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1

Abiotic and Biotic Stress Response Crosstalk in Plants

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1. Introduction

In the course of its evolution, plants have developed mechanisms to cope with and adapt to different types of abiotic and biotic stress imposed by the frequently adverse environment. The biology of a cell or cells in tissues is so complicated that with any given stimulus from the environment, multiple pathways of cellular signaling that have complex interactions or crosstalk are activated; these interactions probably evolved as mechanisms to enable the live systems to respond to stress with minimal and appropriate biological processes. The sensing of biotic and abiotic stress induces signaling cascades that activate ion channels, kinase cascades, production of reactive oxygen species (ROS), accumulation of hormones such as salicylic acid (SA), ethylene (ET), jasmonic acid (JA) and abscisic acid (ABA). These signals ultimately induce expression of specific sub-sets of defense genes that lead to the assembly of the overall defense reaction.

In plants, defense response genes are transcriptionally activated by different forms of environmental stress or by pathogens. The induction of expression of defense genes in the response against certain pathogens is further dependent on temperature and humidity, suggesting the existence of a complex signaling network that allows the plant to recognize and protect itself against pathogens and environmental stress. A body of research has shown that calcium and reactive oxygen species are second messengers in the early response to abiotic and biotic stress. For example, cytosolic calcium (Ca^{2+}) levels increase in plant cells in response to various harsh environmental conditions, including pathogen attack, osmotic stress, water stress, cold and wounding. After the increase of Ca^{2+} concentration in the intracellular space, several simultaneous pathways are activated by calcium-interacting proteins such as Ca^{2+}-dependent protein kinases (CDPKs), calmodulin and calcineurin B-like proteins (CBLs), all proteins with the structural 'EF-hand' calcium-binding motif.

It is also known that plants respond with an oxidative burst to avirulent microbial intruders or to the previously mentioned abiotic stress factors. In this response, NADPH oxidases generate O_2^- that is rapidly converted to H_2O_2. Recent evidence demonstrated that the NADPH oxidases are activated by Ca^{2+} signatures. ROS are generated by NADPH oxidases

in the plasma membrane and increase in concentration in the cytoplasm; these species are also formed in mitochondrion and chloroplast.

The intricate and finely tuned molecular mechanisms activated in plants in response to abiotic and biotic environmental factors are not well understood, and less is known about the integrative signals and convergence points in different sets of partially overlapping reactions. It is now recognized that crosstalk between the second messengers Ca^{2+} and ROS modulates the activity of specific proteins that act at the nuclear level to control the expression of determinate defense genes. Recent studies exploring molecular players have identified and characterized several new genes, including kinases and transcription factors, that are involved in the crosstalk between signaling cascades involved in the responses against two or more types of stress.

Phytohormones also play central roles in abiotic and biotic stress signaling. SA, JA and ET have central roles in biotic stress signaling. ABA is involved in the response to abiotic stress as low temperature drought and osmotic stress. ABA appears to function as a negative regulator in disease resistance, in opposite action to SA, ET and JA. Several transcription factors including AtMYC2, BOS1 and RD26 are mediators in multiple hormone signaling pathways.

In our recent studies of a *Phaseolus vulgaris*/*Colletotrichum lindemuthianum* pathosystem, genes such as *SUMO* (Small Ubiquitin-like MOdifier) and a calcium-binding like protein (*CaM*) were induced to different levels during the time course of the response to avirulent pathogen inoculation, ultraviolet (A-B) light or extreme temperatures. These findings indicate that these two molecules should be included in the category of integrative signals in abiotic and biotic stress response in plants.

Other well known players in plant response to abiotic and biotic stress are members of the WRKY transcription factor family. Expression patterns of *VvWRKY11*, *AtWRKY39* and *AtWRKY53* genes indicate that protein products of these genes are co-regulators of the plant response against pathogens, hydric stress and heat stress. In addition, some WRKY transcription factors (OsWRKY24 and OsWRKY45*)* antagonize ABA function by repression of ABA-inducible promoters, indicating that these molecules operate with versatile capabilities. Clearly, the signaling components in plant responses to different abiotic and biotic stress often overlap. Commonly the activated signaling cascades act via synergistic and antagonistic actions.

Powerful molecular tools, including transcriptome and proteome analysis, sequencing of entire genomes in plants, bioinformatic analysis and functional studies, are enabling the disection of networks and identification of key factors in abiotic and biotic signaling cascade crosstalk, and will reveal novel interplays between parallel signaling pathways in the plant responses to pathogens and abiotic stress.

2. Calcium (Ca^{2+}) and reactive oxygen species (ROS) as second messengers common to abiotic and biotic stress responses

In plants, Ca^{2+} and ROS constitute important and common signaling molecules in the early response to abiotic and biotic stress. Levels of Ca^{2+} and ROS rapidly increase in cells of local tissue soon after pathogen attack or stress exerted by environmental conditions. Calcium is perhaps the main signal transducer in the signaling cascades activated in plant response to any stimulus or stress, and the ubiquitous characteristic of this molecule in stress signaling justifies the role of the Ca^{2+} cation as an important node at which crosstalk between

pathways can occur. Cytosolic Ca^{2+} levels increase in plant cells in response to various harsh environmental conditions, including pathogen challenge, osmotic stress, water stress, cold and wounding (Dey et al., 2010; Takahashi et al., 2011). For example, plant Ca^{2+} signals are involved in an array of intracellular signaling pathways after pest invasion. Upon herbivore feeding there is a dramatic Ca^{2+} influx, followed by the activation of Ca^{2+}-dependent signal transduction pathways that include interacting downstream networks of kinases (Arimura and Maffei, 2010).

In the last three decades, it has become clear that Ca^{2+} is a universal message transducer that acts on sub-cellular and spatio-temporal patterns of accumulation and protein interaction. Ca^{2+} influx through membrane Ca^{2+} ion channels or carriers yields specific spatial and temporal sub-cellular calcium ion elevations (Errakhi et al., 2008). These signals are then transduced downstream through several simultaneous pathways by calcium-interacting proteins such as CDPKs and CBLs; these Ca^{2+}-binding proteins all contain the 'EF-hand' calcium-binding motif (Kim et al., 2009). An example of Ca^{2+} concentration signatures related to specific signaling pathways is observed in tobacco stressed by wounding: Three calmodulin (CaM) isoforms (wound-inducible type I, hypersensitive response-inducible type III, and constitutive type II) are enabled at different cytosolic Ca^{2+} concentrations to activate the target enzymes NO synthase and NAD kinase (Karita et al., 2004).

There is ample evidence that ROS are also crucial second messengers involved in the response to diverse abiotic and biotic forms of stress. An oxidative burst takes place in response to avirulent microbial intruders (Lamb and Dixon, 1997) or to the previously mentioned abiotic stress factors including heat (Wahid et al., 2007), cold (Kwon et al., 2007), drought, salinity (Miller et al., 2010) and others. ROS production in plants by plasma membrane NADPH oxidases and apoplastic oxidases following pathogen recognition is well documented process (Allan and Fluhr, 1997; Lamb and Dixon, 1997; Bolwell et al., 2002; Torres et al., 2006; Galletti et al., 2008). Indeed, in plants a positive feedback mechanism involving NADPH oxidase, ROS and Ca^{2+} has been reported. Reduced levels of ROS stimulate Ca^{2+} influx into the cytoplasm and Ca^{2+} in turn activates NADPH oxidase to produce ROS (Takeda et al., 2008). Plant NADPH oxidases generate O_2^- that is converted to H_2O_2 by superoxide dismutase (SOD) and the peroxide diffuses through the cell wall to the extracellular medium and enters into the cell (Hammond-Kosack and Jones, 1996).

