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Plant Growth Regulators and their Role in Stress Tolerance

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ABSTRACT

Abiotic and biotic stresses affect the growth and yield adversely in agronomicaly important crop plants. Management through avoidance is not possible in plants hence these have developed various kinds of signaling processes that activate/recruit plant growth regulator molecules that are capable of protecting against stress. Major growth regulators include phytohormones, simple ions like Ca^{2+} or various non hormonal molecules. These growth regulators initiate/activate a cascade of events either on their own or by evolving a cross-talk within them that finally recruits various transcription factors those in turn activate or suppress a variety of genes. Accumulation of these gene products or their removal trigger activation of various protectant molecules which may include chaperons, osmolytes, gases, ions or other molecules capable of protecting cell constituents. In the present review, we have tried to bring out the recent advances towards the mechanisms of hormonal regulators such as ethylene, auxin, gibberellins, jasmonic acid, abscissic acid, brassinosteroids, non hormonal regulators like polyamine and salicylic acid and developmental regulators such as heat shock proteins, protein kinases, miRNA, histones and various other genes that are involved in plant stress management. With the advent of modern tools of recombinant DNA technology it could be possible to manipulate these regulators or its associated molecules in developing transgenic varieties that are resistant to stress. This will not only help in reducing losses in agricultural crops but also protect and save elite germplasm when conditions are not conducive.

Keywords: chemical signaling, MAPK, miRNA, osmoprotectant, phytohormone, polyamine, signal transduction

Abbreviations: **ACC**, 1-amino cyclopropane 1-carboxylate; **ABA**, abscisic acid; **ACS**, ACC synthase; **ACO**, ACC oxidase; **BR**, brassinosteroid; **CDPK**, calcium-dependent protein kinase; **CYT**, cytokinin; **ET**, ethylene; **GA**, gibberelin; **GUS**, glucuronidase; **HSP**, heat stress protein; **HMG**, high mobility group, **IAA**, indole-3-acetic acid; **MCP**, methylcyclopropane; **MAPK**, mitogen-activated protein kinase; **PGR**, plant growth regulator; **PA**, polyamine; **SA**, salicylic acid; **SIPK**, SA-induced protein kinase; **TF**, transcription factor; **WAK**, cell wall-associated kinase; **WAKL**, WAK-like kinase; **WIPK**, wound-induced protein kinase

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INTRODUCTION

Plants being non motile organisms have to encounter various kinds of stresses out of their surrounding where they grow. These include climatic, mechanical and biotic stresses (Tuteja 2007b, 2009a, 2009b). The stress management through avoidance is not applicable in case of plants hence they have developed various systems within to counter those stresses. Plants have developed capacities to sense changes/stress around them and recruit various signaling

Received: 31 January, 2009. Accepted: 18 December, 2009.

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molecules to transduce these signals locally or systemically to prepare themselves to manage it. Various phytohormones, biomolecules and chemicals are assigned different roles to manage different kind of stresses. Besides these having a direct role it is now well accepted that these entities work through a cross talk among themselves and a shift in the balance of either concentration or function culminate into a final effect against stress.

Plant development and productivity are negatively affected by environmental stresses (Khan and Singh 2008; Singh *et al.* 2008, 2009; Tuteja 2009a, 2009b). Global effects on desertification, soil salinization, atmospheric CO_2 enrichment and effects of other pollutants are predicted to cause dramatic changes in the climatic conditions of arable lands in this century. Every year India loses hundreds of millions of rupees from reductions in crop productivity caused by abiotic stresses (Mahajan and Tuteja 2005; Khan and Singh 2008). Maintaining crop yields under adverse environmental stress conditions is probably a major challenge facing modern agriculture. Further, in their natural environment, plants encounter a vast array of pathogenic microorganisms such as fungi, bacteria, viruses and nematodes. These diverse pathogens deliver effecter molecules (also called virulence factors) into the plant cell to promote virulence and cause disease. To survive under such conditions, plants have evolved intricate mechanisms to perceive external signals, allowing optimal response to environmental conditions. Phytohormones, such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA) are endogenous, low-molecular-weight molecules that primarily regulate the protective responses of plants against both biotic and abiotic stresses *via* synergistic and antagonistic actions, which are referred to as signaling crosstalk (Tuteja and Sopory 2008). On the other hand without stress effect many perennial plants simply would not survive. Trees, shrubs and herbaceous perennials put forth a flush of growth in spring when temperature, light and moisture are optimal. As summer progresses and rains are more frequent the temperature, humidity and light may rise above those that are conducive to growth. The plants use their signaling mechanisms and enter into dormancy. If it happened differently the plants will continue to grow and invite ultimately to death. To understand this complex phenomenon it is necessary to understand the contrasting adaptations of plants to grow in stressed and unstressed conditions, and the compromises and trade-offs between them.

In this review we have tried to review the knowledge that has been gathered over the last couple of decades with respect to various factors that participate in stress management in plants. The most recent knowledge in this respect includes involvement of various protein kinases and transcription factors which participate in signaling and transcriptional regulation of related genes respectively.

HORMONAL GROWTH REGULATORS AND THEIR ROLE IN STRESS

As mentioned earlier most of the abiotic stress is responded by variation in the levels of abscissic acid whereas, biotic stress enhances ethylene and jasmonic acid levels. It is now believed that other hormones such as gibberellins (GAs), auxin, cytokinin (CYT) and recently brassinosteroids (BRs) do also participate in various types of signal transduction during stress in plants. Recent reviews by Bari and Jones (2009), López *et al.* (2008) and Spoel and Dong (2008) clearly indicate that all phytohormones get activated during any kind of stress and either up regulate or down regulate several genes to let plant exert its effect. Some of the important phytohormones and their relevance in stress are reviewed.

Ethylene

The two carbon gaseous plant hormone ET could be considered as the most important phytohormone for more than one reason. Its involvement in almost every phase of the life cycle of a plant makes it most studied plant hormone so far. From seed germination, to growth and development, pollination to fruit development and ripening and organ abscission to senescence ET has been shown to involve in one way or the other (Ables *et al.* 1992). In the past couple of decades its role in various types of biotic and abiotic stress has been well elucidated. Moreover, one of the most studied signaling processes in plants is ET signaling (Klee and Clark 2004). Several components through which ET signal is transduced have been characterized functionally through transgenics or loss/gain of function approaches in mutants. Recently various other phytohormones are believed to exert their effect through cross talk with components of ET signaling and related transcription factors. This makes ET as a major phytohormone in plant processes. What progress has been made towards the understanding of role of ET in stress condition in plants is described in following paragraphs.

It has been observed that the most common and pronounced responses of plants to various environmental stresses is the enhanced production of ET. ET production of plants was shown to be enhanced by various stresses including biological stresses such as infection with pathogens or infestation with herbivores (Abeles *et al.* 1992; Arimura *et al.* 2002). ET is synthesized from S-adenosyl L methionine (SAM), a key molecule for several metabolic pathways. Two major enzymes which participate in the biosynthesis of ET are 1-amino cyclopropane 1-carboxylate synthase (ACC) and ACC oxidase which act stepwise to produce ET, CO_2 and HCN (Yang and Hoffman 1984; Kende 1993). There exist two systems for the biosynthesis of ET (McMurchie *et al.* 1972). System I is operative throughout the life cycle of plant where a small but variable amount of ET is produced depending upon the physiological need of the plant. System II is operative when a large amount of ET is required such as fruit ripening, senescence and under certain instances of stress. Switch over from system I to II is largely dependent on the type of the plant and the physiological situation. Enzymes ACS and ACO are encoded by multi-gene families, which are regulated independently and in a tissue-specific manner in response to one or a specific set of several environmental effectors. In a particular stress, plant, tissue or the developmental stage, the generation of ACC and/or its conversion into ET is stimulated/suppressed while the generation of SAM from methionine is rather constitutive (Pech *et al.* 2004). Later positive and negative feedback of ET production was established by several workers. We shall review that under various conditions how the transcription of ACS/ACO is affected.

Wounding of mature cucumber (*Cucumis sativus*) fruits by slicing and subsequent cutting induced the accumulation of mRNAs of the genes *CSACS1*, *CS-ACS2* and *CS-ACO1*, while maximum expression of both *CS-ACS1* and *CS-ACO1* coincided with the peak of ET production (Shiomi *et al.* 1998). Mathooko *et al.* (2001) studied the effect of combinations of wounding and applications of the translational inhibitor cycloheximide (CHX), the ET action inhibitor 1-methylcyclopropane (MCP) as well as ET on the ET biosynthetic pathway in peach (*Prunus persica*) fruits. A translation-independent expression of genes of ACS and ACO in wound-induced ET production was found and a positive feedback control of wound-induced expression and activity of ACO was monitored. Further, transgenic lines of *Arabidopsis* expressing the glucuronidase (GUS) and green fluorescence protein (GFP) reporter genes from the promoter of each of the *Arabidopsis* ACS gene family members (Tsuchisaka and Theologis 2004) indicated that wounding of hypocotyls inhibited the constitutive transcription of the genes *ACS1* and *ACS5* in the same tissues, whereas expression of *ACS2*, *ACS4*, *ACS6*, *ACS7*, *ACS8* and *ACS11* was induced. Wang *et al.* (2005) expressed *ACS4*, *ACS5* and *ACS7* in the same plant species using ACS-GUS transgenic lines. They found that wounding of leaves by squeezing with tweezers caused an increased reporter gene activity only in the *ACS4*-

GUS and the *ACS5-GUS* transformed plants. As the expression of *ACS4* and *ACS7* was stimulated by wounding, the authors proposed a coexistence of ET autocatalysis and autoinhibition in vegetative tissues. Katz *et al.* (2005) provided similar evidence that two types of ET production, an autocatalytic and an auto-inhibitory system might operate in leaves, both of which could also be induced by wounding increased ET production can be found after plants having experienced water deficit during fruit development (Gelly *et al.* 2003).

The transcription of *ACS* and *ACO* genes may respond to the water deficit in a very tissue-specific but coordinated manner as described by Nakano *et al.* (2002). Such specific responses were recently detected when *Arabidopsis* seedlings were exposed to a short-term water deficit for 3h (Wang *et al.* 2005). Activity of *GUS*-reporter genes revealed a substantial decrease in expression of the *ACS* gene *ACS5* after this treatment, whereas only a slight decrease of *ACS7* was detected and *ACS4* was not affected at all.

