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Reactive Oxygen in Abiotic Stress Perception - From Genes to Proteins

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1. Introduction

Throughout their life plants have to adapt to variable environmental conditions. Changes in photoperiod, light intensity and quality, nutrient abundance and starvation, drought and flooding, variation in temperature, air and soil pollution and osmotic changes are among the abiotic factors that can cause stress (Apel & Hirt, 2004). To ensure constant monitoring of environmental conditions and a quick and appropriate response, plants have developed elaborate and robust perception and signal transduction mechanisms. The importance of the ability to adapt to a changing environment has been described in numerous research articles and reviews (Hirayama & Shinozaki, 2010). Recent years have seen tremendous progress in our understanding of the mechanisms and processes underlying abiotic stress adaptation and defence in different plant species (Hirayama & Shinozaki, 2010; Jaspers & Kangasjärvi, 2010). Importantly, the analysis of abiotic stress tolerant varieties of *Arabidopsis* and also rice has led to novel ideas for improving the stress resistance of crop species. The diversity of abiotic stresses implies that there should be a strong specific component in the individual stress responses (Jaspers & Kangasjärvi, 2010). However, there is a striking common component in the general response to all abiotic stresses (Vaahtera & Brosché, 2011). Essentially all abiotic stresses lead to the production of reactive oxygen species (ROS) albeit different forms and in different subcellular compartments (Jaspers & Kangasjärvi, 2010). In contrast to their presumed role as simply damaging agents in cells ROS act as signalling molecules in the regulation of stress adaptation but also in developmental regulation (Apel & Hirt, 2004; Jaspers & Kangasjärvi, 2010; Møller et al., 2007). For reviews on other aspects of abiotic stress we refer to reviews (Jaspers & Kangasjärvi, 2010; Miller et al., 2008; Munns & Tester, 2008; Vaahtera & Brosché, 2011; Zhu, 2002).

Despite the wealth of information on abiotic stress defence in plants the mechanisms of stress sensing have remained relatively elusive. In this review we turn our attention to the mechanisms of abiotic stress perception. Generally, stresses, as well as other stimuli, can be perceived in a direct or an indirect manner. In direct perception, the agent causing the stress is perceived through a receptor. Alternatively, in indirect perception, specific effects leading to stress caused by an agent are perceived. Evidence suggests that in abiotic stress perception plants use both modes in parallel. In indirect stress perception ROS are components frequently used as signalling molecules. However, ROS themselves can be

subject to direct or indirect perception mechanisms (Figure 1). Since ROS are a response to common to many abiotic stresses particular emphasis will be placed on their role in stress perception. For general reviews on ROS signalling we refer the reader to recent reviews (Foyer et al., 2009; Foyer & Noctor, 2005; Foyer & Noctor, 2009; Foyer & Noctor, 2011; Jaspers & Kangasjärvi, 2010; Møller et al., 2007).