Reactive oxygen species are usually generated by NADPH oxidases in the plasma membrane, but in tobacco cells in response to abiotic stress as cadmium heavy metal, the anion superoxide is generated in mitochondria (Garnier et al., 2006). Mitochondria also serve as the site of ROS production upon abiotic stress exerted by copper in the marine alga *Ulva compressa* (Gonzalez et al., 2011). The NADPH oxidase is a multicomponent complex known as respiratory burst oxidase (RBO), initially described in mammals (Lambeth, 2004). The RBO enzymatic subunit is the transmembrane $gp91^{phox}$ protein that transfers electrons to molecular oxygen to generate superoxide (Lherminier et al., 2009). In *Arabidopsis thaliana*, ten gp91phox homologs have been reported (Torres and Dangl, 2005). It has been shown that members of the Rboh family mediate the ROS production in defense responses to microorganisms, as well as in response to wounding or mechanical stress (Yoshioka et al., 2003; Torres and Dangl, 2005). In *Arabidopsis*, the NADPH oxidase *AtrbohD*, which contains two EF-hand calcium binding motifs, is synergistically activated by Ca^{2+} and phosphorylation. Phosphorylation levels are correlated with ROS production (Ogasawara et al., 2008).

In the early signaling pathways in the plant defense response to pathogens, the opening of Ca^{2+}-associated of plasma membrane anion channels concomitant with the reactive oxygen species potential response have been described (Jurkowski et al., 2004; Dey et al., 2010). Crosstalk between these two signals in the plant response to abiotic stress has also been reported. In pea plants, the cellular response to long-term cadminum exposure consists of crosstalk between Ca^{2+}- and ROS- activated pathways and signaling mediated by nitric oxide (NO) (Rodriguez-Serrano et al., 2009). In roots in *Arabidopsis thaliana*, mechanical stimulation triggers rapid and transient cytoplasmic Ca^{2+} concentration increases; this mechanical stimulation likewise elicites apoplastic ROS production with the same kinetics (Monshausen et al., 2009). Certainly, the ROS (specifically H_2O_2) production in a Ca^{2+}-dependent manner and then the Ca^{2+}concentration regulation in cytoplasm by ROS through the activation of Ca^{2+} channels in the plasma membrane have been established (Takeda et al., 2008; Mazars et al., 2010).

The co-occurrence and the levels of the induction of Ca^{2+} and ROS signatures vary greatly and is dependent on pathosystem and environmental situation. For example, in callose deposition in *Arabidopsis* in response to the flagelin epitope Flg22 and the polysaccharide chitosan, environmental variability that imposes differential growth conditions is correlated with levels of hydrogen peroxide production. This demonstrates that callose deposition is a multifaceted response controlled by multiple signaling pathways, depending of the environmental conditions and the challenging pathogen-associated molecular pattern (Luna et al., 2011). In another example, pharmacological studies indicate that acclimation to low temperatures requires Ca^{2+} influx across the plasma membrane and a transient increase of Ca^{2+} in the cytoplasm (White and Broadley, 2003), and in *Arabidopsis* mesophyll cells, cold transiently activates Ca^{2+}-permeable channels (Carpaneto et al., 2007). The plant response to low temperature stress also includes production of reactive oxygen species (Heidarvand and Amiri, 2010).

Taking in account the aforementioned antecedents it is clear that responses to two or more forms of stress (biotic or abiotic) may overlap or converge in a common signaling element, for instance, Ca^{2+} or ROS or both, leading to similar downstream events. Calcium and ROS are ubiquitous second messengers in the abiotic and biotic stress signaling pathways and are in variable ways interconnected elements. There is strong evidence that Ca^{2+}-dependent ROS production through respiratory burst oxidase homolog (RBOH) enzyme activation is the first link. Induction of Ca^{2+} plasma membrane channels through the increase of cytoplasmic ROS is a second connection. Although these signals co-occur, their magnitudes, spatial location and timing depend on the biological system. The fine signatures in Ca^{2+} and the recently introduced concept of signatures in ROS (sub-cellular and spatiotemporal patterns of ROS) (Mazars et al., 2010) explain the downstream signaling independence that results in unique molecular responses in plant systems to the environment constraints with specific and adaptive responses.

3. Calcium-dependent protein kinases (CDPKs) and mitogen-activated protein kinases (MAPKs) crosstalk in response to abiotic and biotic stress

The transient changes in cytosolic calcium content with their diverse spatio-temporal signatures observed under biotic or abiotic stress conditions require different calcium sensors. A larger and defined group of calcium sensors are the calcium-dependent protein kinases (CDPKs) which in turn have many different substrates. CDPKs possess a

carboxyterminal calmodulin-like domain containing EF-hand calcium-binding sites plus a N-terminal protein kinase domain (Cheng et al., 2002). Thus, the signaling pathways activated in response to stress stand in part on CDPKs. The *Arabidopsis* genome encodes 34 CDPKs, but few substrates of these enzymes have been identified (Uno et al., 2009). Mitogen-activated protein kinases (MAPKs) are a family of Ser/Thr protein kinases widely conserved among eukaryotes. Them respond to extracellular stimuli and regulate various cellular activities, such as gene expression, mitosis, differentiation, proliferation, and cell survival/apoptosis. They work downstream of sensors/receptors and transmit extracellular stimuli into intracellular responses and at the same time amplifying the transducing signal (Ichimura et al., 2002). Amplification is accomplished by a MPK cascade of three hierarchically arranged, interacting types of kinases. MPK activity is induced upon phosphorylation by MPK kinases (MPKKs, MAPKKs, or MEKs), which are in turn phosphorylation activated by MPKK kinases (MPKKKs, MAPKKKs, or MEKKs). In *Arabidopsis*, there are 20 MPKs, 10 MPKKs, and 80 MPKKKs (Colcombet and Hirt, 2008). MAPKs act as last component in a protein kinase cascade, and one of their major tasks is to transducer an extracellular stimulus into a transcriptional response in the nucleus (Wurzinger et al., 2010).