Salinity may affect the plant during seed germination and role of ET during seed germination is well established. When wheat seeds of two cultivars were germinated in petri plates, the increasing levels of salinity of either Cl^- or SO_4^- type did not accelerate ET evolution though dry matter of seedlings was strongly reduced (Datta *et al.* 1998). However, germination of lettuce (*Lactuca sativa*) seeds of nine cultivars in 150 mM NaCl compared to distilled water increased ET evolution (Zapata *et al.* 2003). When seeds of seven plant species were germinated under similar salinity conditions, this induced enhanced ET production only with four species including lettuce, whereas, even a decrease in ET evolution was found with three other species (Zapata *et al.* 2004). The different responses could be due to plant specific ACO activity. Exposing rice plants (*Oryza sativa*) of four cultivars to increasing concentrations of NaCl up to 50 mM in nutrient solution raised ET production of leaves and ACC concentration in same organs. The responses were highly variable among cultivars, duration of salt stress and leaf age (Lutts *et al.* 1996). In tomato plants, ET evolution in petioles, and ACC levels in roots, petioles, leaves as well as in premature and mature fruits increased with increasing concentration of NaCl in nutrient solution (Botella *et al.* 2000; El-Iklil *et al.* 2002). When rootstocks of *Citrus* were exposed to increasing levels of chloride a dramatic increase in ET evolution of leaves was observed only in the chloride-sensitive genotype, which was associated with an increased ACC level in leaves (Bar *et al.* 1998). This response could be strongly suppressed by the addition of nitrate, which competes with the chloride uptake. Salt shock to seedlings of a *Citrus* sp. by the application of 200 mM NaCl increased ACC levels in roots, in xylem fluid and in leaves, and dramatically raised leaf ET production (Gómez-Cadenas *et al.* 1998). Salinity-induced transcription of various *ACS* isogenes suggests that there exist specific responses of the different gene family members, which obviously depend on salt concentration, tissue and other environmental factors. Thus, when leaves of *Arabidopsis thaliana* were treated with different salt solutions, expression of the *ACS* genes *ACS1*, *ACS3*, *ACS4* and *ACS5* did not respond to either 100 mM NaCl, 50 mM LiCl, or 500 mM $CuCl_2$, whereas, *ACS*6 and *ACC* level were highly responsive to all salts and *ACS2* was only slightly responsive to NaCl (Arteca and Arteca 1999). However, when *Arabidopsis* seedlings were exposed to 300 mM NaCl, *GUS*-reporter gene activity indicated induced expression of the *ACS5* and also of the *ACS7* gene (Wang *et al.* 2005).

During the last decade, evidence has been provided that flooding stimulates the expression of genes for ACS and ACO. Shiu *et al.* (1998) showed that ET production in leaves of waterlogged tomato plants varied and peaked with the light periods. The transcription of the ACS gene *LE-ACS2* was induced in roots after flooding and then fluctuated during the dark periods. Soil flooding increased the ACO activity in petioles of a wild-type tomato within 6 to 12h, which was associated with higher rates of ET production, whereas both responses were reduced in a transgenic tomato line coding an anti-sense construct to the ACO gene *LE-ACO1* (English *et al.* 1995). Water logging of potato seedlings resulted in a rapid and transient induction of *ACO1* and *ACO2* in roots and *ACO1* in leaves, within 2h after flooding and continued to increase up to 15h (Nie *et al.* 2002). Submergence not only entraps but also stimulates production of ET in deepwater rice by increased activities of ACS and ACO (Mekhedov and Kende 1996). Submergence induced the expression of *OS-ACS1* (Zarembinski and Theologis 1997) and of *OS-ACS5*, the latter of which may account for the early accumulation of ACC (Zhou *et al.* 2001).

One major adjustment made by both plant and animal cells in response to hypoxia is the switching from aerobic respiration to lactic or ethanolic fermentation (Roberts *et al.* 1984a, 1984b). The role of ADH has been widely studied during hypoxia in plants. In *Arabidopsis* it was found that the hypoxic induction of ADH can be partially inhibited by AOA, an inhibitor of ET biosynthesis (Peng *et al.* 2001). This partial inhibition can be reversed by adding ACC. It has been now shown by Peng *et al.* (2005) that the expression of 4 of the 12 *Arabidopsis* ACS genes, *ACS2*, *ACS6*, *ACS7*, and *ACS9* are induced during hypoxia with three distinct patterns. The hypoxic induction of *ACS9* is inhibited by aminooxy acetic acid, an inhibitor of ET biosynthesis. In addition, the hypoxic induction of *ACS9* is also reduced in *etr1-1* and *ein2-1*, two ET insensitive mutants in ET-signaling pathways, whereas, the addition of 1-aminocyclopropane-1-carboxylic acid, a direct precursor of ET, does not induce *ACS9* under non toxic conditions. These results indicate that ET is needed, but not sufficient, for the induction of *ACS9* during hypoxia.

Drought, which can induce senescence in older leaves, promotes increased ET production in plants by increasing ACC synthesis and its conversion to ET (Apelbaum and Yang 1981). Foliar chlorophyll content decreases as a function of the severity of a water stress (Baisak *et al.* 1994) and inhibition of ET synthesis reduces the drought-induced loss of chlorophyll and prevents drought-induced senescence (Beltrano *et al.* 1999). ET regulates entry into several types of plant developmental cell death and senescence programs besides mediating plant responses to biotic and abiotic stress. The response of cereals to conditions of drought includes loss of leaf function and premature onset of senescence in older leaves. The ACC synthase (*ACS*) mutants, affecting the first step in ET biosynthesis, were isolated in maize and their effect on leaf function examined. Loss of *ZmACS6* expression resulted in delayed leaf senescence under normal growth conditions and inhibited drought-induced senescence. *ZmACS6* leaves continued to be photosynthetically active under both conditions indicating that leaf function was maintained. The delayed senescence phenotype associated with loss of *ZmACS6* expression was complemented by exogenous ACC (Young *et al.* 2004).

In plants, two classes of stress activated protein kinases, mitogen activated protein kinases (MAPKs) and calcium dependent protein kinases (CDPKs) have been reported to integrate multiple environmental stresses and undergo rapid biochemical activation upon exposure to biotic and abiotic stress (Mishra *et al.* 2006; Tuteja and Mahajan 2007; Mahajan *et al.* 2008; Tuteja 2009a). N-terminal CDPK2 signaling triggered enhanced levels of JA and ET but not SA. Elevated CDPK signaling compromised stress induced MAPK activation and this inhibition required ET synthesis and perception. (Ludwig *et al.* 2005). Recent studies have demonstrated that the activity of ACS can be regulated at the post-translational level by protein phosphorylation and dephosphorylation, which potentially could alter the turnover rate of ACS protein (Spanu *et al.* 1994; Wang *et al.* 2002). Protein phosphorylation and dephosphorylation were implicated in the regulation of ET induction by stresses based on studies using protein kinase and phosphatase inhibitors. However, the kinase(s) involved remains to be determined. Using a conditional gain-of-function transgenic system, it was demonstrated that the activation of SIPK, a tobacco MAPK, by NtMEK2, an active mutant of the upstream kinase of SIPK, resulted in a dramatic increase in ET production. The increase in ET after the activation of SIPK coincided with a dramatic increase in ACC synthase (ACS) activity, which was followed by the activation of a subgroup of *ACS* and *ACO* genes, suggesting that either the activation of unidentified *ACS*(s) or post-transcriptional regulation is involved. Infection with *Tobacco mosaic virus* (TMV), which is known to activate the SIPK cascade and induce ET biosynthesis, also induced the same *ACS*s and *ACO*s (Kim CY *et al.* 2003).

The biochemical properties of *A. thaliana* type II recaptors were also studied and it was found that these receptors can bind ET and possessed serine kinase activity (Moussatche and Klee 2004; O'Malley *et al.* 2005). Similarly, a type II ET receptor, *NTHK1*, from tobacco was well characterized. This protein shows about 50% identity with *ETR2* or *EIN4* and possesses serine/threonine kinase activity (Xie *et al.* 2003). *NTHK1* was found to be localized in the plasma membrane of plant cells (Xie *et al.* 2003). Another tobacco ET receptor, *NTHK2*, was found to possess activities of serine/threonine and histidine kinases in the presence of Mn^{2+} and Ca^{2+}, respectively (Zhang *et al.* 2004). The difference in kinase activities and localization may reflect the divergence of the roles played by these ET receptors. ET receptor genes from other plants were also isolated and characterized (Cao Y *et al.* 2003; Klee 2004; Yau *et al.* 2004). ET has been regarded as a stress hormone involved in many stress responses. However, ET receptors have not been studied for the roles they played under salt stress condition. Previously, an ET receptor gene *NTHK1* from tobacco was characterized and found that *NTHK1* is salt-inducible. Further investigation towards the function of *NTHK1* in response to salt stress by using a transgenic approach was carried out. It was found that *NTHK1* promotes leaf growth in the transgenic tobacco seedlings but affects salt sensitivity in these transgenic seedlings under salt stress condition (Zhou *et al.* 2006). Differential Na^+/K^+ ratio was observed in the control Xanthi and *NTHK1*-transgenic plants after salt stress treatment. It was concluded that the *NTHK1* transgene is also salt-inducible in the transgenic plants, and the higher *NTHK1* expression results in early inductions of the ACC oxidase gene *NtACO3* and ET responsive factor (ERF) genes *NtERF1* and *NtERF4* under salt stress. However, *NTHK1* suppresses the salt-inducible expression of the ACC synthase gene *NtACS1*. These results indicate that *NTHK1* regulates salt stress responses by affecting ion accumulation and related gene expressions, and hence have significance in elucidation of ET receptor functions during stress signal transduction.

The nuclear protein ETHYLENE INSENSITIVE2 (*EIN2*) is a central component of the ET signal transduction pathway in plants, and plays an important role in mediating cross-links between several hormone response pathways. It was shown that *EIN2* gene regulates plant response to osmotic and salt stress through an ABA-dependent pathway in *Arabidopsis*. The expression of the *EIN2* gene is down-regulated by salt and osmotic stress. An *Arabidopsis EIN2* null mutant was supersensitive to both salt and osmotic stress conditions. Disruption of *EIN2* specifically altered the expression pattern of stress marker gene *RD29B* in response to the stresses (Wang *et al.* 2007). *EIN2* encodes an Nramp family protein and is considered a central component in ET signaling pathway because it is the only gene whose null loss-of function mutations result in complete ET insensitivity in *Arabidopsis* (Alonso *et al.* 1999; Shibuya *et al.* 2004). Analyses of loss-of-function mutations indicated that *EIN2* may act as a node mediating cross-talk of multiple hormone signaling pathways and responses to pathogens and pests (Lorenzo *et al.* 2003; Tang *et al.* 2005). Recently, Cao WH *et al.* (2006) proposed that only partial ET signaling pathway may involve in plant response to salt stress and it branched off at *EIN2*. Recent studies revealed a very close connection between a novel tomato ethylene response factor 1 (*TERF1*) integrates ET and osmotic stress pathway. It binds to GCC box and to dehydration response element. Its expression was induced by ET and NaCl. Over expression of *TERF1* activated *GCC* box containing pathogen related genes and also caused a typical triple response. Transgenic *TERF1* tomato exhibited salt tolerance. It might work as linker between ET and osmotic stress pathway (Huang *et al.* 2004).