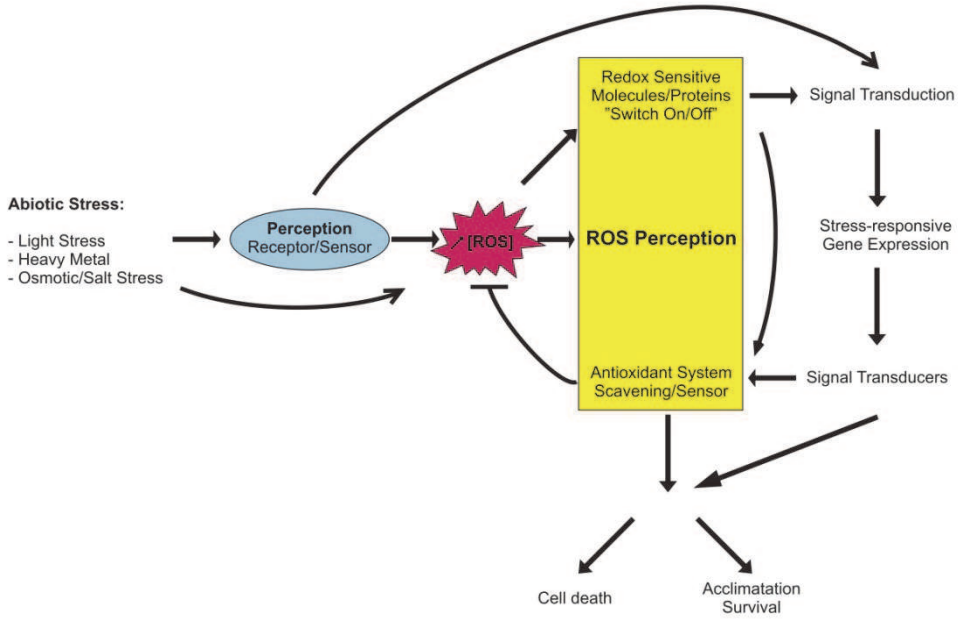

Fig. 1. Hypothetical model of the pathways involved in ROS perception in plants. Abiotic stress or its perception through transmembrane or intracellular receptors results in the overproduction of ROS, including singlet oxygen ($^1O_2$), superoxide ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), or hydroxyl radicals ($HO^{\cdot}$). The increase of ROS levels can be directly sensed by cellular sensors such as redox-sensitive proteins, e.g. transcription factors which can activate signal transduction to induce expression of stress-responsive genes. This results in differential regulation of gene expression that will affect pathways including the induction of the ROS scavenging system and repression of the ROS-producing mechanisms. Ultimately this sensing, signalling and transcriptional reprogramming will be critical for the future fate of the cell leading to adaptation to the stress or to cell death.

2. Perception of salt and osmotic stresses

Salt stress is an abiotic stress, for which some perception components have been identified. Salt stress, as induced by elevated concentrations of NaCl, can be separated into two components: an osmotic stress component and an ionic stress component, i.e., Na toxicity (Munns & Tester, 2008). Osmotic stress can also be caused by other osmotically active substances; mannitol is a frequently used chemical to analyze osmotic stress perception and regulation under laboratory conditions. To sense osmotic stress, a cell could employ either

direct or indirect perception mechanisms. A direct sensing of osmotic stress would be difficult to imagine. If a putative direct osmosensor would act like a classical ligand-specific receptor, it would have to detect water activity (Wood et al., 2001). Alternatively, through indirect perception mechanisms, an osmosensor could sense other cellular properties that are affected by osmotic changes including cell volume, turgor pressure, membrane strain, individual solute concentrations, ionic strength and crowding of macromolecules in the cytoplasm (Wood et al., 2001).

Promising candidates as receptors for salt and osmotic stress are histidine kinases and their cognate response regulators. Histidine kinases are well known for their roles in hormone responses, e.g. cytokinin and ethylene perception (Urao et al., 2000; Urao et al., 2001). In prokaryotes and in yeast histidine kinases have been identified as osmosensors but the system is also conserved in other organisms (Heermann et al., 2009; Heermann & Jung, 2010; Maeda et al., 2006). In the photosynthetic cyanobacterium *Synechocystis* sp. PCC 6803 several different histidine kinases together with their response regulators (Hik33-Rre31, Hik34-Rre1, Hik10-Rre3, Hik16-Hik41-Rre17, Hik2-Rre1) regulate the transcription of distinct gene sets in response to osmotic and salt stress and are likely involved in stress perception (Paithoonrangsarid et al., 2004; Shoumskaya et al., 2005). In the model plant species *Arabidopsis thaliana* a hybrid-type histidine kinase *ARABIDOPSIS THALIANA HISTIDINE KINASE 1 (ATHK1*) has been proposed as an osmosensor as early as the late Nineteen-Nineties (Tran et al., 2007; Urao et al., 1999). Interestingly, ATHK1 is also involved in the regulation of the desiccation process during seed maturation, a process which seems to be connected to drought tolerance (Wohlbach et al., 2008). Similar osmosensors have also been identified in other plant species including the woody plant *Populus deltoides* (Chefdor et al., 2006). While the evidence supports a role for histidine kinases as sensors for salt and osmotic stress, the mechanism of this stress perception is still unclear. Much information originates from gene expression analysis of stress responses and from phenotypic analysis of mutant plants; direct biochemical evidence for salt or osmotic stress sensing is however lacking. Investigation of the homologous histidine kinase-response regulator system KpdD/KpdE from *Escherichia coli* identified different parts of the proteins in the perception of low potassium conditions compared to osmotic stress (Heermann et al., 2009). It has been proposed that histidine kinases as transmembrane proteins might perceive changes in turgor or some associated effect (Epstein, 1992; Laimins et al., 1981). However, for the bacterial histidine kinase KpdD turgor reduction appears not to be the stimulus; and similarity of the histidine kinases suggests that this might be the case also for other species (Hamann et al., 2008). It is abundantly clear, that histidine kinases have important roles during the regulation of salt and osmotic stress responses in addition to their roles in hormone signalling and they are probably very early elements in the perception machinery. However, their precise biochemical roles have yet to be clarified.