In eukaryotes, CDPKs together with MAPKs are two signaling cascades widely activated in response to changing environmental abiotic and biotic stresses. In several pathosystems both cascades could be activated in response to the same stressing factor suggesting a crosstalk between those pathways (Wurzinger et al., 2010), or a specific CDPK or MAPK could be induced or activated in response to different biotic and abiotic stresses. Several studies in *Arabidopsis* demonstrate that: a) upon challenge exposure to biotic (bacterial pathogens) or abiotic (BTH, SA, and 4-chloro-SA) stress, MPK3 and MPK6 are activated and their respective mRNAs accumulate (Gerold et al., 2009); b) MKK2 is a key regulator of the cold- and salt-stress response (Teige et al., 2004) but, it was similarly involved in disease resistance to *Pseudomonas syringae* (Brader et al., 2007); c) the actived MKK9 protein in transgenic plants, induces the synthesis of ethylene and camalexin through the activation of the endogenous MPK3 and MPK6 kinases, moreover enhances the sensitivity to salt stress (Xu et al., 2008). In other hand, CDPKs CPK6 and CPK3 operate in ABA regulation of guard cell S-type anion- and Ca2+- permeable channels and stomatal closure (Mori et al., 2006), but besides its well-established role in abiotic stress adaptation, recent results in rice plants indicate that ABA is also involved in the regulation of pathogen defense responses, and mediates the repression of pathogen-induced ethylene signaling pathway in an MPK5-dependent manner (De Vleesschauwer et al., 2010).

From the accumulated data, the biological significance of crosstalk among signaling pathways under stress conditions that operate by CDPKs alone or together with MAPKs and viceversa, demonstrate that these two groups of calcium-dependent enzymes and the mitogen-activated protein kinases are involved in signaling pathways that in plants, in some cases signify the establishment of cellular mechanisms that lead to the simultaneous reinforcement of the defense responses to pathogens as well to other forms of abiotic stress. We are just to begin to uncover convergence points that command the crosstalk between these signaling pathways under various stress conditions.

4. Genetic pathways crosstalk in response to abiotic and biotic stress

A body of research demonstrates that plant defense response genes are transcriptionally activated by pathogens, as well by different forms of abiotic stress, or even more, the

induction of specific defense genes in the response against certain pathogens, are dependent on specific environmental conditions, suggesting the existence of a complex signaling network that allows the plant to recognize and protect itself against pathogens and environmental stress. Similar induction patterns of members of the *14.3.3* gene family (*GF14b* and *GF14c*) by abiotic and biotic stresses such as salinity, drought, ABA and fungal inoculation have been documented in rice. The rice *GF14* genes contain *cis*-elements in their promoter regions that are responsive to abiotic stress and pathogen attack. The *14-3-3s* family genes are also subject to the regulation by certain transcript factors (Chen et al., 2006). In rice, the *RO-292* gene is up-regulated in roots by salt or drought stresses and by blast fungus infection (Hashimoto et al., 2004). Similarly, the *Mlo* gene in barley (*Hordeum vulgare*) act as modulators of defense and cell death in response to *Blumeria graminis* f. sp. *tritici* or *Magnaporte grisea* inoculation, and to wounding or the herbicide paraquat (Piffanelli et al., 2002). In *Arabidopsis*, at least five of the 29 *cytochrome P450* genes are induced by abiotic and biotic stress including *Alternaria brassicicola* or *Alternaria alternata*, paraquat, rose bengal, UV stress (UV-C), heavy metal stress (CuSO4), mechanical wounding, drought, high salinity, low temperature or hormones (salicylic acid, jasmonic acid, ethylene and abscisic acid). These five *cytochrome P450* genes (*CYP81D11*, *CYP710A1*, *CYP81D8*, *Cyp71B6* and *CYP76C2*) are co-induced by metal stress ($CuSO_4$), paraquat, salinity, ABA and pathogen inoculation. A common characteristic shared by all of these induced genes, as in the 14.3.3 genes family, is the presence of *cis*-acting elements in regulatory regions of the gene; W-box (DNA binding sites for WRKY transcription factors), P-box (a positive *cis*-acting regulator of pathogen defense) and MYB recognition sites are common (Narusaka et al., 2004). A collection of genes, including transcription factors are co-activated by pathogen challenge and abiotic stress, examples of these genes mediating crosstalk between signaling pathways for biotic and abiotic stress responses are *DEAR1*, *BOS1* and *SlERF5*. *DEAR1* is a transcriptional repressor of DREB protein that mediates plant defense and freezing stress responses in *Arabidopsis*; the *DEAR1* mRNA accumulates in response to both pathogen infection (*Pseudomonas syringae*) and cold treatment (Tsutsui et al., 2009). *BOS1* codes for a R2R3MYB protein that acts as transcription factor that in *Arabidopsis* regulates responses to *Botrytis cinerea* infection and to water deficit, increased salinity and oxidative stress (Mengiste et al., 2003). *SlERF5* is highly expressed in response to the harpin protein coded in the *hrp* gene clusters in many Gram-negative phytopathogens; the over-expression of *SlERF5* is involved in the induction of the dehydration-responsive genes through the ABA-mediated abiotic stress response (Chuang et al., 2010).

Studies in our laboratory in common bean (*Phaseolus vulgaris*) leaves detached, inoculated with fungal pathogen, and maintained in humid chamber demonstrate that *chalcone synthase* (*CHS*), a gene implicated in the biosynthesis of phytoalexins in response to pathogen challenge (Ferrer et al., 1999), is also responsive to wounding at early times after stress. As shown in Figure 1, *CHS* mRNA is detected 6 hours post-wounding of leaves or at latter times post-inoculation with *Colletotrichum lindemuthianum*; the mRNA disappears by 12 hours post-wounding stress. In plants, following exposure to environmental stresses including pathogen attack and wounding, the phenylpropanoid pathway has important functions in the production of compounds including lignin, flavonoids and phytoalexins. Chalcone synthase (CHS) is a key enzyme in this pathway, catalyzing the first step in flavonoid biosynthesis, whose expression can be induced in response to environmental stress (Richard et al., 2000). This evidence exhibits the importance of molecular events in

downstream levels from the initial key factors (transcription factors), where secondary genes as chalcone synthase and phenylalanine ammonia-lyase (PAL) are able also to respond to abiotic and biotic stress, and are committed to achieve the relevant functions of biosynthesis of compounds with more direct actions toward microorganisms intruders, through phytoalexins; or the reinforcement of the cell wall with lignin, a macromolecule composed of highly cross-linked phenolic molecules, as a major component of secondary walls.

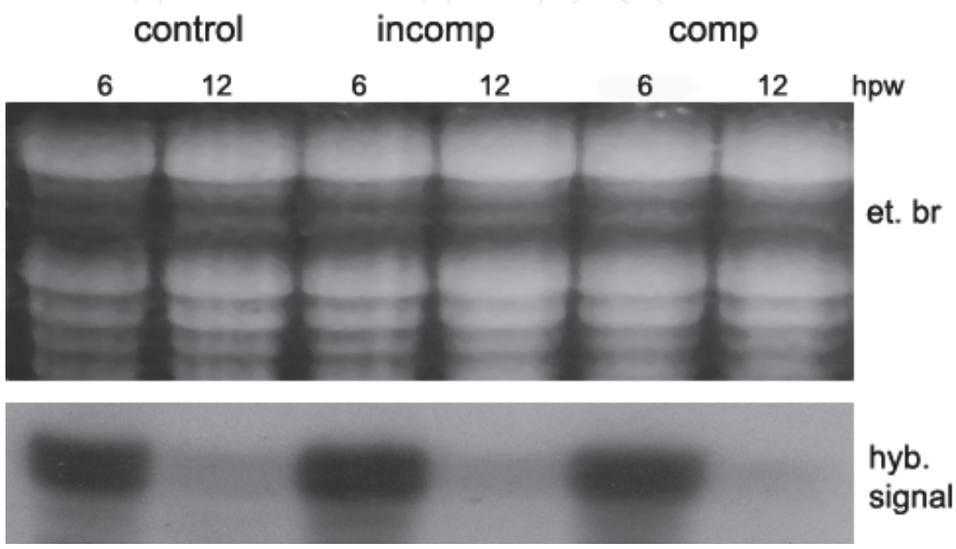

Fig. 1. *Chalcone synthase* mRNA levels in *Phaseolus vulgaris* leaves 6 and 12 hours after wounding besides pathogen interaction. Other leaves were inoculated with conidial suspensions of avirulent (incompatible) and virulent (compatible) *Colletotrichum lindemuthianum* pathotypes and total RNA was isolated after 6 and 12 hours. In the upper panel, total RNA (14 μg per lane) was stained with ethidium bromide; in bottom panel, the hybridization signal with a radiolabeled chalcone synthase cDNA probe is shown.