The tomato ERF protein *TSRF1*, is transcriptionally upregulated by ET, SA, or *Ralstonia solanacearum* strain BJ1057 infection. Biochemical analysis indicates that *TSRF1* specifically interacts *in vitro* with the *GCC* box, an element present in the promoters of many pathogenesis-related (PR) genes. Further investigation indicated that *TSRF1* activates *in vivo* the expression of reporter β-glucuronidase gene controlled by *GCC* box. More importantly, over expressing *TSRF1* in tobacco and tomato constitutively activates the expression of PR genes, and subsequently enhancing transgenic plant resistance to the bacterial wilt caused by *Ralstonia solanacearum* strain BJ1057 (Zhang *et al.* 2004).

The *AtNAC2* expression was induced by salt stress and this induction was reduced in magnitude in the transgenic *Arabidopsis* plants overexpressing tobacco ET receptor gene *NTHK1*. *AtNAC2* is localized in the nucleus and has transcriptional activation activity. It can form a homodimer in yeast. *AtNAC2* was highly expressed in roots and flowers, but less expressed in other organs examined. In addition to the salt induction, the *AtNAC2* can also be induced by ABA ACC and NAA. The salt induction was enhanced in the ET overproducer mutant *etol-1*, but suppressed in the ET-insensitive mutants *etr1-1* and *ein2-1*, and in the auxin-insensitive mutant *tir1-1* when compared with that in wild-type plants (He XJ *et al.* 2005).

Four rice genes, *OsBIERF1* to *OsBIERF4* (*Oryza sativa* benzothiadiazole (BTH)- that induced ET responsive transcriptional factors (ERF)) were identified and analyzed their expressions in rice disease resistance response and under various abiotic stress conditions. The *OsBIERF1-4* proteins contain conserved ERF domains, but are categorized into different classes of the previously characterized ERF proteins based on their structural organizations. *OsBIERF3* and *OsBIERF2* belong to Classes I and II, respectively; while *OsBIRERF1* and *OsBIERF4* are members of Class IV. *OsBIERF3* could bind specifically to the *GCC* box sequence and was targeted to nucleus when transiently expressed in onion epidermis cells. Expression of *OsBIERF1*, *OsBIERF3* and *OsBIERF4* was induced by treatments with BTH and SA, chemical inducers capable of inducing disease resistance response in rice. In the BTH-treated rice seedlings, expression of *OsBIERF1*, *OsBIERF3* and *OsBIERF4* was further induced by infection with *Magnaporthe grisea*, the rice blast fungus, as compared with those in water-treated seedlings. *OsBIERF1* and *OsBIERF3* were activated in an incompatible interaction but not in compatible interaction between rice and *M. grisea*. Moreover, *OsBIERF1*, *OsBIERF3* and *OsBIERF4* were also upregulated by salt, cold, drought and wounding. These results suggest that *OsBIERF* proteins may participate in different signaling pathways that mediate disease resistance response and stress responses to abiotic factors (Cao Y *et al.* 2006). *Hahb-4* is a member of transcription factor belonging to subfamily I of HD-zip protein that is transcriptionally regulated by water availability and ABA. Manarella *et al.* (2006) have shown that this is a new component of ET signaling pathway that induces marked delay in senescence. *Hahb-4* over expressing lines show strong tolerance to water stress. These lines are less sensitive to ET. This has a major repressive effect on ACS and SAM and on *ERF2* and *ERF5*. Qin *et al.* (2006) have shown that *GbERF* belonging to *ERF* family that regulates *GCC* box containing PR genes when over expressed did not change endogenous levels of ET. However, expression profile of several PR genes, osmotin, *CHN50*, *ACS* and *ACO* were altered.

Jasmonic acid

JA is a key signaling phytohormones in numerous plant responses to stresses (Kunkel and Brooks 2002). It is one of the final products of the octadecanoid pathway. This molecule functions as a signal, together with other intermediates in this pathway and with biologically active derivatives (referred collectively as jasmonates), in response to biotic or abiotic stress. JA are fundamental to the mediation of responses to stress, such as wounding and elicitor molecules (Doares *et al*. 1995; Parchmann *et al*. 1997; León *et al*. 2001), ultraviolet light and ozone exposure (Overmyer *et al*. 2000; Rao *et al*. 2000), drought (Sugano *et al*. 2003), defences against insects (McConn *et al*. 1997), pathogens (Kloek *et al*. 2001) as well as in plant growth and development. Recent studies suggest that, JA plays an important role in defense mechanisms in rice (Rakwal and Komatsu 2000; Kim JA *et al*. 2003). Also, in symbiotic interactions such as arbuscular mycorrhiza, plant defense responses are triggered during early stages (Liu *et al*. 2003). In barley, colonization by an arbuscular fungus leads to elevated levels of JA (Hause *et al*. 2002). Plant responses to the activation of JA signaling eventually involve the induction of genes, such as those encoding the vegetative storage proteins (VSPs) (Benedetti *et al*. 1995), thionin (Thi2.1) (Epple *et al*. 1995; Vignutelli *et al*. 1998) and a plant defensin (PDF1.2) (Penninckx *et al*. 1998). JAs also enhance the transcription of genes involved in JA synthesis, such as *DAD1*, *LOX2*, *AOS*, *OPR3* and *JMT* (Heitz *et al*. 1997; Laudert and Weiler 1998; Mussig *et al*. 2000; Ishiguro *et al*. 2001; Seo *et al*. 2001). Microarray analyses have confirmed the methyl jasmonate (MeJA) inducibility and organspecific expression of genes required for JA biosynthesis, corroborating the existence of a positive feedback regulatory system for JA biosynthesis (Sasaki *et al*. 2001). Wasternack (2007) reported that JA alters gene expression positively or negatively in a regulatory network with synergistic and antagonistic effects in relation to other plant hormones such as salicylate, auxin, ET and ABA. It is reported in tobacco that, wounding causes rapid activation of two MAPKs, wound-induced protein kinase (WIPK) and SA-induced protein kinase (SIPK), and the subsequent accumulation of JA. It is found that activation of WIPK is required for the production of wound-induced JA. Seo *et al*. (2007) suggested that WIPK and SIPK play an important role in JA production in response to wounding, and that they function cooperatively to control SA biosynthesis. In *Arabidopsis* the systemic immunity uses conserved defense signaling pathways, which is found to mediate by jasmonates (Truman *et al*. 2007). These authors suggested that JA signaling mediate long-distance information transmission. Moreover, the systemic transcriptional response shares extraordinary overlap with local herbivory and wounding responses, indicating that JA may be pivotal to an evolutionarily conserved signaling network that decodes multiple abiotic and biotic stress signals. Recently, Walia *et al*. (2007) reported the JA mediated adaptation of barley to salinity stress. The JA-pre-treated salt-stressed plants accumulated low levels of Na^+ in the shoot tissue compared with untreated salt-stressed barley plants after several days of exposure to stress. Their study suggested that three JA-regulated genes, arginine decarboxylase, ribulose 1,5-bisphosphate carboxylase/ oxygenase (Rubisco) activase and apoplastic invertase are possibly involved in salinity tolerance mediated by JA.

Abscisic acid

ABA, a class of metabolites known as isoprenoids, in any particular tissue in a plant is determined by the rate of biosynthesis and catabolism of the hormone. Although it contains 15 carbon atoms, in plants it is not synthesised directly from the C_{15} sesquiterpene precursor, farnesyl diphosphate, but is rather formed by cleavage of C_{40} carotenoids originating from the mevalonate pathway (Nambara and Marion-Poll 2005). ABA regulates plant growth and development such as germination, lateral root development, seedling growth, seed development, seed dormancy, transition from vegetative to reproductive phase and abiotic stress tolerance (Wasilewskaa *et al*. 2008). Interestingly, ABA also plays a recently discovered role in hydroid regeneration, stress-adaptation in sponges, pathogenesis of *Toxoplasma gondii* and in human immune responses, thus indicating a conservation of ABA signaling across kingdoms (Bruzzone *et al*. 2007; Nagamune *et al*. 2008). Although ABA signaling pathways in plants are not thoroughly understood, it is established that most of the ABA responses are regulated by ABA-mediated transcriptional regulation, which have been reviewed extensively (Nambara and Marion-Poll 2005; Yamaguchi-Shinozaki and Shinozaki 2006; Wasilewska *et al*. 2008). Genome-wide transcriptome analyses have identified more than a thousand genes that are differentially regulated by ABA, and these ABA-mediated changes in gene expression translate to major changes in proteome expression. It has been proposed that Phospholipids, heterotrimeric G proteins, modulation of intracellular calcium levels and the action of protein kinases and phosphatases are involved in ABA signaling (Hirayama and Shinozaki 2007). Knockout lines and RNA-interference technology, together with protein interaction analyses, have been used to identify many of the cellular components that regulate or modulate ABA responses (Tuteja 2007a; Tuteja and Sopory 2008). Recent discoveries reveal that besides genetic reguation, epigenetic regulation plays a key role in ABA-mediated plant processes (Chinnusamy *et al*. 2008). In addition to this, characterization of ABA-sensitivity mutations in RNA-binding proteins has led to the establishing of a functional link between post-transcriptional mRNA processing and the ABA signal transduction machinery. By influencing transcript abundance, these RNA-binding proteins may modulate ABA signaling through the alteration of mRNA processing events such as splicing, 3′ processing, nuclear export, transcript stability and RNA degradation (Kuhn *et al*. 2008). Diverse roles of ABA in plants growth as well as in biotic and abiotic stress response suggest the existence of multiple receptors and signal transduction pathways. Tol date, only three possible ABA-receptors, namely, FCA (flowering time control protein A) (Razem *et al*. 2006), ABAR (ABA receptor) (Shen *et al*. 2006) and G protein-coupled receptor (GCR2) (Liu *et al*. 2007) have been identified.

In plants, ABA accumulates in response to different environmental stresses such as high salt, cold and drought. As an integral part of stress signal transduction, ABA regulates important cellular reactions such as stomatal closure in guard cells, mediating by solute efflux, and regulates the expression of many genes that may function in tolerance to stresses (Himmelbach *et al*. 2003). These ABA-regulated genes contain a conserved, ABA-responsive, *cis*-acting element named *ABRE* (ABA-responsive element; PyACGT GGC) in their promoter regions. This *ABRE* functions as a *cis*-acting element involved in ABA-regulated gene expression but a single copy of *ABRE* is not sufficient for ABA response. *ABRE* and coupling elements having similarity with *ABREs* constitute an ABA-responsive complex in the regulation of many genes (Shen *et al*. 1996). *Arabidopsis* cDNAs encoding the bZIP transcription factors referred to as *ABRE*-binding (AREB) proteins or *ABRE*-binding factors (*ABF*s) interacting with *ABRE* were isolated using the yeast one-hybrid screening method (Uno *et al*. 2000; Choi *et al*. 2000). Among these *AREB*/*ABF* proteins, expression of *AREB1*/*ABF2*, *AREB2*/*ABF4*, and *ABF3* was upregulated by ABA, dehydration, and high-salinity stresses. Their activities were reduced in the ABA-deficient *aba2* mutant and in the ABA-insensitive *abi1* mutant, but were enhanced in the ABA-hypersensitive *era1* mutant (Koornneef *et al*. 1984; Uno *et al*. 2000). Most of the AREB subfamily proteins in *Arabidopsis* are involved in ABA-responsive signal transduction pathways in vegetative tissues or seeds. Though ABA has been suggested to play important role in stress tolerance but based on the observation that only a subset of stress inducible genes responds to ABA, ABA-dependent and independent regulatory pathways have been suggested to mediate stress response (Yamaguchi-Shinozaki and Shinozaki 2006). The *Arabidipsis RD29A*/*COR78*/*LTI78* gene is induced by drought, cold, and ABA. However, this gene is induced in *aba* or *abi* mutants by both drought and cold stresses, which suggests that it is governed by both ABA-dependent and ABA-independent regulation under drought and cold conditions (Zhou *et al*. 2004).