Histidine kinases are not the only candidates for sensors for osmotic and ionic stress. There is evidence linking several transporters to osmosensing thereby unifying osmoperception and osmoregulation in bacteria (Wood et al., 2001). Receptor-transporters in *E. coli* seem to respond specifically to internal solvents (Culham et al., 2003a; Culham et al., 2003b; Rübenhagen et al., 2000; van der Heide et al., 2001; Wood et al., 2001). Several transmembrane transporter proteins have been identified in plants including the plasma membrane Na^+/H^+ antiporter SALT-OVERLY-SENSITIVE 1 (SOS1) and the HIGH-AFFINITY K^+ TRANSPORTER 1 (HKT1), which mediates Na^+-K^+ co-transport (Horie et al.,

2009; Mäser et al., 2002a; Mäser et al., 2002b; Schachtman & Schroeder, 1994; Shi et al., 2000; Shi et al., 2002). SOS1 interacts with an important regulator of abiotic stress responses, RADICAL-INDUCED CELL DEATH 1 (RCD1; Katiyar-Agarwal et al., 2006). Another group of transporters, the Na^+/H^+ EXCHANGER AtNHX1, and the close orthologues AtNHX2, 3, 4, 5 and 6 are involved in compartmentalization of Na^+ to the vacuole (Horie et al., 2009; Qiu et al., 2004; Yokoi et al., 2002). While these transporters are critical determinants of salt tolerance there is only little evidence linking them to salt stress perception (Horie et al., 2009). SOS1 is regulated through phosphorylation of its autoinhibitory C-terminal domain by the SALT-OVERLY-SENSITIVE 2 (SOS2) protein kinase, a member of the Sucrose non-fermenting 1-related protein family (Quintero et al., 2011). SOS2 is regulated through interaction with the Ca^{2+}-sensing protein SALT-OVERLY-SENSITIVE 3 (SOS3). This suggests that calcium is a critical regulator of Na^+-transport and osmotic/ionic stress regulation. It is still unclear however, which sensory mechanism and which signaling events lead to the required changes in cellular Ca^{2+} concentrations that subsequently result in differential regulation of SOS1. Other Ca^{2+} signalling proteins seem to be involved in the acclimation to abiotic stresses as well. The Ca^{2+}-DEPENDENT PROTEIN KINASE 3 (CPK3) provides a parallel pathway to MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) signalling in *Arabidopsis thaliana* (Mehlmer et al., 2010; Wurzinger et al., 2011). In these cases, just as in the example of SOS1, the importance of Ca^{2+} signalling is recognized, but the components that induce Ca^{2+} signalling in response to the initial stress remain unknown.

Recent research suggests a novel mechanism of osmoperception through salt-dependent protein-nucleic acid interactions (Novak et al., 2011). In the cyanobacterium *Synechocystis* sp. PCC6803 the key enzyme of the glucosyl-glycerol pathway (GgpS) can be non-competitively inhibited by nucleic acids in a sequence- and length-independent manner *via* a salt-dependent electrostatic interaction. The intracellular salt concentration thus could serve as a trigger for GgpS regulation leading to inactivation through nucleic acid binding at low salt concentrations. An increase in salt concentration leads to liberation of GgpS and the accumulation of glucosyl-glycerol facilitates the acclimatization to salt stress. It is unclear if this mechanism is also conserved in plants and other organisms, future research will have to answer this question.

3. Heavy metal sensing

Heavy metals (HMs) have biological importance in plant development and growth, where they play key roles affecting cellular processes such as homeostasis and photosynthesis (Terry, 1980). Many cellular processes are regulated by enzymes whose activities require the presence of heavy metals such as Fe, Zn, Mn, and Cu in the active site or in another position important for the proper enzyme functioning (Hänsch & Mendel, 2009). Thus, some HMs serve as cofactors of different enzymes and are important micronutrients, essential for plant growth. The variety and concentration of HMs depend on different sources. Natural sources include volcanic activity and continental dust. Alternatively HM can originate from human activities. Increased availability (concentration) of HMs strongly affects plant growth and development, resulting mostly in the inhibition of plant growth and toxicity symptoms. Toxic effect of HMs can be subdivided into production of ROS and oxidative stress, inhibition of enzyme activities *via* displacement of essential cofactors, and blocking of protein or metabolite functional groups, for example, by binding to thiol, carboxyl, and

histidyl groups (Sharma & Dietz, 2009). The identification and characterization of heavy metal transporters in plants is still ongoing and the mechanisms underlying HM perception through "sensor proteins" are poorly understood. However evidence suggests the existence of HM sensors in plants to perceive the availability of HMs in the environment.