The signaling pathways in plants in response to microorganism intruders and to wound could be with a relevant level of crosstalk. In both cases, cytoplasmic Ca^{2+} increase and the reactive oxygen species production occur (Jurkowski et al., 2004; Karita et al., 2004; Dey et al., 2010), moreover the induction of *WRKY* and pathogenesis related (*PR*) gene expression (Leon et al., 2001; Takemoto et al., 2003; Huang et al., 2010). The level of crosstalk between different genetic pathways in the plant response to abiotic and biotic stress often vary, as expected, in accordance with the specificity of the stressors. On the biotic side, the response depends on the pathogen identity; on the abiotic side, it depends on the level of the stressing factor and the general environmental conditions. The commonality between different genetic pathways vary greater in relation with the species and the genotype in the plant species. In chickpea, the batteries of expressed genes identified in response to high salinity, drought, cold or pathogen inoculation show marked differential coincidences. It was found that the genes up-regulated in response to pathogens were more similar to these induced by high salinity than those up-regulated in response to cold or drought conditions. In 51 transcripts differentially expressed in plants inoculated with pathogen, 21 were common among *Ascochyta rabiei* inoculation and one or more of the other three abiotic conditions. It is noteworthy that no transcript was commonly differentially expressed across all the four

stresses assessed. Conversely, other sets of genes were found to be specifically induced by only one treatment, indicating the existence of specific signaling routes in addition to shared pathways (Mantri et al., 2010). A similar convergence of signaling pathways was reported for systemin, oligosaccharide elicitors and UV-B radiation at the level of mitogen-activated protein kinases (MAPKs) in *Lycopersicon peruvianum* suspension-cultured cells. LeMPK1 and LeMPK2, were activated in response to systemin, four different oligosaccharide elicitors, and UV-B radiation, whereas LeMPK3, was only activated by UV-B radiation. The common activation of LeMPK1 and LeMPK2 by many stress signals is consistent with a substantial overlap among stress responses; while UV-B induces specific responses (Holley et al., 2003). In our studies, in a *Phaseolus vulgaris*/*Colletotrichum lindemuthianum* pathosystem, the *SUMO* gene and the *EF-hand calcium-binding protein* gene were responsive to pathogen as well to the abiotic stresses UV light (UV-A and UV-B), and extreme temperatures (8° and 38°C). These two genes are induced to different levels by UV light and extreme temperatures conditions. The highest expression for the *SUMO* mRNA upon UV treatment was lower than of the *EF-hand calcium-binding protein* mRNA: After 4 hours of heat (38°C) treatment, the *EF-hand calcium-binding protein* mRNA levels surpass the *SUMO* mRNA levels (Fig. 2) (Alvarado-Gutiérrez et al., 2008). Thus, clearly the levels of individual defense genes are differentially regulated transcriptionally by abiotic and biotic forms of stress. In relation to *SUMO*, five WRKY transcription factors are SUMO1 targets (WRKY3, WRKY4, WRKY6, WRKY33, WRKY72); many WRKY transcription factors are commonly involved in plant defense reaction to pathogens, moreover several forms of abiotic stresses. Therefore, resistance protein signaling and SUMO conjugation also converge at transcription complexes. It is known that SUMO conjugation is essential to suppress defense signaling in non-infected plants, and recently was suggested a model in which SUMO conjugation can transform transcription activators into repressors, thereby preventing defense induction in the absence of a pathogen (Burg and Takken, 2010).

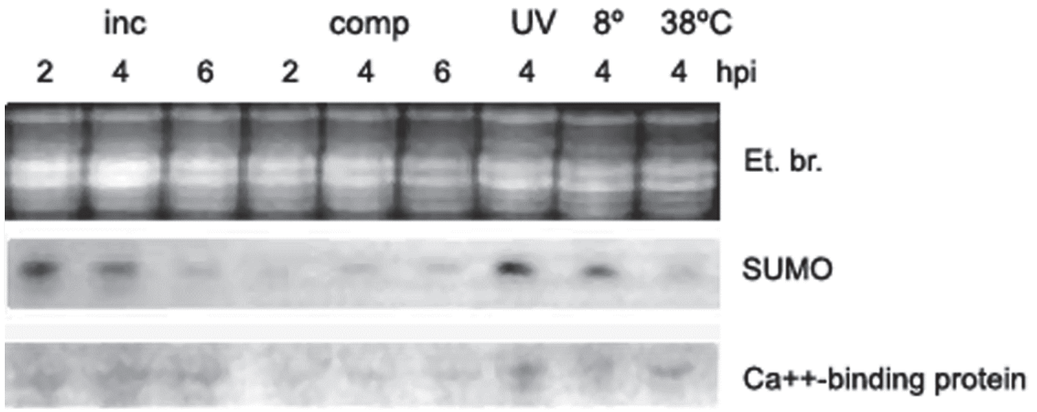

Fig. 2. *SUMO* and *EF-hand calcium-binding protein* mRNA levels in common bean plants after fungal infection or treatment with abiotic stresses UV light or extreme temperatures. Shown are northern blot assays of 12 μg of total RNA each lane. Radiolabeled probes for the two mRNAs were used. In the upper panel, total RNA was stained with ethidium bromide; in middle and bottom panels, signals for each gene are shown. Similar results were obtained from three independent experiments. Figure from previously reported results (Alvarado-Gutiérrez et al., 2008).

A complexity of the stress response in plants is evident when it is considered the natural fluctuating environmental conditions within a day or over longer periods of time. In the environment, changing states in light intensities, temperatures and pressures exerted by wind are normal. The dynamism inherent to factors that compose the environment impacts in changes in the profile of expression of some plant defense genes. As previously we reported, the *SUMO* and the *EF-hand calcium-binding protein* genes in the plant-pathogen interaction exhibit similar kinetics in the dark period, but not in the light period. For the *EF-hand calcium-binding protein* gene, the transcript levels in light in the control treated (H_2O sprinkled) leaves surpass those in the pathogen-treated leaves (Fig. 3) (Alvarado-Gutiérrez et al., 2008). Thus, these two genes, which are co-induced by two or more types of biotic and abiotic stresses, are also differentially regulated by the daily photoperiod advance and possibly by the circadian rhythm. These findings indicate that these two molecules should be included in the category of integrative signals in abiotic and biotic stress response in plants.