Several groups have reported that ABA plays important roles in plant defence responses (Mauch-Mani and Mauch 2005; Adie *et al*. 2007; de Torres-Zabala *et al*. 2007). However, the role of ABA in plant defence appears to be more complex, and vary among different types of plant-pathogen interactions. In general, ABA is shown to be involved in the negative regulation of plant defence against various biotrophic and necrotrophic pathogens. ABA-deficient (sitiens) mutant of tomato showed more resistance to *B. cinerea* (Audenaert *et al*. 2002), Pst (Thaler and Bostock 2004), *Oidium neolycopersici* (Achuo *et al*. 2006) and *Erwinia chrysanthemi* (Asselbergh *et al*. 2008) in comparison to wild type plants. Similarly, the ABA-deficient *aba2-1* mutant of *Arabidopsis* showed more resistance to *Fusarium oxysporum* (Anderson *et al*. 2004) and the *aba1-1* mutant showed less susceptibility to *Hyaloperonospora arabidopsidis* (Mohr and Cahill 2003) compared to wild type plants. Similarly, *Arabidopsis* mutants impaired in ABA biosynthesis or sensitivity show more resistance to Pst DC3000 (de Torres-Zabala *et al*. 2007) and *B. cinerea* (Adie *et al*. 2007). Taken together, these results suggest that ABA acts as a negative regulator of defence responses in various plant pathosystems. This negative effect have been shown to be due to the interference of ABA with biotic stress signaling that is regulated by SA, JA and ET, and to an additional effect of ABA on shared components of stress signaling. However, the role of ABA as a positive regulator of defence 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 Pst. In addition, treatment with ABA protects plants against *A. brassicicola* and *P. cucumerina* indicating that ABA acts as a positive signal for defence (Ton and Mauch-Mani 2004). Accumulating evidence suggests that ABA regulates defence responses through its effects on callose deposition, production of reactive oxygen intermediates and regulation of defence gene expression (Bari and Jones 2009). However, the exact molecular mechanism of ABA action on plant defence responses against diverse pathogens remains unclear. Since ABA is involved in both biotic and abiotic stress signaling, the cross-talk between these signaling pathways and the molecular mechanisms involved remain obscure.

Gibberellins

GAs are diterpene plant hormones that are biosynthesized from geranylgeranyl diphosphate (GGDP), a common C20 precursor for diterpenoids and control diverse aspects of growth and development including seed germination, stem elongation, flowering, fruit development and the regulation of gene expression in the cereal aleurone layer. These GAs are produced not only by higher plants, but also by fungi and bacteria (MacMillan 2001). It is supposed that GAs in fungi and bacteria are secondary metabolites that act as signaling factors to establish the interaction with host plants. Genes encoding enzymes of GA biosynthesis have been identified through conventional enzyme purification from rich sources of GA enzymes, functional screening of a cDNA expression library, or molecular genetic approaches using dwarf mutants defective in GA biosynthesis (Yamaguchi 2008). Among more than hundred GAs, the major bioactive GAs, including GA_1, GA_3, GA_4, and GA_7, commonly have a hydroxyl group on C-3β, a carboxyl group on C-6, and a lactone between C-4 and C-10. GA_1 has been identified frequently in a variety of plant species (MacMillan 2002), implying that it acts as a widespread bioactive hormone. However, GA_4 also exists in most species, and is thought to be the major bioactive GA in *Arabidopsis thaliana* and some *Cucurbitaceae* members. Recent studies have highlighted the occurrence of previously unrecognized deactivation mechanisms. It is now clear that both GA biosynthesis and deactivation pathways are tightly regulated by developmental, hormonal, and environmental signals, consistent with the role of GAs as key growth regulators. In contrast to the GA-biosynthesis cascade, the mechanisms of GA signal transduction are still poorly understood. GAs promote plant growth by stimulating degradation of negative regulators of growth called DELLA proteins, which are considered to be a ‘molecular switch’ for GA signaling. The rice soluble GA receptor gibberellin insensitive *dwarf1* (*GID1*) interacts with the rice DELLA protein slender *rice1* (*SLR1*) in a GA-dependent manner. The *GID1* gene encodes a member of the serine hydrolase family, which includes esterases, lipases, and proteases (Ueguchi-Tanaka *et al.* 2005). Although the enzymatic function of *GID1* has not yet been identified, analysis of a *gid1* and *slr1* double mutant has revealed that *SLR1* is epistatic to *GID1*. The binding of *GID1* to *DELLA* results in ubiquitination and degradation of *DELLA via* a ubiquitin E3 ligase SCF complex and the 26S proteasome (Ueguchi-Tanaka *et al*. 2005; Griffiths *et al*. 2006). To elucidate the function of *gid1*, proteins regulated downstream of *gid1* were analysed using a proteomic approach. The results suggest that the expression of *PBZ1* (probenazole inducible protein) is regulated by GA signaling and stress stimuli, and that *gid1* is involved in tolerance to cold stress and resistance to blast fungus (Tanaka *et al*. 2006).

GA regulates positively many genes leading to GA-associated phenotype. GA-regulated *MYB* transcription factor (*GAMYB*) that was first identified as an activator of alpha-amylase expression in barley aleurone cells have also been demonstrated to be involved in anther development in barley (Murray *et al*. 2002). Furthermore, *GAMYB* interacts with *KGM* (KINASE-ASSOCIATED WITH GAMYB), which is a member of an emerging subgroup of protein kinases and it represses *GAMYB* function in barley aleurone (Woodger *et al*. 2003). Although the phosphorylation of *GAMYB* by *KGM* has not been demonstrated the characterisation of *KGM* function will provide new insights into GA signaling pathways. Transgenic tobacco plants expressing a dominant-negative form of repressor of shoot growth (RSG) had a dwarf phenotype and a reduced concentration of the active GA_1. RSG, which contains a basic leucine-zipper (bZIP) domain, transactivated the expression of the ent-kaurene oxidase gene through interaction with its promoter sequence (Fukazawa *et al*. 2002). Recently, it has been demonstrated that 14-3-3 proteins bind RSG and control its subcellular localisation, thus regulating its efficiency as a transcriptional effector of GA-synthesis genes in the nucleus (Igarashi *et al*. 2001).

Arabidopsis DELLA proteins, which act as negative regulators of GA signaling, control plant immune responses by modulating SA and JA dependent defence responses. Studies suggest that DELLA proteins promote resistance to necrotrophs by activating JA/ET-dependent defence responses but susceptibility to biotrophs by repressing SA-dependent defence responses in *Arabidopsis*. Thus, DELLA proteins appear to integrate plant defence response pathways involving SA and JA/ET (Navarro *et al*. 2008). It seems that DELLA proteins regulate plant defence responses against various biotrophic and necrotrophic pathogens at least in part through the modulation of ROS levels in plants. How DELLA proteins regulate the expression of ROS detoxification enzymes and how DELLA-mediated modulation of ROS levels act as biological signals to regulate plant growth and stress responses remains unclear (Achard *et al*. 2008).

Brassinosteroids

BRs are a family of poly-hydroxylated steroid hormones that are involved in many aspects of plant growth and development (Rao *et al.* 2002; Sasse 2003). BRs are localized in all parts of plants and their presence unveiled in 27 families of higher plants and three families of lower plants including roots and have the capability of long distance transport, especially from root to shoot (Bajguz and Tretyn 2003; Sasse 2003). The biosynthesis of biologically active BRs involves a series of cytochrome P450 and steroid 5a-reductase enzymes. BRs bind to the extracellular domain of the leucine-rich-repeat receptor-like kinase (LRR-RLK) *BRI1* (Brassinosteroid Insensitive 1) (Kinoshita *et al.* 2005) and activate its kinase function. *BRI1* and its coreceptor *BAK1* - another *LRR-RLK* (Nam and Li 2002) - transduces the BR signal through an unknown mechanism to soluble downstream components. Two of these components -*BIN2* (*BR-Insensitive 2*) (Li and Nam 2002) and *BSU1* (*bri1 Suppressor 1*) (Mora-Garcia *et al.* 2004), a GSK3 kinase and a Ser-Thr phosphatase, respectively, control the phosphorylation states of a family of nuclear transcription factors that include *BZR1* (*Brassinazole Resistant 1*) (Wang *et al.* 2002; He JX *et al.* 2005) and *BES1* (*bri1 EMS Suppressor 1*), also known as *BZR2* (Yin *et al.* 2005). *BZR1* and *BZR2*/*BES1* were identified as dominant gain-of-function mutants that are resistant to brassinazole (BRZ) (a BR biosynthesis inhibitor) and suppress the dwarf phenotype of *bri1* mutants. Phosphorylation of *BZR1* and *BZR2*/*BES1* inhibits their activity through multiple mechanisms, including proteasome degradation, cytoplasmic retention, and abolishment of DNA binding (Gampala *et al.* 2007; Gendron and Wang 2007). BR-induced dephosphorylation activates *BZR1* and *BZR2*/*BES1* proteins, which directly regulate the transcription of BR-responsive genes.