Among HMs iron is of a special importance for plants due to its requirement for photosynthesis and most of the cellular redox-dependent processes. Many studies have been focusing on the iron deficiency response (Briat et al., 2007; Walker & Connolly, 2008; Wintz et al., 2003), less is known about signalling pathways induced by iron excess. Excess of iron is harmful for cells due to its high reactivity with oxygen which leads to ROS production. Accumulation of ferritins, iron storage proteins, in plastids is one of the early responses to iron excess in plants (Lobreaux et al., 1992; Petit et al., 2001). Ferritin gene expression is regulated by other environmental factors including drought, cold, and light intensity (Briat et al., 2010). Recent studies have shown that ferritins participate in defence against oxidative stress by buffering and sequestering free iron (Arosio et al., 2009; Ravet et al., 2009). Detailed gene expression analyses have allowed the identification of HM stress-specific transcriptional profiles and suggested the existence of HM sensors. Transcriptional analysis of plant responses to different HMs suggested the presence of a Zn^{2+} sensor in the cell. Interestingly, this Zn^{2+} sensor might have an important role in response to Cd^{2+} through competitive binding of Cd^{2+} or Zn^{2+}. However, this Zn^{2+} sensor is not yet identified. Following Cd^{2+} exposure expression of AtZIP9, a putative Zn^{2+}/Cd^{2+} transporter, increased in *Arabidopsis thaliana* (Weber et al., 2006). AtZIP9 is also known as a marker of Zn^{2+} depletion (Wintz et al., 2003). Although Zn^{2+} depletion is also rapidly observed under Cd^{2+} treatment, Cd^{2+}-induced gene expression is suggested to be rather a consequence of the competitive binding of Cd^{2+} to the Zn^{2+} sensor in response to Cd^{2+} exposure. Recently, HEAVY METAL ATPase 4 (AtHMA4), a heavy metal pump in *Arabidopsis thaliana,* has been proposed to have a dual role as Zn^{2+} and Cd^{2+} sensor and as a regulator of Zn^{2+} and Cu^{2+} export (Baekgaard et al., 2010). AtHMA4 has an extended C-terminal domain which exhibits high affinity to Zn^{2+} and Cd^{2+}. Heterologous expression of the C-terminal domain, containing 13 cysteine pairs, in the Zn^{2+}-sensitive *zrc1 cot1* yeast strain confers zinc and cadmium tolerance and decreased the accumulation of Zn^{2+} and Cd^{2+}. Another Zn^{2+}/H^{+} antiporter, METAL TOLERANCE PROTEIN 1 (AtMTP1), localizes to the vacuolar membrane and is involved in Zn^{2+} homeostasis. It drives Zn^{2+} detoxification and accumulation in the leaves. Interestingly, a histidine-rich loop might serve as a Zn^{2+} buffering pocket and Zn^{2+} sensor thus being crucial in maintaining proper levels of cytoplasmic Zn^{2+} (Kawachi et al., 2008). It is clear that metal transporters perform the task of metal sensing to regulate import or export of metal ions. How that subsequently translates into a downstream response as reflected in transcriptional adaptation however, is still unclear.

Detoxification of HMs occurs in the cytosol where high affinity targets of HM, so called chelators, bind and sequester HM in order to detoxify the cell. A variety of molecules are able to chelate HM, including both low molecular weight molecules such as organic acids, amino acids, peptides, as well as proteins, such as metallothioneins or phytochelatins (PC). After chelation, HM are transported and further sequestered in the vacuole (Hong-Bo et al., 2010). Indeed, vacuolar compartmentalization is considered as the major tolerance mechanism allowing HM accumulation in plants, mainly in the vacuoles of root cells. However, it has been demonstrated for some HM hyperaccumulator species, that shoots can

