α-bergamontene	TMTT	Geranyl acetate	(*E*)-nerolidol	β-caryophyllene	(*E*)-β-ocimene	Methyl salicylate	1-penten-3-ol	(*Z*)-Hexen-1-ol	(*E*)-2-Hexenal	(*E*)-3-Hexenal	LOX products	α-Thujene	α-Pinene	Sabinene	Limonene	β-Elements	B-sesquiphellandrene
Zea mays	*SL*	Increased soil humidity (20 to 60–80 %)	↓	↑	n.s	n.s	n.s	↑	↕	↕	n.s	n.s	↕	n.s	↕	–	–	–	–	–	–	–	–	–	–	–	–	–
Zea mays	*SL*	Increased air humidity (20 to 45–65 %)	↑	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	–	–	–	–	–	–	–	–	–	–	–	–	–
Zea mays	*SL*	Increased temperature (17–37 °C)	↑	↑	n.s	n.s	n.s	n.s	n.s	n.s	n.s	↑	n.s	↑	↑	–	–	–	–	–	–	–	–	–	–	–	–	–
Zea mays	*SL*	High light intensity (0 to 15,000–20,000 lm/m^2)	↑	↓	n.s	↓	n.s	↑	n.s	↑	n.s	↑	↑	↑	↑	–	–	–	–	–	–	–	–	–	–	–	–	–
Zea mays	*SL*	Reduced fertilisation	↓	n.s	n.s	↓	n.s	↕	↓	↓	n.s	↓	↓	↓	↓	–	–	–	–	–	–	–	–	–	–	–	–	–
Zea mays	*SF*	Increased copper (0–80 μM)	↑	↑	–	–	↑	n.s	n.s	n.s	↑	n.s	–	n.s	n.s	–	–	–	↑	↑	n.s	–	–	–	–	–	–	↑
Alnus glutinosa	*MP*	Drought	↑	n.s	–	–	–	–	↑	–	–	–	–	–	–	↑	↑	–	–	–	–	↑	–	–	–	–	↑	–

Table 9.1 (continued)

Plant species	Biotic stress	Abiotic stress	Total VOCs in dual stress	(*Z*)-3-hexen-1-yl acetate	β-myrcene	(*E*, *E*)-α-farnesene	(*E*)-β-farnesene	linalool	DMNT	Indole	α-bergamontene	TMTT	Geranyl acetate	(*E*)-nerolidol	β-caryophyllene	(*E*)-β-ocimene	Methyl salicylate	1-penten-3-ol	(*Z*)-Hexen-1-ol	(*E*)-2-Hexenal	(*E*)-3-Hexenal	LOX products	α-Thujene	α-Pinene	Sabinene	Limonene	β-Elements	B-sesquiphellandrene
Brassica napus	*PX*	Elevated O_3 (100 nL/L)	n.s	–	n.s	–	–	–	n.s	–	–	–	–	–	–	–	–	–	–	–	–	–	n.s	n.s	n.s	n.s	n.s	–
Brassica napus	*PX*	Elevated CO_2 (750 μL/L)	↑	–	↑	–	–	–	↑	–	–	–	–	–	–	–	–	–	–	–	–	–	↑	↑	↑	↑	↑	–
Phaseolus lunatus	*TU*	Elevated O_3 (150–200 nL/L)	↑	n.s	–	–	–	–	↑	–	–	n.s	–	–	–	↑	–	–	–	–	–	–	–	–	–	–	–	–

Plant pathogens: *SL Spodoptera littorali*, *SF Spodoptera frugiperda*, *MP Monsoma pulveratum*, *PX Plutella xylostella*, *TU Tetranychus urticae*

n.s. not significant, – not determined in particular study, ↕ no regular pattern but fluctuates significantly with the stresses, ↑ significant increase, ↓ significant decrease, *DMNT* (*E*)-4,8-dimethyl-1,3,7-nonatriene, *TMTT* (*E*, *E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene components of the pathways in rice responding to multiple environmental stresses have already been elucidated. Members of the WRKY family of TFs are responsive to both biotic and abiotic stresses and play a vital role in fine-tuning plants' response to simultaneous stress. In rice, *WRKY13* antagonistically regulates the response to drought and bacterial disease by selectively binding to the *cis*-acting elements and specific sequences in the promoters of *SNAC1* and *WRKY45–1*. It can also autoregulate its own expression by binding to its promoter (Xiao et al. 2013). *WRKY45* imparts resistance against the fungal and bacterial pathogens in rice by differential mechanisms (Shimono et al. 2012). The *WRKY45-1* allele negatively regulates ABA signalling and also increases plant susceptibility to bacterial pathogens, whilst the *WRKY45-2* allele positively regulates ABA signalling and increases resistance to bacterial pathogens (Tao et al. 2011). Both alleles positively regulate resistance to fungal blast disease (Tao et al. 2009). *WRKY76* transcription repressor plays opposite role in response to rice blast disease and cold stress; over-expression of the *WRKY76* results in increased susceptibility towards blast infection but increases tolerance to cold stress (Yokotani et al. 2013a). *WRKY82* enhances defence against biotic pathogens and tolerance against abiotic stress via the JA/ET pathways (Peng et al. 2011).