BRs play a significant role in the amelioration various abiotic stresses (Hasan *et al.* 2008). Moreover, BRs are also recognized as regulators of transcription and translation (Bajguz 2000) thereby improving the level of total proteins (Bajguz 2000), enzymes (Hayat and Ahmad 2003a; Hayat *et al.* 2003; Fariduddin *et al.* 2004), the rate of nitrogen fixation (Vardhini and Rao 1999) and finally the seed yield, at harvest (Hayat and Ahmad 2003b; Hayat *et al.* 2003; Fariduddin *et al.* 2004, 2005). BRs elicit various physiological responses in plants, including stem elongation, pollen tube growth, leaf bending and epinasty, root growth inhibition, induced synthesis of ethylene, activation of proton pump, xylem differentiation, synthesis of nucleic acids and proteins, activation of enzymes and photosynthesis (Clouse and Sasse 1998; Khripach *et al.* 1999; Hayat and Ahmad 2003a; Yu *et al.* 2004; Hayat *et al.* 2007). It has been proposed that the changes induced by BRs are mediated through the repression and/or depression of specific genes (Fellner 2003). The treatment rice and tomato plants (Kamuro and Takatsuto 1991), maize (He *et al.* 1991), cucumber (Katsumi 1991) and brome grass (Wilen *et al.* 1995), with BRs improved their capacity of resistance to low temperature. Similarly, BRs increased the degree of tolerance, to high temperature, in wheat (Kulaeva *et al.* 1991) and brome grass (Wilen *et al.* 1995). BRs also countered the drought stress in sugarbeet (Schilling *et al.* 1991), moisture stress in wheat (Sairam 1994), nickel toxicity in mustard (Alam *et al.* 2007), saline stress in chickpea (Ali *et al.* 2007), cadmium stress in chickpea and mustard (Hayat *et al.* 2007; Hasan *et al.* 2008), aluminium stress in mung bean (Ali *et al.* 2008) and induced seed germination and seedling growth in *Eucalyptus* (Sasse *et al.* 1995) and rice (Anuradha and Rao 2001), under salinity stress. Moreover, BRs activate antioxidative enzymatic defense system in rice seedlings, grown under salt stress (Nuñez *et al.* 2003). Furthermore, BRs have been successfully employed for economic gains, since treated plants develop stress resistance and produce more seeds, at harvest (Hayat and Ahmad 2003a; Fariduddin *et al.* 2004, 2005; Ali *et al.* 2008; Hasan *et al.* 2008).

Cytokinins

In plants, CYT, the N6-substituted adenine-based molecules, are mainly synthesized by the addition of an isoprene moiety to ATP or ADP. These have been associated diverse processes including stem-cell control, vascular differentiation, chloroplast biogenesis, seed development, growth and branching of root, shoot and inflorescence, leaf senescence, nutrient balance and stress tolerance (Muller and Sheen 2007). CYT has also been linked to nodulation in legumes, interactions with pathogens and circadian rhythms (To and Kieber 2008). CYT signal transduction has similarities to the two-component system of bacteria (Kakimoto 2003) in which a sensor histidine (His) kinase perceives a stimulus and autophosphorylates on a conserved His residue in the kinase domain (West and Stock 2001). Further, signal is transduced *via* phosphoryl transfer to a conserved aspartic acid present on the receiver domain of a response regulator, which activates downstream responses (West and Stock 2001). The cytokinin receptors *ARABIDOPSIS* HIS KINASE 4 (AHK4), AHK2 and AHK3 are hybrid kinases similar to HKs in two-component systems. These three transmembrane hybrid kinases have an extracellular cytokinin-binding domain and cytoplasmic His transmitter and receiver domains (Heyl and Schmulling 2003).

CYT have also been shown to be an important signal travelling from roots to the shoots. Root-produced CYT are clearly involved in responses to nutrient deprivation (Schachtman and Shin 2007). Because these are produced mainly in roots, could be important in drought responses. There are evidences that provide information on the CYT content of xylem sap changes under drought conditions. In grapevines, reduction in zeatin (Z) and zeatin riboside (ZR) was found in plants that had been subjected to partial root-zone drying (Stoll *et al.* 2000). In sunflower, xylem sap, combined Z and ZR and combined isopentenyladenine and isopentenyladenosine concentrations in xylem sap decreased under drought-stressed conditions (Hansen and Dorffling 2003). This suggests that the ABA: CYT ratios in xylem sap may play important role in signaling. Increase in transpiration rate was observed in transgenic plants that overexpressed the isopentenyltransferase, causing the plants to produce more CYT after a heat shock treatment. Though role of CYT has been reported but strong conclusions are premature because the complexity of the CYT profiles has not been fully explored (Davies *et al.* 2005).

Role of CYT in plant defence against diseases has also been documented (Bari and Jones 2009). Down-regulation of genes involved in CYT homeostasis (cytokinin synthases and cytokinin oxidases/dehydrogenases) in *Plasmodiophora brassicae* infected *Arabidopsis* suggests that CYT plays an important role in the development of club root disease caused by *P. brassicae* in *Arabidopsis* (Siemens *et al.* 2006). Transgenic plants overexpressing cytokinin oxidase/dehydrogenase genes showed resistance against *P. brassicae* infection suggesting that CYT acts as a key factor in the development of club root disease in *Arabidopsis* (Siemens *et al.* 2006). Modulation in CYT metabolism in *Arabidopsis* after infection with *Rhodococcus fascians* has also been reported (Depuydt *et al.* 2008).

Auxin

Auxin biology is among the oldest fields of experimental plant research because auxins influence virtually every aspect of plant growth and development. One of the earliest noted auxin effects was phototropism, the curvature of stems toward a light source. Some early effects of auxin was noted where it promoted rooting from undifferentiated callus (Skoog and Miller 1957). Along with the phytohormone CYT, which induces shoot formation, auxin allows regeneration of plants from cultured callus (Krikorian 1995). Many naturally occurring compounds that exert auxin-like effects have been identified and assayed such indole-3-acetic acid (IAA), an extensively studied endogenous auxin, a chlorinated form of IAA with high auxin activity, 4-Cl-IAA, (Slovin *et al.* 1999), indole-3-butyric acid (IBA), identical to IAA except for two additional methylene groups in the side chain, (Zolman *et al.* 2000) etc. Two main types of synthetic plant growth regulators (PGRs) with auxin-like activity have been described: 1-naphthalacetic acid (NAA) and 2,4-D-related compounds. Both compounds exert auxin-like influences, including root elongation inhibition and lateral root promotion. The auxin group of compounds is synthesized from tryptophan using both tryptophan (Trp)-dependent and Trp-independent routes. Multiple IAA biosynthetic pathways may contribute to the regulation of IAA production. A detailed account of auxin biology and biochemistry has been reviewed by Woodward and Bartel (2005). Auxin rapidly and transiently induces accumulation of at least three families of transcripts: *SMALL AUXIN-UP RNAs* (*SAURs*), *GH3*-related transcripts and *AUXIN/INDOLE-3-ACETIC ACID* (*Aux/IAA*) as reviewed by Guilfoyle (1999) and Hagen and Guilfoyle (2002). Most of the genes in these three families are primary/early response genes which mean that they are activated rapidly after auxin treatment and that the protein synthesis is not required for their activation. At least one promoter DNA sequence that is involved with the auxin regulation of primary/early auxin response genes is the *TGTCTC* or auxin response element (*AuxRE*). The auxin response elements allow binding of auxin response factors (*ARFs*) which are transcription factors and could be transcriptional activators or repressors (Tewari *et al.* 2003). The identification of the auxin response sequence element led to the isolation of first *ARF1* from *Arabidopsis* (Ulmasov *et al.* 1997). The auxin signaling is one of the most complicated pathways in plant signaling. Though lot of research has gone into auxin signaling still it is not well characterized. The molecular and biochemical studies of several auxin resistant mutants have positioned the SCF^{TIR1} ubiquitin-ligase complex as a central regulator of auxin signaling (Quint and Gray 2006). The picture on the role of MAP kinases mediated auxin signaling is getting little bit clearer.

Though auxins have long been considered as the phytohormone responsible for plant growth and phototropism recent evidences indicate that it may have a direct/indirect role in plant stress management as well. Some of the recent works in this direction are reviewed. Auxin responsive *GH3* genes have been shown to play role in plant defence response in *Arabidopsis*. The *GH3-5* may be acting as bi functional modular for SA and auxin signaling during pathogen infection (Zhang *et al.* 2007). Over expression of another gene of this class, *GH3-8* resulted in enhanced resistance to *Xanthomonas* in rice which causes bacterial blight disease. Interestingly this resistance was independent of SA and JA signaling (Ding *et al.* 2008). Treatment of *Arabidopsis* plants with an SA analog BTH resulted in the repression of several auxin responsive genes (Wang *et al.* 2007). SA is known to be the most responsive molecule in pathogen infection. Very recently it was shown that over expression of *OsGH3.1* in rice caused auxin biosynthesis and auxin signaling inhibition genes induced and repressed, respectively. *OsGH3.1* over expression did also activate a significant number of defense-related genes and genes related to cell wall morphogenesis and loosening (Domingo *et al.* 2009). Interference with auxin signaling or its transport compromises resistance of *Arabidopsis* plants to the necrotrophic fungi *P. cucumerina* and *B. cinerea* (Llorente *et al.* 2008). Further, periwinkle shoots infected with different 'Candidatus Phytoplasma' when treated with IAA and IBA showed recovery. It was concluded that auxin mediates phytoplasma infection and can be used to eliminate phytoplasma *in vitro* conditions (Ćurković *et al.* 2008). Ellis *et al.* (2005) showed that *ARF1* and *ARF2* genes regulate floral organ senescence and abscission in *Arabidopsis*. The HR programmed cell death initiated by a bacterial type III secretion system dependent proteinaceous elicitor harpin (from *Erwinia amylovora*) can be reversed till very late in the process by the PGR auxin (Gopalan 2008). NPK1 is a mitogen-activated protein kinase kinase kinase identified in *Nicotiana tabacum* and plays important roles in cytokinesis and auxin signaling transduction and responses to multiple stresses. Expression analysis of *OsNPKL* genes under abiotic stresses suggests that the stress-responsive genes are mainly from the same subgroup. Especially interesting is that all the clustered genes are induced by drought, salt, or cold stress (Hu *et al.* 2008).

NON-HORMONAL GROWTH REGULATORS AND THEIR ROLE IN STRESS

Plants respond and adapt to the continuous environmental fluctuations with appropriate physiological, developmental and biochemical changes to cope with these stress conditions. There is biological evidence suggesting that plants use a general and conserved response mechanism to deal with abiotic stress. PGRs (auxins, CYT, GAs, ABA and ET) are known to influence plant development in general and floral development, fruit set, fruit ripening and senescence in particular (Srivastava and Handa 2005). Other growth regulators such as polyamines (PAs), SA, BRs and JA are becoming known as signaling molecules in diverse plant processes (Mattoo and Handa 2004; Srivastava *et al.* 2007). Furthermore, the use of ions for osmotic adjustment may be energetically more favorable than biosynthesis of organic osmolyte under osmotic stresses; many plants accumulate organic osmolytes to tolerate osmotic stresses. These compounds fall into several groups - amino acids (e.g. proline), quaternary ammonium compounds (GB), polyols and sugars (mannitol, dononitil, trehalose, sucrose, fructan, etc.). This part of review deals with the possible role of non hormonal PGRs in abiotic stress tolerance.