A number of *Arabidopsis thaliana* lesion-mimic mutants that show alterations in the responses to abiotic and biotic stresses have been reported. One class of these mutants exhibits constitutively increased *PR* gene expression, SA levels and heightened resistance to pathogen infection (Yoshioka et al., 2001; Jambunathan and McNellis, 2003; Jurkowski et al., 2004; Mosher et al., 2010); this class includes the *cpr22* mutant, which has mutations in two cyclic nucleotide-gated ion channels that impart the phenotype of spontaneous lesion formation, SA accumulation, constitutive *PR-1*, *PR-2* and *PR-5*gene expression and enhanced resistance to various pathogens (Mosher et al., 2010). Noteworthy, in the aforementioned mutants, the phenotypes exhibited are suppressed under high relative humidity and high temperature and are enhanced by low humidity and cold temperatures (Yoshioka et al., 2001; Mosher et al., 2010). Similarly, the effects on basal and resistance (*R*) gene-mediated resistance in *A. thaliana* and *Nicotiana benthamiana*/*Pseudomonas syringae* pathosystems are reduced at moderately elevated temperatures (Wang et al., 2009). In accordance with this data, a number of mutants in plants with de-regulated expression of R proteins have been shown temperature-dependent defense responses (Alcazar et al., 2009; Huang et al., 2010; Zhou et al., 2010). These data indicates that in these mutants, the resistance phenotypes are dependent on environmental conditions or that, at least, there are humidity and temperature sensitive steps (Mosher et al., 2010). Indeed, the resistance response mediated by *R* genes as well the basal resistance is attenuated when the temperature increases.

Collectively, these data suggest that specific batteries of defense genes are involved in different signaling cascades that converge with a degree of overlap in the response programs for pathogen defense and abiotic stress protection. There is a balanced interplay with fine-tuning between parallel signaling branches by different sets of partially overlapping reactions. Moreover, the genes that are the convergence points between different genetic pathways are differentially regulated, more evidently, when these genes are analyzed in the time scale, and definitely, the genetic pathways activated by *R* genes are modulated in variable levels by environmental factors. There are common factors in the defense signaling pathways to abiotic (humidity and temperatures variable conditions) and biotic (pathogen infection) stresses. These convergence points expose the superimposed complexity levels in the response to environmental changes. A pending task is the deciphering of the specificity of the signal transduction processes that conduit to the establishment of the commonality among different stress responses.

5. Phytohormones have central roles in abiotic and biotic stress signaling

Plant hormones, also called phytohormones, were first defined as "a substance which, being produced in any one part of the organism, is transferred to another part and there influences a specific physiological process" in the classical book *Phytohormones* written by Frits Went and Kenneth in 1937. The five classical phytohormones: auxin, cytokinin, ET, gibberellins, ABA and the recently identified brassinosteroids, JA and SA, are chemical messengers present in trace quantities; their synthesis and accumulation are tightly regulated. Depending on the context, they are subject to positive or negative feedback control and often are affected by crosstalk due to environmental inputs. Phytohormones move throughout the plant body via the xylem or phloem transport stream, move short distances between cells or are maintained in their site of synthesis to exert their influence on target cells where they bind transmembrane receptors located at the plasma membrane or endoplasmic reticulum or interact with intracellular receptors. The downstream effects of hormonal signaling include alterations in gene expression patterns and in some cases non-genomic responses. Changes in plant hormones concentrations and tissue sensitivity to them regulate a whole range of physiological process that have profound effects on growth and development. The phytohormomes affect all phases of the plant life cycle and their responses to environmental stresses, both biotic and abiotic. Hormonal signalling is critical for plant defenses against abiotic and biotic stresses (Crozier et al., 2000; Taiz and Zeiger, 2010; Williams, 2010).

Typically the phytohormones that regulate the responses against adverse cues are grouped into two types: those that play a major role in response to biotic stress (ET, JA and SA) and those that have pivotal roles regulating the abiotic stress responses (mainly ABA). Commonly the biotic defense signaling networks mediated by phytohormones are dependent on the nature of the pathogen and its mode of pathogenicity. SA plays a central role in the activation of defense responses against biotrophic and hemi-biotrophic pathogens as well as the establishment of systemic acquired resistance. By contrast, JA and ET are usually associated with defense against necrotrophic pathogens and herbivorous insects. Concerning to abiotic stress, ABA is the most studied stress-responsive hormone; it is involved in the responses to drought, osmotic and cold stress (Peleg and Blumwald, 2011; Wasilewska et al., 2008; Bari and Jones, 2009; Vlot et al., 2009).

5.1.2 Salicylic acid, ethylene, jasmonic acid and abscisic acid: are they working alone?

In addition to roles in activation of defense responses against biotrophic and hemi-biotrophic pathogens, SA is also important to the establishment of systemic acquired resistance (SAR) (Grant and Lamb, 2006; Vlot et al., 2009). When resistant tobacco and cucumber plants are inoculated with pathogens, the levels of SA increase (Malamy et al., 1990; Rasmussen et al., 1991). Exogenous applications of this chemical messenger result in the induction of *PR* genes increasing resistance to a broad range of pathogens (Vlot et al., 2009). In addition, transgenic plants and mutants of tobacco and *Arabidopsis* in which endogenous SA levels are reduced, fail to develop SAR or express *PR* genes; instead, they displayed heightened susceptibility to both virulent and avirulent pathogens. When these plants are treated with the SA synthetic analog, 2,6-dichloro-isonicotinic acid, resistance and *PR* genes expression are restored (Gaffney et al., 1993; Delaney et al., 1994; Vernooij et al., 1995.; Nawrath and Métraux, 1999; Nawrath et al., 2002; Genger et al., 2008; Vlot et al., 2009).

By contrast, over-expression of bacterial SA biosynthetic genes in transgenic tobacco confers highly elevated SA levels, *PR* gene expression, and enhanced resistance (Verberne et al., 2000). The SAR is induced systemically by a signal generated in the inoculated leaf; this signal is transmitted via the phloem to the uninfected portions of the plant (Grant and Lamb, 2006; Parker, 2009). SA levels rise coincidently with or just prior to SAR and systemic *PR* gene expression or peroxidase activation in pathogen-infected tobacco or cucumber, also was detected in the phloem of pathogen-infected cucumber and tobacco, and radio-tracer studies suggest that a significant amount of SA in the systemic leaves of pathogen-infected tobacco and cucumber is transported from the inoculated leaf. This was initially proposed to serve as signal in systemic acquired resistance; however, leaf detachment assays show that the mobile signal moves out of the infected leaf before increased SA levels are detected in petiole exudates from that leaf (Malamy et al., 1990; Rasmussen et al., 1991; Vlot et al., 2009). SA can be methylated to form methyl salicylate, in tobacco by the esterase SABP2 (an SA-binding protein). Recently, it has been shown that, methyl salicylate, which is induced upon pathogen infection, acts as an internal plant signal and also as an airborne defense signal (Forouhar et al., 2005; Park et al., 2007).