contain higher HM levels than roots (Hong-Bo et al., 2010). It is possible that chelators act as HM sensors and that the modification of these HM sensors/scavengers might be recognized by other proteins to decipher the information. On the other hand, indirect HM sensing *via* ROS signalling is well documented. After Cd^{2+} transport into the plant cell, glutathione (GSH) could act as an initial ligand to form GS_2-Cd^{2+} complexes. Cd^{2+} can also interact with GSH-derived peptides such as phytochelatins (PC) (Cobbett & Goldsbrough, 2002; Grill et al., 1985). The GS_2-Cd^{2+} and PC-Cd^{2+} complexes formation lead to GSH depletion which will induce oxidative stress through redox imbalance (De Vos et al., 1992; Ortega-Villasante et al., 2005; Schützendubel & Polle, 2002). *Arabidopsis* mutants deficient in GSH such as *cad2* are very sensitive to Cd^{2+} and other HMs (Howden et al., 1995; Hugouvieux et al., 2009). To date, PC synthesis is suggested to be at least one of the specific responses to heavy metal accumulation, since it has been described only after metal excess challenges. Indeed, although the PC synthase gene is constitutively expressed, the protein activity depends on metal ions and/or metal-GS complexes (Maier et al., 2003; Vatamaniuk et al., 2000). PC generation can thus be considered as a direct sensor of the presence of metal in plant tissues. In addition to PCs other potential metal binding targets might be used as markers of the metal perception if their activity and or function are altered after reacting with metal. However, their specificity to heavy metal stress should be assessed. Moreover, reverse genetic will help to understand the role of the specifically induced genes in response to heavy metal during metal stress signalling.

4. Sensing light stress

Similarly to salts and some heavy metals, which are important nutrients required for plant life, plants require light in order to thrive. However, excessive exposure to high light intensities can cause considerable damage to plants. Plants utilize light as their primary source of energy converting light to usable chemical energy through photosynthesis. Light is an essential prerequisite for Chlorophyll (Chl) biosynthesis and chloroplast development; events that do not take place in darkness. Early light perception involves three classes of wavelength-specific photoreceptors, phytochromes (PHYs), cryptochromes (CRYs) and phototropines (PHOTs).

PHYs, sensing red and far-red light, are synthesized in darkness in an inactive Pr form and localize to the cytosol. Upon light perception, PHYs are converted into the biologically active Pfr form and translocate to the nucleus to initiate signalling pathways through direct interaction with PHYTOCHROME INTERACTING FACTORS (PIFs), a subfamily of basic helix-loop-helix (bHLH) transcription factors (Castillon et al., 2007; Leivar & Quail, 2011). *Arabidopsis* contains 5 genes encoding PHY apoproteins, PHYA-E, with PHYA and PHYB playing the main role in the photomorphogenetic response. Isolation of a quintuple mutant lacking all five *PHY* genes has shown that the PHYs are the major but not the sole sensors of red-light in *Arabidopsis* since the mutant is able to respond to red light and accumulate chlorophyll (Strasser et al., 2010). The quintuple mutant has several developmental defects; some of these defects can be bypassed by blue light exposure indicating functional CRYs in the absence of PHYs. In contrast to the red light receptor complement in *Arabidopsis thaliana*, PHYs are the only red light photoreceptors in rice, since *phyA phyB phyC* triple mutant lack chlorophyll biosynthesis and changes in gene expression in response to red light (Takano et al., 2009). Inactive CRY1 and CRY2 are localized to the nucleus where they interact with

CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), an E3 ubiquitin ligase, a key regulator of light signalling. Blue light induces activation and translocation of CRY1 to the cytoplasm, whereas CRY2 remains in the nucleus.