Polyamines

PAs a group of small aliphatic amines are reported to play important role in plant development. PAs, mainly diamine putrescine (Put), triamine spermidine (Spd) and tetra amine spermine (Spm), are low molecular organic cations that are found in a wide range of organisms from bacteria to plants and animals. In plants, PAs are involved in various physiological events such as development, senescence and stress responses. Production of Put in plants is different from that in animals owing to the presence of the arginine decarboxylase (ADC) pathway through arginine in addition to the ornithine decarboxylase (ODC) pathway through ornithine. Spd is synthesized from Put *via* spermidine synthase (SPDS) with the addition of an aminopropyl moiety provided by decarboxylated S-adenosylmethionine (dcSAM), which is catalyzed by the enzyme of S-adenosylmethionine decarboxylase (SAMDC) using S-adenosylmethionine (SAM) as a substrate. Similarly, Spm is produced from Spd *via* spermine synthase (SPMS) with the same aminopropyl moiety rendered by dcSAM. It has been proposed that PAs are a new category of PGRs which are found to be involved in a wide range of physiological processes, such as tolerance to stresses, embryogenesis, cell division, morphogenesis, and development (Papadakis and Roubelakis-Angelakis 2005; Alcazar *et al.* 2006; Yang *et al.* 2007; Kuznetsov and Shevyakova 2007; Pang *et al.* 2007). These are also known to accumulate under salt stress conditions in different plant systems, resulting in protective effects, acting as free radical scavengers, stabilizing cellular membranes and maintaining cellular ionic balance under these conditions. Jiménez-Bremont *et al.* (2007) reported that in response to long-term salt stress the levels Spd and Spm were modulated suggesting their role in salt stress. It has been suggested that there is a connection between PA metabolism, abiotic stress and abscisic acid. The measurement of PAs levels in different rice cultivars showed that salt-tolerant rice cultivars maintains a high level of higher PAs, e.g. Spd and Spm, whereas, salt-sensitive rice cultivars maintains only a high level of Put (Basu and Ghosh 1991; Krishnamurthy and Bhagwat 1989). The salt tolerant cultivars

'AU1', 'Co43', and 'CSC1' were effective in maintaining high concentrations of Spd and Spm, while the content of Put was not significantly altered in the growth stages analysed when plants were exposed to salinity. The salt sensitivity in rice was associated with excessive accumulation of Put and with low levels of Spd and Spm in the shoot system of the salt-sensitive cultivars 'Co36', 'CSC2', 'GR3', 'IR20', 'TKM4', and 'TKM9' under saline conditions (Krishnamurthy and Bhagwat 1989). Free and bound PAs content in root tonoplast vesicles were closely related to salt tolerance of barley plants. It is reported that 200 mM NaCl induced reductions in the contents of phospholipids and PAs in tonoplast vesicles isolated from barley seedling roots, while exogenous Put or Spd (0.5 mM) application partially restored this effect, attenuating salt injury in barley seedlings (Zhao and Qin 2004). PAs accumulated in *Arabidopsis* wild-type plants ('Col-0' and 'Ler-0') that were pre-treated with 100 mM NaCl before transfer to 125 mM NaCl, but not in plants that were directly transferred to 125 mM NaCl (Kasinathan and Wingler 2004). On the other hand, the salt treatment that induced PA accumulation in wild-type plants did not lead to PA accumulation in the *spe1-1* and *spe2-1* mutants with reduced activity of ADC (Kasinathan and Wingler 2004), demonstrating that decreased PA formation due to lower ADC activity lead to reduced salt tolerance. Mutlu and Bozcuk (2005) reported the potential role of PAs to overcome the adverse effect of salinity. They also reported an increase of free, acid-soluble bound, and total Spm in leaf tissues of sunflower plants subjected to 50, 100, and 150 mM NaCl. Zapata *et al.* (2004) observed increased levels of polyamines in several plant species such as spinach, lettuce, melon, pepper, broccoli, beetroot and tomato under salt stress. They observed that except beetroot, Put concentration was lower in seedlings grown under saline conditions. However, salinity caused a significant increase in Spd and Spm in almost all the plant species studied. This meant that the pool of Put was directed to Spd and Spm synthesis. The (SpdþSpm) = Put ratio increased with salinity, which would be in agreement with the idea of a protective role of higher PAs (Spd and Spm) against salt stress. Significant increase in the accumulation of Spm and Spd associated with a decrease in Put content in wheat cultivars under salinity stress was reported by El-Shintinawy (2000). However, in another study Imai *et al.* (2004) found that 200mM NaCl did not significantly change the *OsSPDS2* (a SPDS gene) mRNA levels in rice plants. These results indicated that endogenous Put also plays an important role in salt tolerance in *Arabidopsis* (Urano *et al.* 2004). In order to differentiate the ionic and osmotic components of salt stress, Legocka and Kluk (2005) found that 260 mM NaCl and 360 mM sorbitol trigger organ-specific changes in PAs levels and in the activity of ADC in *Lupinus luteus*, a drought-tolerant plant. After a shortterm exposure (4 h) of seedlings to both stresses, Put and Spd accumulated in roots and leaves. Long (24 h) salt and osmotic stress conditions produced a decline of Put and Spd in roots, and an increase in hypocotyls and leaves. During this period of time, the concentration of free Put significantly raised in the leaves without increasing ADC activity. This may indicate that during longer times of action for both stresses, Put synthesized in roots was carried through hypocotyl to leaves. Also, in roots and leaves of *Lupinus luteus* growing for 24 h on salt or sorbitol, a higher level of PAs bound to microsomal membranes was observed (Legocka and Kluk 2005). In relation to the consequences of water deficiency, it was observed that when an oat ADC gene was overexpressed in rice, the plants showed improved drought tolerance in terms of chlorophyll loss. Wild-type plants of *Datura stramonium* responded to the onset of drought stress by increasing endogenous Put levels, but this was not enough to trigger the conversion of Put into Spd and Spm, (the agents that are believed to protect plants against water deficit (Capell *et al.* 2004). The use of difluromethylarginine (DFMA) and α-difluromethylornithine (DFMO), the biosynthetic inhibitors of Put biosynthesis, as well as cyclohexylamine (CHA), biosynthetic inhibitor of Spd and Spm biosynthesis, supported the role of PAs in mediating the differential sensitivity of chickpea Barley seedlings treated with Spd prior to a water deficit period, reverted the increase in catalase and guaiacol peroxidase activities produced by this stress, suggesting that PAs are able to influence the activity of H_2O_2-scavenging enzymes, moderating this signal molecule level (Kubis 2003). In the *Arabidopsis* genome, eight genes involved in PA biosynthesis have been recently identified (two genes for ADC, two genes for SAMDC, two genes for SPDS and two genes for SPMS) and their expression profiles were analyzed in response to different abiotic stress conditions (Urano *et al.* 2003). Yamaguchi *et al.* (2006) reported that an *Arabidopsis* double knock out plant that cannot produce Spm showed higher sensitivity to high salt. This mutant was also later found to be sensitive to drought and the mutant phenotype could be cured by the addition of Spm but not by Spd (Yamaguchi *et al.* 2007) The genes involved in Spm and Spd synthesis have also been found to be regulated by salinity and abcissic acid (Jiménez-Bremont *et al.* 2007). By using patch clamp techniques to protoplasts, it was found that polyamines affect K^+/Na^+ homeostasis (Zhao *et al.* 2007). This could be one of the mechanism by which polyamines could help in salinity tolerance in plants. Regulation of PAs biosynthesis has also been reported in plants under drought stress. In cacao, expression pattern of five genes encoding enzymes involved in polyamines biosynthesis were studied in response to drought and correlated with the levels of Put, Spm and Spd (Bae *et al.* 2008). In many studies overexpression of these genes has also been shown to confer stress tolerance in plants (Groppa and Benavides 2008). There is evidence of cross-talk of PA with NO. Exogenous addition of PA has been shown to induce the production of NO although the mechanism for this is still not understood and needs more experiments (Yamasaki and Cohen 2006).

Salicylic acid

SA is a common plant-produced phenolic compound that can function as a plant growth regulator. SA has been known to be present in some plant tissues for quite some time, but has only recently been recognized as a potential plant growth regulator. SA is synthesized from the amino acid phenylalanine. The role of SA in biotic and abiotic stress tolerance has been well documented. In plants, SA biosynthesis occurs *via* the shikimate-phenylpropanoid pathway, where, phenylalanine is first converted to *trans*-cinnamic acid (t-CA) by phenylalanine ammonia lyase. Two pathways for the formation of salicylic acid have been reported in plants. t-CA is either hydroxylated to *O*-coumaric acid before oxidation of the side chain, or the t-CA side chain is shortened to benzoic acid, which is in turn hydroxylated to SA. It has been reported that the exogenous application of SA influence several developmental and physiological processes in plants such as seed germination, transpiration rate, stomatal closure, membrane permeability, growth and photosynthesis (Hayat and Ahmad 2007). Guo *et al* (2009) hypothesized that SA may accelerate the cell death of cadmium (Cd)-stressed roots to avoid Cd uptake by plants or may play positive roles in protecting the stressed roots from Cd-induced damage. They found that SA pretreatment in rice plants elevated the enzymatic and non-enzymatic antioxidants, and the concentrations of GSH and NPT in roots and shoots, hence leading to alleviation of the oxidative damage as indicated by the lowered H_2O_2 and MDA levels. SA pretreatment also mitigated the Cd-induced growth inhibition in both roots and shoots and increased transpiration compared with non-SA-pretreatment under Cd exposed rice plants. The SA-enhanced Cd tolerance in rice can be attributed to SA-elevated enzymatic and non-enzymatic antioxidants and NPT, and to SA-regulated Cd uptake, transport and distribution in plant organs. Other workers also reported that SA can alleviate Cd induced growth inhibition in *Hordeum vulgare* (Metwally *et al.*