In plant defense responses against insects and microbial pathogens, JA is a crucial component. In *Arabidopsis* leaves, jasmonates control the expression of an estimated 67-85% of wound- and insect-regulated genes. Treatment of plants with JA results in enhanced resistance to herbivore challenge. Mutants defective in the biosynthesis or perception of JA show compromised resistance to herbivore attackers (Bari and Jones, 2009). Attack of herbivores such as *Manduca sexta* in tobacco induces the JA signaling activity (Paschold et al., 2007). Similarly, JA signaling is induced in tomato and *Arabidopsis* by *Tetranychus urticae* and *Pieris rapae*, respectably (Li et al., 2002; Reymond et al., 2004; De Vos et al., 2005). However, not all herbivores activate JA signaling in plants (Bari and Jones, 2009). The production of proteinase inhibitors (PIs) and other anti-nutritive compounds such as polyphenol oxidase (PPO), threonine deaminase (TD), leucine amino peptidase and acid phosphatase (VSP2) are mediated by JA in order to deter, sicken or kill the attacking insect (Howe and Jander, 2008). Also terpenoids and other volatile compounds produced by an herbivore-attacked plant are recognized by other carnivorous and parasitoid insects. The blends of compounds are specific to the particular plant/herbivore interaction, and the discerning carnivore uses this information to find its favorite meal (Howe and Jander, 2008; Williams, 2011).

5.1.2.1 Phytohormone signaling networks act together

Necrotrophic pathogens include most fungi and oomycetes as well as some bacteria. Defenses to these types of pathogens are often mediated by JA and ET. JA and ethylene operate synergistically to activate the expression of a subset of defense genes following pathogen inoculation in *Arabidopsis* (Thomma et al., 2001; Glazebrook, 2005). Experimental data confirm that JA and ethylene signaling pathways act together. Analysis of the mutants *coi1* (jasmonate insensitive) and *ein2* (ethylene insensitive) revealed that the induction of JA response marker gene *PDF1.2* by *Alternaria brassicicola* requires both JA and ethylene signaling pathways (Penninckx et al., 1998; Thomma et al., 2001). Genes acting as point controls between these two pathways have been described: *CEV1* acts as a negative regulator and *ERF1* (ethylene response factor 1) is a positive regulator (Ellis et al., 2002; Lorenzo et al., 2003).

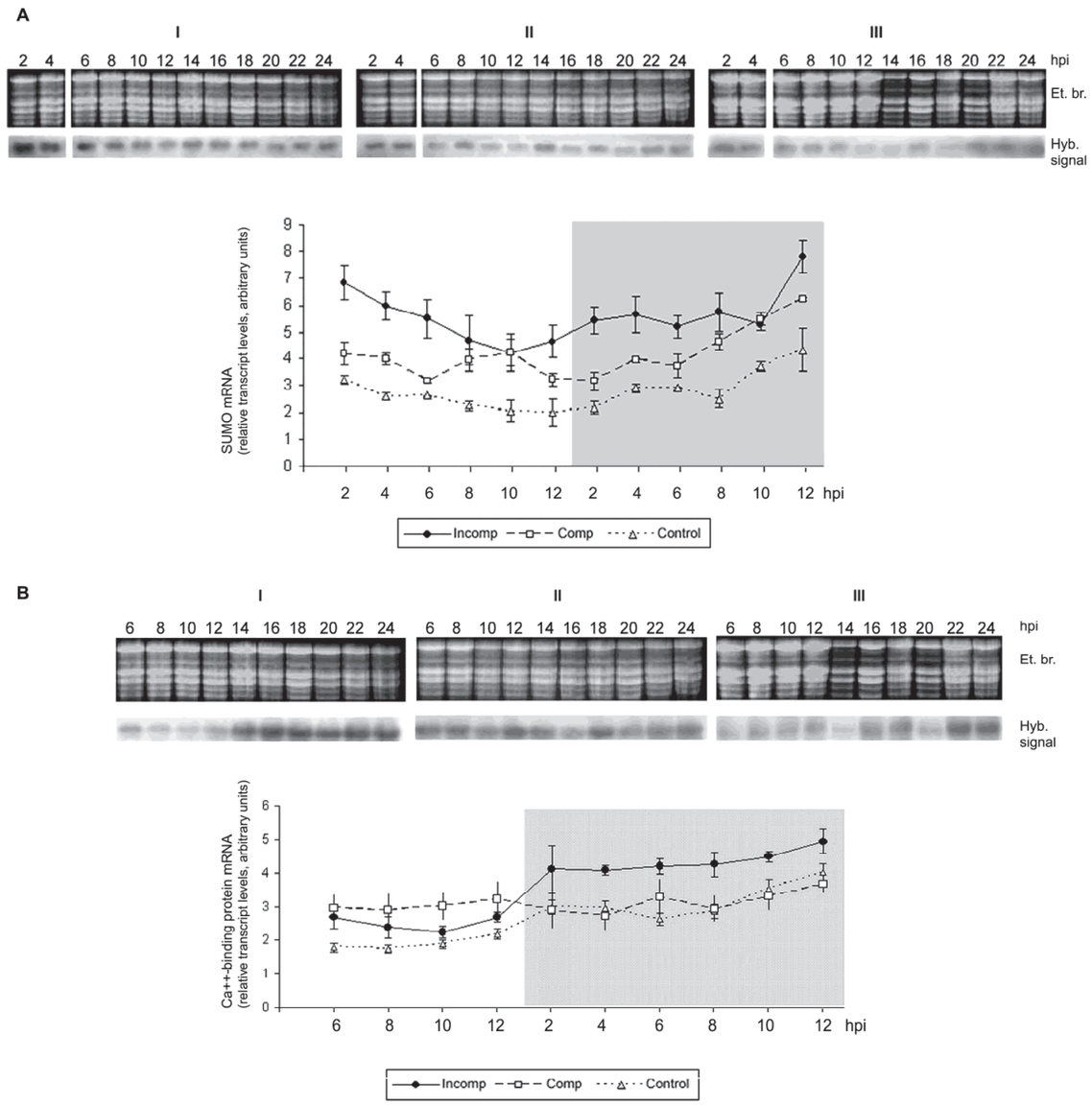

Fig. 3. *SUMO* and *EF-hand calcium-binding protein* mRNA levels in common bean plants infected with fungus through 24 hours with normal light and dark periods. Shown are northern blot assays with 14 µg of total RNA each lane. In panel A, RNA was hybridized with radiolabeled probe for *SUMO* mRNA. In panel B, a radiolabeled probe for the *EF-hand calcium-binding protein* mRNA was used. In A and B, from left to right: I, resistant interaction; II, susceptible interaction; and III, control plants in white background for day (light) period and in gray background for night (dark) period. The level of expression in the plot indicates transcript abundance relative to the 28S rRNA. Values are expressed as means of three independent experiments (± SE). Figure from previously reported results (Alvarado-Gutiérrez et al., 2008).