The proteins acting downstream of PHYs and CRYs are mainly transcription factors regulating photosynthesis-related genes necessary for chloroplast biogenesis (Vandenbussche et al., 2007; Waters & Langdale, 2009). PIFs are transcriptional inhibitors, and their degradation upon phytochrome activation promotes the expression of photomorphogenesis-related genes. PIF1 regulates the expression of *PORC*, encoding Pchlide oxidoreductase, an enzyme in chlorophyll biosynthesis pathway (Huq et al., 2004). PIF3 is a negative regulator of genes *HEMA1* and *GENOMES UNCOUPLED 5* (*GUN5)*, encoding enzymes of Chl biosynthesis, and also genes encoding for components of Photosystem I (PSI) (Shin et al., 2009). Consequently, *pif1* and *pif3* mutants accumulate high amounts of the Chl intermediates when grown in darkness which leads to photobleaching after transfer to light. Quadruple mutant *pif1 pif3 pif4 pif5* (*pifQ*) is constitutively photomorphogenic and the gene expression profiles of the dark-grown *pifQ* mutant and the red-light-grown wild type *Arabidopsis* are similar (Shin et al., 2009). LONG HYPOCOTYLS 5 (HY5) is a bHLH transcription factor, acting downstream of light signalling cascades induced by activation of photoreceptors. HY5 positively regulates a number of photosynthesis-related genes (Andronis et al., 2008; Lee et al., 2007a). Activity of HY5 is mediated by protein phosphorylation and degradation, where COP1 plays an important role. CRY1 and HY5 have been shown to regulate many highlight responsive genes, including EARLY LIGHT INDUCIBLE PROTEINs (ELIPs) and ASCORBATE PEROXIDASE 2 (APX2), in young seedlings (Kleine et al., 2007). The *cry1* mutant has enhanced sensitivity to high irradiance which is demonstrated by photobleaching and increased photoinhibition of the photosystem II (PSII) under high light (Kleine et al., 2007).

Belonging to another class of blue light photoreceptors, PHOT1 and PHOT2 have a minor role in blue light dependent photomorphogenesis compared to CRYs. However, PHOT1 and PHOT2 play a key role in blue light-dependent chloroplast movement, which serves as a rapid response to different light regimes (Celaya & Liscum, 2005; Demarsy & Fankhauser, 2009). Knockout of both PHOTs is sufficient to eliminate all chloroplast movements (Sakai et al., 2001). Analysis of single *phot* mutants demonstrated the exclusive role of PHOT2 in high light response and redundant role of both PHOT proteins in low light response (Ohgishi et al., 2004). PHOTs have also partially redundant functions in the regulation of phototropism and stomatal opening (Kinoshita et al., 2001). PHOT proteins are plasma membrane localized protein kinases, containing two light oxygen voltage (LOV) domains, essential for their function. PHOT1 and PHOT2 can autophosphorylate (Inoue et al., 2008; Matsuoka & Tokutomi, 2005). This autophosphorylation mediates *in vivo* interaction of PHOT with 14-3-3 proteins (Sullivan et al., 2009). In addition, PHOT interacts directly with PHYTOCHROME KINASE SUBSTRATE family proteins (de Carbonnel et al., 2010).

Unlike light in the visible spectrum, even moderate levels of UV-B irradiation cause oxidative stress. Studies of UV-B light signalling suggested its perception by a specific receptor, different from those discussed above (Ulm & Nagy, 2005). UV RESPONSE LOCUS 8 (UVR8) was recently shown to be a direct sensor of UV-B in *Arabidopsis* (Rizzini et al., 2011). The signalling pathway leading to transcriptional response includes also COP1 and HY5 (Brown & Jenkins, 2008; Oravecz et al., 2006). In the absence of UV-B UVR8 localizes to the nucleus and to the cytosol (Kaiserli & Jenkins, 2007). Upon UV-B irradiation UVR8

translocates to the nucleus where it interacts directly with COP1 in a UV-B dependent manner which, in turn, affects the interaction between COP1 and HY5 (Favory et al., 2009; Kaiserli & Jenkins, 2007).

Mature chloroplasts, in turn, work as environmental sensors regulating stress response and dynamic acclimation of the photosynthetic mechanism to environmental fluctuations. Environmental factors such as light, temperature and nutrient availability exert a strong effect on the function of plant chloroplasts. Changes in light intensity lead to rearrangement of the light harvesting antenna complexes and changes in composition of the two photosystems. Low light requires optimizing of light harvesting whereas high light leads to increased energy dissipation and photoinhibition. Mechanisms of regulation are referred to as nonphotochemical quenching (NPQ) (Bailey & Grossman, 2008; Holt et al., 2004). The *Arabidopsis npq4* mutant, lacking the minor subunit S of PSII (PSBS), is deficient in dissipation of excess energy and is more sensitive for photoinhibition during high light. Overexpession of *PsbS* leads to enhanced resistance to high light stress (Li et al., 2002). Moreover, the transcript and protein levels of *PsbS* are elevated upon exposure of *Arabidopsis* to high light (Giacomelli et al., 2006; Kimura et al., 2003). Screens for *npq* mutants in *Chlamydomonas* identified stress-related chlorophyll a/b binding proteins 2 and 3 as proteins required for proper energy dissipation (Bonente et al., 2011; Peers et al., 2009).