2003), *Glycine max* (Drazic and Mihailovic 2005) and in *Oryza sativa* (Guo *et al.* 2007). Szepesi *et al.* (2005) found that pretreatment of tomato seeds with 10^{-7} M SA decreased the osmotic stress-induced reduction in relative water content. SA pretreatments also reduced K^+ contents of leaves under salt and non-ionic osmotic stress. SA decreased the Na^+/K^+ ratio in the roots and increased it significantly in the leaves in comparison to the NaCl-treated plants. It has been reported that SA improved the photosynthetic performance of plants under stress conditions, and chlorophyll a fluorescence gave insight into the ability of plant to tolerate environmental stresses (Ananieva *et al.* 2002). It has been reported that at low photosynthetic light intensity (165 μmol m^{-2} s^{-1}) the effective quantum yield was only slightly affected in NaCl-treated tomato samples, but it was significantly reduced under non-ionic osmotic stress (Szepesi *et al.* 2005). This was partially overcome when the plants were pretreated with SA. SA pretreatment might improve the gross rate of carbon assimilation during osmotic stress. Gunes *et al.* (2007) reported that exogenous application of SA increased plant growth of maize significantly both in saline and non-saline conditions. Under salinity stress, lipid peroxidation and membrane permeability decreased by SA treatment. SA has also received much attention due to its role in plant responses to various other abiotic stresses such as ozone, UV-B, heat stress, drought, oxidative stress, salt and osmotic stress (Hayat and Ahmad 2007). SA is considered to serve as a signal in the induction of expression of genes (Metraux 2001). The application of SA has been found to increase tolerance of wheat and maize seedlings to salinity (Arfan *et al.* 2007; Gunes *et al.* 2007), water deficit (Bezrukova *et al.* 2001), of tomato and bean plants to low and high temperature (Senaratna *et al.* 2003) as well as of heavy metals of rice plants (Choudhury and Panda 2004). The SA pathway, thus considered to be a key factor in inducing tolerance. This acid is phenol, ubiquitous in plants generating a significant impact on plant growth and development, photosynthesis, transpiration, ion uptake and transport. It also plays a role in thermogenesis in lily, induces flowering in a range of plants, controls ion uptake by roots and stomatal conductivity (Raskin 1992). SA has been found in signal regulation and gene expression in the course of leaf senescence in *Arabidopsis* (Morris *et al.* 2000), inhibitor of fruit ripening (Srivastava and Dwivedi 2000). Borsani *et al.* (2001) showed an evidence for a role of SA in the oxidative damage generated by NaCl and osmotic stress in *Arabidopsis* seedlings. Szepesi *et al.* (2005) reported that SA pretreatment decreased catalase activity in the roots and leaves of tomato, but the activity of other enzymes associated with the antioxidative defense, superoxide dismutase, peroxidase, ascorbate peroxidase and glutathione reductase exhibited different changes at 10^{-7} M SA or 10^{-4} M SA. The activity of these enzymes decreased compared to the control in the leaves of tomato plants at 10^{-7} M SA pretreatment, while at 10^{-4} M concentration their activity was enhanced. Salt tolerance induced by 10^{-4} M SA was associated with the activation of the oxidative defense mechanisms and with the accumulation of osmolytes. Shim *et al.* (2003) reported a significant and dose-dependent increase in SA content in the NaCl-treated leaves of rice seedlings. They negatively correlated this increase in SA content with catalase activity and concluded that the formation of SA could be induced by salt stress. Mahajan *et al.* (2006) have earlier reported that the CBL and CIPK genes from pea were induced in response to SA and wounding. Pan *et al.* (2006) reported that SA application reduced leaf injury in pea caused by heat stress and induced the synthesis of heat shock proteins (*Hsp70* and *Hsp17.6*). Several SA-responsive genes are known to regulate by basic/leucine zipper-type transcription factors of the *TGA* family. *TGA* factors interact with *NPR1*, a central regulator of many SA induced defense responses including SA/JA antagonism. An *ATPaseC* gene from *Pennisetum* was found to be upregulated by SA and its promoter was found to bind nuclear factors to *TGA cis* elements (Tyagi *et al.* 2005). Ndamukong *et al.* (2007) reported that glutaredoxin acts as regulatory protein of SA-dependent signaling pathways. Koo *et al.* (2007) reported that overexpression of SA carboxyl methyltransferase reduces SA-mediated pathogen resistance in *Arabidopsis thaliana*. Their results indicated that in the absence of SA, methyl salicylate alone cannot induce a defense response, yet it serves as an airborne signal for plant-to-plant communication. Recently, Wang *et al.* (2007) reported that SA inhibits pathogen growth in plants through repression of the auxin signaling pathway. It may be said that SA could be used as a potential growth regulator in abiotic stress tolerance.

DEVELOPMENTALLY REGULATED GENES AND THEIR ROLE IN STRESS

In plants, as in other organisms many developmental processes and responses to different stress stimuli are under the regulation of complex gene regulatory network. Many genes that are known to be regulated developmentally are also responsive in certain stress conditions.

Heat shock proteins

In tomato it has been shown recently that a class of small Heat stress proteins (sHSPs) is expressed during zygotic embryogenesis and in normal temperature without any external stress. In plants the developmental regulation of HSP is related to only a specific class of Hsps. Most of class1 sHSPs that are developmentally present in seeds also respond to stress not only in vegetative tissues but also in seeds.

It was shown by differential analyses that the *cis*-regulatory HSE (heat shock response elements) that are involved in heat stress response are also involved in developmental responses (Waters 1996). This suggested the involvement of Heat shock responsive transcription factors in the developmental responses also. However later experiments showed that the mutageneis of HSE in sunflower promoter completely abolished heat stress response but only weakly reduced the experession in dessicating embryos. Another sunflower promoter Ha hsp 17.6 G1 promoter does not respond to stress but is transcriptionally activated by Hsfs in developing embryos. These observations suggested that the developmental regulation of genes by Hsfs using the HSE may be different in mechanism from that of Heat stress response (Carranco *et al.* 1997).

The plant co-chaperones FK506 binding proteins (FKBS) function in protein folding, signal transduction and chaperone activity (Aviezer-Hagai *et al.* 2007). In *Arabidopsis* the expression of two large FKBS (ROF1 and ROF2) has been shown to be regulated in a developmental specific manner and also by heat stress. The ROF1 has been shown to bind HSP90, and the expressions of ROF2 and AtHSP90-3 and expressions of ROF1 and AtHSP90-1 coincides. The promoter regions of ROF and HSP90 share many elements known to mediate heat shock and other stress stimuli. The study suggests that ROF and HSP form protein complexes that are functional in vivo and affect development and stress responses.

SNF1- kinases and wall-associated kinases

The Sucrose Non-Fermenting-1 like kinases are involved in adaptation of metabolism to environmental conditions such as nutrition, energy and stress. It was shown by Radchuk *et al.* (2006) that SNRK-1 kinases in pea interacts with the ABA signal transduction and is a key regulator in controlling developmental programming associated with the switch from prestorage to maturation.

The plant cell wall associated kinases (WAK) and WAK-like kinases (WAKL) are a family of receptor like kinases genes that encode transmembrane proteins with a serine/threonine kinase domain and an extracellular region containing epidermal growth factor like repeats. Studies have shown that some members are responsive in defence and heavy metal response whereas some members are involved in plant development and cell elongation.

Aquaporin genes

Aquaporin genes are a class of major intrinsic proteins and are involved in water transport, by making channels across the plasma membrane. One of the subclass of Aquaporin genes are the PIP genes or plasma membrane intrinsic protein that are mainly targeted to the plasma membrane. A large number of these genes are expressed in plants in developmental and tissue specific manner. In cotton plants three aquaporin genes *GhPIP1*;*1 GhPIP2*;*1* and *GhPIP2*;*2* have been shown to be involved in the development of roots (Li *et al*. 2009). The expression of these genes increases during early root development and then declines thereafter. These genes were also shown to be regulated by different stress treatments like NaCl, cold, and PEG. Under drought stress the *GhPIP*;*1* and *GhPIP2*;*1* expression was upregulated unlike that in *AtPIP* genes, suggesting that these genes may be facilitating water transport during drought stress by forming special water channels.

MAP kinases

MAP kinases play important roles in plant growth and development. In many instances these genes are also shown to be responsive of environmental stress stimuli like drought, salt, cold, etc. (Mishra *et al*. 2006). Two rice MAP kinases OsMSRMK3 (multiple stress responsive) and OsWJUMK1 (wound- and JA-uninducible) were shown to be upregulated by diverse stress responses and were also shown to be developmentally upregulated (Agarwal *et al*. 2002). sMSRMK3 and OsWJUMK1 encode 369 and 569 amino acid polypeptides having the MAPK family signature and phosphorylation activation motifs TEY and TDY, respectively. Steady state mRNA analyses of these MAPKs with constitutive expression in leaves of two- week-old seedlings revealed that OsMSRMK3 was up-regulated upon wounding (by cut), JA, SA, ET, ABA, H_2O_2, protein phosphatase inhibitors, chitosan, high salt/sugar, and heavy metals, whereas, OsWJUMK1 not induced by either wounding, JA or SA, showed up-regulation only by H_2O_2, heavy metals, and cold stress (12°C). The expression of these genes increased with panicle development in rice seedlings, suggesting their role in development also. Apart from this study there have been other reports about the role of MAPK in developmental responses, too.

In *Arabidopsis* MAPK 9 is shown be involved in ET biosynthesis and salt stress (Xu *et al*. 2009). Expression of active MKK9 protein in transgenic plants induces the synthesis of ET and camalexin through the activation of the endogenous MPK3 and MPK6 kinases. As a consequence, transcription of multiple genes responsible for ET biosynthesis, ET responses, and camalexin biosynthesis is coordinately up-regulated. The activation of MKK9 inhibits hypocotyl elongation in the etiolated seedlings. MKK9-mediated effects on hypocotyl elongation were blocked by the ET biosynthesis inhibitor, aminoethoxyvinylglycine, and ET receptor antagonist, Ag(+). Expression of active MKK9 protein enhances the sensitivity of transgenic seedlings to salt stress, whereas loss of MKK9 activity reduces salt sensitivity indicating a role for MKK9 in the salt stress response.

In a recent study C1 subgroup MAP kinase cDNA, PsMPK2, was isolated from *Pisum sativum*. PsMPK2 is expressed in vegetative (root and leaf) and reproductive (stamen, pistil and fruit) organs. Expression of PsMPK2 in *Arabidopsis thaliana* shows that mechanical injury and other stress signals as ABA, JA and H_2O_2 increase its kinase activity, extending previous results indicating that C1 subgroup MAPKs may be involved in the response to stress (Ortiz-Masia *et al*. 2008).

Transcription factors

In *Arabidopsis* a *bZIP* transcription factor *bZIP60* was identified in ER mediated stress response (Iwata *et al*. 2008). When compared with wild-type *Arabidopsis* plants, homozygous *bZIP60* mutant plants show a markedly weaker induction of many ER stress-responsive genes. The *bZIP60* protein resides in the ER membrane under unstressed condition and is cleaved in response to ER stress caused by either tunicamycin or DTT. The N-terminal fragment containing the *bZIP* domain is then translocated into the nucleus. In *Arabidopsis*, expression of the *bZIP60* gene and cleavage of the *bZIP60* protein are observed in anthers in the absence of stress treatment, suggesting that the ER stress response functions in the normal development of active secretory cells.