SA and JA are mutually antagonistic. Mutations that disrupt JA signaling (*coi1*) lead to the enhanced basal and inducible expression of the SA marker gene *PR1*, whereas mutations that disrupt SA signaling (*npr1*) lead to concomitant increases in the basal or induced levels of the JA marker gene *PDF1.2* (Kazan and Manners, 2008). Plants inoculated with virulent strains of *Pseudomonas syringae* pv. tomato treated with SA show compromised resistance to necrotrophic pathogen *Alternaria brassicicola*, which is sensitive to JA-dependent defenses (Spoel et al., 2007). The non-expresser of PR genes 1 (NPR1) is a master regulator of SA signaling. *Arabidopsis npr1* mutants fail in SA-mediated suppression of JA responsive genes suggesting that NPR1 plays an important role in the SA-JA interaction (Spoel et al., 2007). Acting downstream from NPR1, WRKY70, a transcription factor (TF) acts as a positive regulator of SA-dependent defenses and a negative regulator of JA-dependent defenses and plays central role in determining the balance between these two pathways. Suppression of *WRKY70* expression allows increased expression from JA-responsive genes and increased resistance to a pathogen sensitive to JA-dependent defenses. In contrast, over-expression of WRKY70 results in the constitutive expression of SA-responsive *PR* genes and enhanced resistance to SA-sensitive pathogens but reduces resistance to JA-sensitive pathogens (Li et al., 2004). Recently, WRKY6, WRKY53, mitogen activated protein kinase 4 (MPK4) and GRX480 (glutaredoxin) were reported to affect antagonism between SA- and JA-mediated signaling (Petersen et al., 2000; Brodersen et al., 2006; Mao et al., 2007; Miao and Zentgraf, 2007; Ndamukong et al., 2007). As we explained, plant hormone signaling pathways extensively interact during plant defense again pathogens and herbivores. Lifestyles of different pathogens are not often readily classifiable as purely biotrophic or necrotrophic. Therefore, those interacting points or crosstalk between SA and JA/ET pathways may be regulated in a pathogen-specific manner (Adie et al., 2007; Bari and Jones, 2009).

5.1.2.2 Abscisic acid in abiotic and biotic responses cross talk in plants

As sessile organisms, plants often have to cope with multiple environmental stresses; therefore most plants employ complex regulatory mechanisms to trigger effective responses against various biotic and abiotic stresses. In this scenario, phytohormones are the main players regulating these responses. To coordinate the complex interactions, an intense crosstalk among the regulatory networks is necessary. ABA is involved in the regulation of many aspects of plant growth and development and also is the major hormone that controls plant responses to abiotic stresses (Wasilewska et al., 2008).

In the last decade, our understanding of ABA involvement to pathogen susceptibility and its relationship to other phytohormones involved in biotic stress response have increased. Exogeneous ABA treatment increases the susceptibility of various plant species to bacterial and fungal pathogens (Heinfling et al., 1980; McDonald and Cahill, 1999; Thaler and Bostock, 2004; Mohr and Cahill, 2007)(Henfling et al., 1980; McDonald & Cahill., 1999; Mohr & Cahill, 2003; Thaler & Bostock, 2004; Ward et al., 1989). ABA-deficient tomato mutants show a reduction in susceptibility to the necrotroph *Botrytis cinerea* (Audenaert et al., 2002) and virulent isolates of *Pseudomonas syringae* pv tomato DC3000 (Thaler and Bostock, 2004; de Torres-Zabala et al., 2007), and ABA-deficient *Arabidopsis* has reduced susceptibility to the oomycete *Hyaloperonospora parasitica* (Mohr and Cahill, 2003). In general, ABA is involved in the negative regulation of plant defenses against various biotrophic and necrotrophic pathogens. However, the role of ABA appears to be complex and may vary depending on the pathosystem. The role of ABA as a positive regulator of defense has also been reported (Mauch-Mani and Mauch, 2005). ABA activates stomatal closure that acts as a

barrier against bacterial infection (Melotto et al., 2006). As a result, ABA-deficient mutants show more susceptibility to *Pseudomonas syringae* pv. tomato. In addition, treatment with ABA protects plants against *Alternaria brassicicola* and *Plectosphaerella cucumerina* indicating that ABA acts as a positive signal for defense against some necrotrophs (Ton and Mauch-Mani, 2004). Pathogen challenge results in the alteration of ABA levels in plants. For example, tobacco plants infected with tobacco mosaic virus (TMV) have increased ABA levels, and treatment with ABA enhances TMV resistance in tobacco (Whenham et al., 1986). Similarly, *Arabidopsis* plants challenged with virulent isolates of *Pseudomonas syringae* pv tomato DC3000, accumulate higher levels of ABA and JA than unchallenged plants (de Torres-Zabala et al., 2007). Additionally, mutants deficient in ABA are more sensitive to infection by the fungal pathogens *Pythium irregulare* (Adie et al., 2007) and *Leptosphaeria maculans* (Kaliff et al., 2007). The situation becomes even more complicated when pathogens are tested on ABA signaling mutants, such as *abi4,* which displays opposite resistance responses towards these two fungi. Along the same line, the mutations *abi1-1* and *abi2-1* actually foster differential resistance responses against *Leptosphaeria maucans* (Kaliff et al., 2007; Wasilewska et al., 2008). Transcriptome and meta analyses of expression profiles altered by infection with the necrotroph *Pythium irregulare* identified many JA-induced genes but also highlighted the importance of ABA as a regulator, as the ABA responsive element (ABRE) appears in the promoters of many of the defense genes (Adie et al., 2007; Wasilewska et al., 2008). This indicates that ABA plays an important role in the activation of plant defense through transcriptional reprogramming of plant cell metabolism. Moreover, ABA is required for JA biosynthesis and the expression of JA responsive genes after *Phytium irregular* infection (Adie et al., 2007). Recently, it has been identified the first molecular component in crosstalk between biotic and abiotic stress, the rice *MAP* gene *OsMPK5*. ABA antagonize pathogen-activated ET signaling via OsMPK5 (De Vleesschauwer et al., 2010).
The exact molecular mechanism of ABA action on plant defense responses against diverse pathogens started to be elucidated. Identification of more factors involved in ABA-mediated crosstalk between biotic and abiotic stress signaling merits extensive future study.

6. WRKY and other transcription factors as players in plant response to abiotic and biotic stress

Plant responses to environmental stimuli involve a network of molecular mechanisms that vary depending on the nature of environmental signal. In the signal transduction network that leads from the perception of stress signals to the expression of stress-responsive genes, transcription factors play an essential role. TFs are a group of master proteins that interact with *cis*-elements present in promoter regions upstream of genes and regulate their expression. Most TFs impact multiple physiologic processes such as metabolism, cell cycle progression, growth, development and reproduction (Fujita et al., 2009; Zhou et al., 2010; Hussain et al., 2011). Several transcription factors are mediators of multiple phytohormone signaling networks.