Changes in light quality induce imbalanced excitation of the two photosystems which have distinct absorption spectra. The mechanisms of acclimation include reversible phosphorylation and migration of a part of the light-harvesting antenna complexes between photosystems to balance the energy distribution (so-called state transitions). The process is controlled by the redox status of the plastoquinone pool (PQ). The genetic screen for mutants with impaired state transitions in *Chlamydomonas* resulted in identification of Stt7 protein kinase responsible for phosphorylation of LHCII (Depège et al., 2003). Two orthologs of Stt7 with different substrate specificity exist in *Arabidopsis*: STN7 protein kinase phosphorylates Light Harvesting Complex II (LHCII), and STATE TRANSITION 8 (STN8) protein kinase is involved in phosphorylation of PSII core proteins (Bonardi et al., 2005; Vainonen et al., 2005). STN7, activated by the reduced PQ pool, is required for state transitions (Bonardi et al., 2005) and supposed to be involved in retrograde signalling *via* a yet unknown mechanism (Pesaresi et al., 2010; Pfannschmidt, 2010). Oxidation of the PQ pool inactivates the STN7 kinase which leads to dephosphorylation of light-harvesting proteins by THYLAKOID-ASSOCIATED PHOSPHATASE 38 (TAP38/PPH1) protein phosphatase identified in a reverse genetics screens (Pribil et al., 2010; Shapiguzov et al., 2010). Thus, the pair STN7/TAP38(PPH1) is a key regulator of state transitions and short-term acclimation in *Arabidopsis*. The lack of STN8 protein kinase in *stn8* and *stn7 stn8* single and double mutants results in ineffective repair of PSII and higher susceptibility to photoinhibition under high light stress (Tikkanen et al., 2008).

The photosynthetic reactions in chloroplasts are a continuous source of ROS: several different ROS are produced inside plastids as by-products of photosynthesis. Superoxide ($O_2^{\cdot-}$) is converted to hydrogen peroxide (H_2O_2) by a chloroplast-associated superoxide dismutase (SOD). Singlet oxygen ($^1O_2$) is produced at PSII by energy transfer from excited chlorophyll molecules to oxygen. Imbalanced electron flow due to high light or environmental stress favour production of $^1O_2$ inside plastids. Production of ROS in chloroplasts leads to dramatic changes in nuclear gene expression including genes encoding

for photosystem subunits (Bechtold et al., 2008; Fey et al., 2005). The extensive study of the molecular mechanisms of signalling suggests several partially overlapping and redundant pathways (Nott et al., 2006).

The *Arabidopsis fluorescent in blue light* (*flu*) mutant (Meskauskiene et al., 2001) has played a key role as a tool in dissecting signalling pathways specific to singlet oxygen generation within plastids and it has been used to identify genes specifically regulated by singlet oxygen release within plastids (op den Camp et al., 2003). FLU is a nuclear-encoded plastid protein and a negative regulator of Chl biosynthesis. Dark-grown *flu* seedlings overaccumulate protochlorophyllide (Pchlide), an intermediate in the Chl biosynthetic pathway. Pchlide acts as a photosensitizer and produces singlet oxygen upon illumination. Transfer of *flu* seedlings from dark to light leads to their rapid bleaching and death. Light is required for the induction of early responsive genes and the onset of programmed cell death (PCD) in *flu* seedlings after the dark-light shift. CRY1 was shown to mediate the transcriptional response, thus, linking ROS signalling to photomorphogenesis (Danon et al., 2006). Under continuous light the *flu* mutant grows as wild type; however, placing mature *flu* plants in darkness followed by transfer to light, results in growth inhibition.

Extensive mutant screens have been made with mutagenized *flu* seeds to identify second-site mutants that do not show bleaching of seedlings or growth inhibition of mature plants after the dark-to-light shift (Lee et al., 2007b; Wagner et al., 2004). Another approach has utilised a transgenic line of the *flu* mutant with a $^1O_2$-responsive reporter gene (Baruah et al., 2009a; Baruah et al., 2009b). The majority of mapped mutations targets genes encoding for chloroplast proteins. EXECUTER 1 (EX1), identified in a suppressor screen, is required for induction of a larger part of $^1O_2$-responsive genes. The double mutant *ex1 flu* accumulates the same level of the chlorophyll intermediate in darkness, but grows similarly to wild type and does not bleach after a transfer to light. This result suggests that in *ex1 flu* the signalling pathway from $^1O_2$ in chloroplasts to the nucleus is impaired. The closely related EXECUTER 2 works as a modulator of EX1 activity. Both nuclear-encoded proteins are localized to the thylakoid membranes inside chloroplasts; the molecular mechanism of their action is so far unknown.