Several disease-resistant cultivars have different natural expression levels of *OsMYB4* leading to varying degrees of resistance to sheath blight and leaf blight diseases in rice (Singh et al. 2013). Ectopic expression of the rice *OsMYB4* TF enhances abiotic and biotic stress tolerance in many plants including *Arabidopsis*, tomato and apple (Pasquali et al. 2008; Vannini et al. 2006, 2007). The JA-induced *MYB* gene, *JAmyb,* is induced by high salinity, osmotic stress and ROS and its over-expression results in induction of JA-induced TFs that play an important role in biotic stress response (Yokotani et al. 2013b).

The *OsNAC6* gene acts as a transcription inducer for biotic and abiotic stress responses in rice. Constitutive over-expression of *OsNAC6* results in increased tolerance to dehydration and salt stress along with greater resistance to blast disease, but with growth and yield penalty (Nakashima et al. 2007). *OsNAC5* also enhances abiotic stress tolerance in rice and is responsive to JA, but does not cause any negative effect on plant growth (Takasaki et al. 2010). A plant-specific TF family, ethylene-responsive factor TFs, bind to the GCC sequence specifically found in the *PR* genes. These TFs are mainly involved in abiotic stress responses in plants. Four ethylene-responsive genes, *BIERF1-4,* are up-regulated by salt, drought, wounding and fungal pathogens (Cao et al. 2006).

In addition to TFs, various protein kinases (PKs) also act as the convergence points in biotic and abiotic stress pathways in rice. Out of the 17 known rice MAPK genes, five are induced by both biotic and abiotic stresses (Rohila and Yang 2007). *OsMAPK5* is the most studied rice MAPK; it confers ABA-mediated tolerance to abiotic stress and resistance to brown spot, whilst negatively regulating the response to rice blast fungus (Sharma et al. 2013). Members of the rice CDPK family are also involved in crosstalk between biotic and abiotic stresses. OsCDPK12 regulates genes involved in ROS scavenging in stressed plant cells resulting in reduced accumulation of H_2O_2. The over-expression of *OsCDPK12* leads to positive regulation of salt tolerance and negative regulation of blast resistance (Asano et al. 2012). *OsCDPK13* is involved in the gibberellic acid-mediated response in rice leaf sheath and cold tolerance (Abbasi et al. 2004). Four CIPK PKs (*OsCIPK 2*, *OsCIPK 10*, *OsCIPK 11* and *OsCIPK 14*) also play important roles in the crosstalk between biotic and abiotic stresses (Chen et al. 2011). Another family of PKs, known as dual specificity PKs (*OsDPK*), also shows response to biotic and abiotic stresses. *OsDPK1*, *OsDPK2* and *OsDPK3* are all induced by exogenous application of ABA, drought, salinity and in response to the rice blast fungus (Gu et al. 2005). Involvement of these rice gene families in biotic as well as abiotic stress responses presents them as candidates for transgenic improvement of multiple stress tolerance.

9.7 Future Perspectives

Studies describing the effects of individual and combinatorial stresses have facilitated an initial understanding of the molecular interactions controlling plant stress responses. Plants respond to the exact set of conditions they encounter by activating both specific and non-specific stress responses. Signal specificity is achieved through the precise interplay between components of each pathway, particularly the hormones ABA, SA and JA, TFs, HSFs, ROS and small RNAs. In the past, individual plant stress factors, which trigger linear signalling pathways, have been studied in isolation. It seems that this model is no longer sufficient, as both biotic and abiotic stress pathways are inextricably linked in a network of molecular interactions.

The development of new crop varieties will depend on understanding crucial stress-regulatory networks and the potential effects of different combinations of adverse conditions. Studies of multiple stress responses in the model plants *Arabidopsis* and rice, as well as work on other species, have greatly increased our knowledge. Plant efficiency in sensing and responding to each unique set of environmental conditions means that different methods of imposing stress can lead to drastically different transcriptional profiles (Bray 2004). Commonalities between biotic and abiotic signalling pathways that have been identified may lead to their antagonistic nature. Nodes that act in both biotic and abiotic stress response systems are excellent candidates for manipulating stress tolerance (Baena-González and Sheen 2008; Miller et al. 2010). To provide a model for crop stress responses, an integrated approach should be adopted, whereby future experiments are carried out in conditions that reproduce natural or field conditions as accurately as possible (Deyholos 2010; Mittler and Blumwald 2010; Suzuki et al. 2014).

The impacts of climate change pose further challenges for plant breeding and biotechnology. Crops must be developed that can cope with multiple concurrent stresses whilst still fulfilling their genetic potential to provide maximum yields and thus ensure future global food security.

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