6.1 Transcription factors in crosstalk stress responses

The TFs are involved in responses against biotic and abiotic stress, and they play an esential role in regulation of plant adaptation to environmental changes. A few TFs have been reported to take part in the crosstalk between abiotic and biotic stress signaling nethworks. The basic helix-loop-helix (bHLH) domain-containing transcription factor AtMYC2 is a

positive regulator of ABA signaling. The genetic lession of *AtMYC2* results in elevated levels of basal and activated transcription from JA-ethylene responsive defense genes (Abe et al., 2003; Anderson et al., 2004). MYC2 differentially regulates two branches of JA-mediated responses; it positively regulates wound-responsive genes, including *VSP2, LOX3*, and *TAT*, but represses the expression of pathogen-responsive genes such as *PR4*, *PR1*, and *PDF1.2*. These complex interactions are co-mediated by the ethylene-responsive transcription factor ERF1 (Lorenzo et al., 2003; Lorenzo et al., 2004). The botrytis susceptible 1 (*BOS1*) gene of *Arabidopsis* encodes an R2R3MYB transcription factor that mediates responses to certain signals, possibly through ROS intermediates from both biotic and abiotic stress agents (Mengiste et al., 2003). There are also four members of the *NAC* family of genes that encode plant-specific transcription factors involved in diverse biological processes. *OsNAC6, Arabidopsis transcription activation factor 1* (*ATAF1*), *ATAF2* and *dehydration 26* (*RD26*) are potentially involved in regulation of responses to abiotic and biotic stresses (Wu et al., 2009).

6.2 WRKY transcription factors

WRKY proteins are a recently identified class of DNA-binding proteins that recognize the TTGAC(C/T) W-box elements found in the promoters of a large number of plant defense-related genes (Dong et al., 2003). These TFs contain WRKY domains that appear to be unique to plants (Eulgem and Somssich, 2007). The name of the WRKY family is derived from its highly conserved 60 amino acid long WRKY domain, comprising highly conserved WRKYGQK at N-terminus and a novel metal chelating zinc finger signature at C-terminus. *WRKY* genes thought to be plant-specific TFs that have been subject to a large plant-specific diversification. Phylogenetic analysis shows that the *WRKY* genes are clustered into several different groups on the basis of their amino acid sequences (Yamasaki et al., 2005; Eulgem and Somssich, 2007). *WRKY* genes probably originated concurrently with the major plant phyla.

Current information suggests that WRKY factors play a key role in regulating the pathogen-induced defense program. From the beginning of research into WRKY transcription factors, it was evident that they play roles in regulating several different plant processes. It is common for a single WRKY transcription factor to regulate transcriptional reprogramming associated with multiple plant processes. The dynamic web of signaling in which WRKY factors operate has multiple inputs and outputs (Rushton et al., 2010). It is expected that a single WRKY transcription factor has activity on both abiotic and biotic stress pathways and cross talks with different signal transduction pathways. The rice *WRKY45 (OsWRKY45)* gene expression is markedly induced in response to ABA and various abiotic stress factors such as NaCl, dehydration; in addition expression is induced by pathogens such as *Pyricularia oryzae Cav*. and *Xanthomonas oryzae* pv. oryzae. Moreover, *OsWRKY45*-over-expressing plants exhibited several changes: a) the constitutive expression of ABA-induced responses and abiotic-related stress factors, b) markedly enhanced drought resistance and c) increased expression of *PR* genes and resistance to the bacterial pathogen *Pseudomonas syringae*. Thus, OsWRKY45 shows a dual role, acting as a regulator and as a protective molecule upon water deficit and pathogen attack (Qiu and Yu, 2009). *VvWRKY11* from *Vitis vinnifera* is a nuclear protein that is expressed rapidly and transiently in response to treatment with SA or pathogen *Plasmopara viticola*. Transgenic *Arabidopsis* seedlings over-expressing *VvWRKY11* have higher tolerance to water stress induced by mannitol than wild-type plants. These

results demonstrate that the *VvWRKY11* gene is involved in the response to dehydration and biotic stress (Liu et al., 2011). Other well known players in plant responses to abiotic and biotic stresses are members of the WRKY transcription factor family. Expression patterns of *VvWRKY11*, *AtWRKY39* and *AtWRKY53* indicate that these genes are co-regulator of the plant response against pathogens and hydric and heat stress. In addition, some WRKY transcription factors (OsWRKY24 and OsWRKY45) antagonize ABA function, repressing an ABA-inducible promoter, indicating that these molecules operate with versatile capabilities.

7. Conclusion

Crop growth and crop yield are affected by environmental cues. There is a need of greater understanding of plant physiological responses to the abiotic and biotic stresses. We can understand stress as a stimulus or influence that is outside the normal range of homeostatic control in a given organism: If a stress tolerance is exceeded, mechanisms are activated at molecular, biochemical, physiological and morphological levels; once stress is controlled, a new physiological state is established, and homeostasis is re-established. When the stress is retired the plant may return to the original state or a new physiological state.

Plants continually encounter stress even under environmental conditions that we think of as normal. The environment changes during the day, day to day and throughout the year, thus plants must respond to stress over the course of each day and often must respond to several stresses at the same time. Study of stress responses show that there is much crosstalk among signaling networks during specific stress responses. Thus, plants may respond to stress perception by an initial global response and follow with specific stress responses.

As we discussed in this chapter, convergence points between biotic and abiotic stress signaling pathways have begun to be analyzed. Specific factors including transcription factors such as *WRKYs, ATAF1 and 2, MYC2, RD2, BOS1, OsNAC6* and OsMPK5 kinase are molecular player, common to multiple networks or involved in crosstalk between stress signaling pathways regulated by abscisic acid, salicylic acid, jasmonic acid and ethylene as well as ROS signaling. Powerful molecular tools, including transcriptome and proteome analyses, sequencing of entire genomes in plants, bioinformatic analyses and functional studies, will enable the dissection of networks and identification of key factors in abiotic and biotic signaling cascade crosstalk, which will reveal novel interplays between parallel signaling pathways in the plant responses to biotic and abiotic stress.

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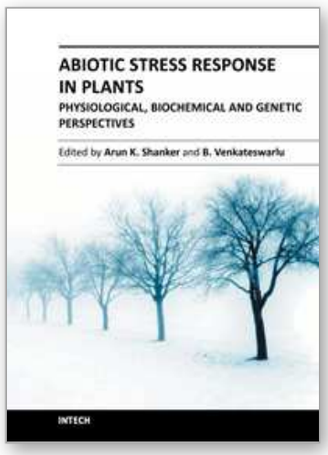

Abiotic Stress Response in Plants - Physiological, Biochemical and Genetic Perspectives

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Plants, unlike animals, are sessile. This demands that adverse changes in their environment are quickly recognized, distinguished and responded to with suitable reactions. Drought, heat, cold and salinity are among the major abiotic stresses that adversely affect plant growth and productivity. In general, abiotic stress often causes a series of morphological, physiological, biochemical and molecular changes that unfavorably affect plant growth, development and productivity. Drought, salinity, extreme temperatures (cold and heat) and oxidative stress are often interrelated; these conditions singularly or in combination induce cellular damage. To cope with abiotic stresses, of paramount significance is to understand plant responses to abiotic stresses that disturb the homeostatic equilibrium at cellular and molecular level in order to identify a common mechanism for multiple stress tolerance. This multi authored edited compilation attempts to put forth an all-inclusive biochemical and molecular picture in a systems approach wherein mechanism and adaptation aspects of abiotic stress are dealt with. The chief objective of the book hence is to deliver state of the art information for comprehending the effects of abiotic stress in plants at the cellular level.

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