RING finger proteins comprise a large family and play key roles in regulating growth/developmental processes, hormone signaling and responses to biotic and abiotic stresses in plants. Expression of rice *OsBIRF1* was up-regulated in rice seedlings after treatment with benzothaidiazole, SA, l-aminocyclopropane-1-carboxylic acid and JA, and was induced differentially in incompatible but not compatible interactions between rice and *Magnaporthe grisea*, the causal agent of blast disease. Transgenic tobacco plants that constitutively express *OsBIRF1* exhibit enhanced disease resistance against tobacco mosaic virus and *Pseudomonas syringae* pv. *tabaci* and elevated expression levels of defense-related genes, e.g. *PR-1*, *PR-2*, *PR-3* and *PR-5*. The *OsBIRF1*-overexpressing transgenic tobacco plants show increased oxidative stress tolerance to exogenous treatment with methyl viologen and H_2O_2, and upregulate expression of oxidative stress-related genes. Reduced ABA sensitivity in root elongation and increased drought tolerance in seed germination were also observed in *OsBIRF1* transgenic tobacco plants. Furthermore, the transgenic tobacco plants show longer roots and higher plant heights as compared with the wild-type plants, suggesting that overexpression of *OsBIRF1* promotes the plant growth. The study showed that *OsBIRF1* has pleiotropic effects on growth and defense response against multiple abiotic and biotic stresses (Liu *et al*. 2008).

miRNA

Important developmental processes in both plants and animals are partly regulated by genes whose expression is modulated at the post-transcriptional level by processes such as RNA interference (RNAi). Dicers, Argonautes and RNA-dependent RNA polymerases (RDR) form the core components that facilitate gene silencing and have been implicated in the initiation and maintenance of the trigger RNA molecules, central to process of RNAi. A genome wide analysis of rice Dicer-like, Argonaute and RDR gene families including gene structure, genomic localization and phylogenetic relatedness among gene family members and microarray-based expression profiling of these genes during 14 stages of reproductive and 5 stages of vegetative development and in response to cold, salt and dehydration stress was carried out (Kapoor *et al*. 2008). This investigation has identified 23 rice genes belonging to DCL, Argonaute and RDR gene families that could potentially be involved in reproductive development-specific gene regulatory mechanisms. These data provide an insight into probable domains of activity of these genes and a basis for further, more detailed investigations aimed at understanding the contribution of individual components of RNA silencing machinery during reproductive phase of plant development. In *Medicago* 15 new miRNAs were identified and their expression was shown to be differentially regulated in different plant growth stages and in response to heavy metal stresses (Hg, Cd, and Al) (Zhou *et al*. 2008).

HMG and histones

High mobility group (HMG) proteins of the HMGB family are small and relatively abundant chromatin-associated proteins that are involved in the regulation of transcription and other DNA-dependent processes. Analysis of *Arabidopsis* mutant plants lacking the HMGB1 protein, transgenic plants overexpressing HMGB1 and mutant plants that were transformed with the HMGB1 genomic region (complementation plants) revealed that despite the presence of several other HMGB proteins, the lack and overexpression of HMGB1 affect certain aspects of plant growth and stress tolerance and it has a marked impact on the transcriptome, suggesting that HMGB1 has (partially) specialized functions in *Arabidopsis* (Lildballe *et al.* 2008). Both the absence and overexpression of HMGB1 caused shorter primary roots and affected the sensitivity towards the genotoxic agent methyl methanesulfonate. The overexpression of HMGB1 decreased the seed germination rate in the presence of elevated concentrations of NaCl. The complementation plants that expressed HMGB1 at wild-type levels did not show phenotypic differences compared to the control plants. Transcript profiling by microarray hybridization revealed that a remarkably large number of genes were differentially expressed (up- and down-regulated) in plants lacking HMGB1 compared to control plants. Among the down-regulated genes, the gene ontology category of stress-responsive genes was overrepresented. Neither microscopic analyses nor micrococcal nuclease digestion experiments revealed notable differences in overall chromatin structure, when comparing chromatin from HMGB1-deficient and control plants.

In another study of HMGB proteins in *Cucumis* it was demonstrated that transgenic *Arabidopsis* plants overexpressing *CsHMGB* showed retarded germination compared with the wild-type plants when grown under high salt or dehydration stress conditions (Jang *et al.* 2008). Germination of the transgenic plants was delayed by the addition of ABA, implying that *CsHMGB* affects germination through an ABA-dependent way. The expression of *CsHMGB* had affected only the germination stage, and *CsHMGB* did not affect the seedling growth of the transgenic plants under the stress conditions. These results suggest that ectopic expression of a *CsHMGB* in *Arabidopsis* modulates the expression of several germination-responsive genes, and thereby affects the germination of *Arabidopsis* plants under different stress conditions.

Arabidopsis GCN5 is a major histone acetyltransferase. The mutation of the gene induces pleiotropic effects on plant development, and affects the expression of a large number of genes. *GCN5* was shown to interact specifically with a phosphatase 2C protein (*AtPP2C-6-6*). *GCN5* phosphorylated by activities in cellular extracts could be dephosphorylated by *AtPP2C-6-6 in vitro*. Analysis of T-DNA insertion mutants revealed a positive role of *AtPP2C-6-6* in salt induction of stress-inducible genes, while the *gcn5* mutation seemed to have no effect on the induction but showed up-regulation of a subset of the stress-inducible genes under non-induced conditions. In addition, the *gcn5* mutation seriously reduced acetylation of histone *H3K14* and *H3K27*, whereas the T-DNA insertions of the *AtPP2C6-6* gene enhanced the acetylation of these lysine residues (Servet *et al.* 2008).

Other genes

The plant enzyme 4-coumarate:coenzyme A ligase (*4CL*) is part of a family of adenylate-forming enzymes present in all organisms. Expression patterns of a conserved set of *Arabidopsis* and poplar 4CL-like acyl-CoA synthetase (*ACS*) genes were assayed. Expression analysis revealed conserved developmental and stress-induced expression patterns of *Arabidopsis* and poplar genes. Evolutionary and gene expression data, combined with *in vitro* and limited *in vivo* protein function data, suggest that angiosperm *ACS* enzymes play conserved roles in octadecanoid and fatty acid metabolism, and play roles in organ development, for example in anthers Fasciclin-like arabinogalactan proteins (FLAs), a subclass of arabinogalactan proteins (AGPs), are usually involved in cell development in plants. Recently, in cotton the expressions of the *GhFLA* genes were shown to be regulated in fiber development and in response to phytohormones and NaCl (Huang *et al.* 2008).

Another group of proteins that are involved in development and stress responses are Phospholipase D (*PLD*) *PLD* encoding genes constitute a large gene family that is present in higher plants. There are 12 members of the *PLD* family in *A. thaliana* and several of them have been functionally characterized, recent genome-wide analysis in rice identified 17 *PLD* members in different chromosomes. Expression pattern analysis indicates that most *PLD*-encoding genes are differentially expressed in various tissues, or are induced by hormones or stress conditions, suggesting the involvement of *PLD* in multiple developmental processes. Transgenic studies have shown that the suppressed expression of rice *PLD beta 1* results in reduced sensitivity to exogenous ABA during seed germination. Further analysis of the expression of ABA signaling-related genes has revealed that *PLD beta 1* stimulates ABA signaling by activating SAPK, thus repressing *GAmyb* expression and inhibiting seed germination (Li *et al.* 2007).

In a genetic screen for mutants with altered drought stress responses, an ABA-overly sensitive mutant, the *abo 1* mutant, which showed a drought-resistant phenotype was identified (Chen *et al.* 2006). The abo1 mutation enhances ABA-induced stomatal closing and increases ABA sensitivity in inhibiting seedling growth. *abo1* mutants are more resistant to oxidative stress than the wild type and show reduced levels of transcripts of several stress- or ABA-responsive genes. The mutation also differentially modulates the development and growth of adjacent guard cells. Map-based cloning identified *ABO1* as a new allele of *ELO2*, which encodes a homolog of *Saccharomyces cerevisiae Iki3*/*Elp1*/*Tot1* and human *IkappaB* kinase-associated protein. *Iki3*/*Elp1*/*Tot1* is the largest subunit of Elongator, a multifunctional complex with roles in transcription elongation, secretion, and tRNA modification.

Cryptochromes (CRYs) are blue light receptors important for plant growth and development. A recent study identified two CRY genes, *TaCRY1a* and *TaCRY2*, from the monocot wheat (Xu *et al.* 2009). The expression of *TaCRY1a* was most abundant in seedling leaves and barely detected in roots and germinating embryos under normal growth conditions. The expression of *TaCRY2* in germinating embryos was equivalent to that in leaves and much higher than the *TaCRY1a* counterpart. Treatment of seedlings with high salt, PEG and ABA up-regulated *TaCRY2* in roots and germinating embryos. The transgenic *Arabidopsis* plants over-expressing *TaCRY1a* and *TaCRY2* showed higher sensitivity to high salt, osmotic stress and ABA treatment during germination and post-germination development, and they displayed altered expression of stress/ABA responsive genes. The primary root growth in transgenic seedlings was less tolerant of ABA.

There are three iron superoxide dismutases in *Arabidopsis thaliana*: FE SUPEROXIDE DISMUTASE1 (*FSD1*), *FSD2*, and *FSD3*. Myuoga *et al.* (2008) showed that *FSD2* and *FSD3* play essential roles in early chloroplast development, whereas, *FSD1*, which is found in the cytoplasm, does not. An *fsd2-1 fsd3-1* double mutant had a severe albino phenotype on agar plates, whereas *fsd2* and *fsd3* single knockout mutants had pale green phenotypes. Chloroplast development was arrested in young seedlings of the double mutant. The mutant plants were highly sensitive to oxidative stress and developed increased levels of ROS during extended darkness. Furthermore, transgenic *Arabidopsis* plants overexpressing both the *FSD2* and *FSD3* genes showed greater tolerance to oxidative stress induced by methyl viologen than did the wild type or single *FSD2*- or *FSD3*-overexpressing lines. It was proposed in the study that heteromeric *FSD2* and *FSD3* act as ROS scavengers in the maintenance of early chloroplast development by protecting the chloroplast nucleoids from ROS.

CONCLUSIONS AND FUTURE PROSPECTIVES

The conclusions which can be drawn from the studies encompassed in this review are as follows:

1. Stress is an unavoidable and integral part in the plant growth, development and evolution. Though it causes great deal of losses towards the yield in crop plants the recent studies in this respect are providing leads to develop sustainable varities.
2. The stress signal is sensed by various hormonal, non hormonal and developmental tools of the plants and dissipated/transduced in the system to overcome variety of stress.
3. SA, JA and ET are the major signaling molecules for biotic stress, whereas, ABA, Ca^{2+} and ET evoke signal response in abiotic stress.
4. Most hormone including GAs, CYT, auxin and BRs besides the ones mentioned above enter into a cross talk during any stress and adjust their levels/activities through various mechanisms such as activating/deactivating various protein kinases in order to enable plants manage stress.
5. Various transcription factors appear to play most important task by way of activating/repressing target genes to help produce metabolites, enzymes, osmolytes, osmoprotectants and other chaperon molecules which provide protection to cell components.

The major challenge before plant scientists is to identify some or few central regulator which can be used stably or transiently to manage stress response without altering normal metabolism of the plant. High throughput analysis including microarray, transcriptomics, metabolomics, reverse genetics etc supported by a high quality bioinformatics should answer some of these questions related to stress response. A good transformation system of major crop plants needs to be developed in order to produce stress resistant transgenic varieties.

ACKNOWLEDGEMENTS

Works on plant stress tolerance in NT's and PN's laboratories are partially supported by Department of Science and Technology (DST), Government of India and Department of Biotechnology (DBT), Government of India.

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