Another group of second site mutants, *soldat* mutants, suppress the PCD of *flu* seedlings after the dark-light shift. Both characterized mutants (*soldat8 flu*, *soldat10 flu*) accumulate the same level of Pchlide and exhibit almost the same transcriptional response as the parental *flu* plants but their seedlings remain green after illumination. Identification of impaired genes resulted in SIGMA6 factor of plastid RNA polymerase in *soldat8* and mTERF-related plastid protein in *soldat10*. The only non-plastid regulator identified so far in the mutant screens is PLEIOTROPHIC RESPONSE LOCUS 1 (PRL1) protein, localized to the nucleus and known to mediate multiple stress responses, including energy deprivation (Baruah et al., 2009a). The mutant was isolated by constitutive expression of a $^1O_2$-responsive gene. Gene expression data showed that PRL1 regulates only a subset of $^1O_2$-responsive genes and, in addition, it regulates other genes. The *prl1* mutant has enhanced resistance to combined (cold/high light) stress than wild type (Baruah et al., 2009a). In summary, using the *flu* mutant and genetic approaches, it has been shown that $^1O_2$ signalling from plastids is mediated by several signal transduction pathway and is linked to a variety of environmental stresses.

5. ROS are a common factor of abiotic stresses

A common factor between most stresses is the active production of reactive oxygen species (ROS) (Jaspers & Kangasjärvi, 2010). Also salt acclimation and osmotic stress result in the

increased production of ROS (Miller et al., 2010). It has become clear that ROS are not only toxic to cells but serve important functions as signalling molecules. However, we do not currently have a clear understanding of how ROS signalling works and how ROS signals are perceived. The regulation of ROS production occurs in different subcellular locations including the chloroplasts, peroxisomes, mitochondria and in the apoplast. Important components of the apoplastic oxidative burst are the NADPH oxidases respiratory burst oxidase homologues (AtRBOH). AtRBOHD and AtRBOHF have important functions during the defence against pathogens but also in the response to abiotic stress (Miller et al., 2009). It has been proposed that the ROS produced by the NADPH oxidases in the extracellular space serve mostly as signalling molecules rather than being directly cytotoxic (Jaspers & Kangasjärvi, 2010). While the importance of ROS in signalling during stress adaptation and development in plants has been recognized, their perception has remained largely elusive. Several regulators of transcription have been found to be redox regulated in plants, most notably NONEXPRESSER OF PR GENES 1 (NPR1) and the transcription factor TGA2 (see below) (Després et al., 2003; Fan & Dong, 2002; Fobert & Després, 2005). In addition, methionine oxidation of proteins might be another way to regulate the enzymatic activity of proteins directly through redox control (Hardin et al., 2009). These proteins however rely on intracellular ROS for redox regulation. The perception of apoplastic ROS is so far not well understood. Extracellular ROS might be perceived in different ways. Either proteins might be redox modified leading to ROS sensing, or other components of cell wall or membranes might be oxidized and those in turn sensed by receptors, leading to signalling into the cytosol (Hancock et al., 2006; Jaspers & Kangasjärvi, 2010). In particular cysteine-rich proteins have been proposed as candidates for ROS perception in the apoplast (Reddie & Carroll, 2008). Candidates include receptor-like kinases (RLKs) and small apoplastic proteins and peptides. The members of the Cysteine-rich receptor-like kinase (CRKs) subfamily of the receptor-like kinases (RLKs) contain two copies of a conserved cysteine motif C-8X-C-2X-C which has been proposed to serve as a suitable target for redox regulation (Acharya et al., 2007; Chen et al., 2003; Chen et al., 2004; Czernic et al., 1999). *CRKs* have been found to be transcriptionally regulated by oxidative stress, pathogen attack and plant hormones (Chen et al., 2004; Czernic et al., 1999; Wrzaczek et al., 2010). Plants ectopically overexpressing CRKs have altered responses to pathogens and show spontaneous induction of cell death (Acharya et al., 2007; Chen et al., 2003; Chen et al., 2004). The small extracellular GRIM REAPER (GRI) protein is another candidate for ROS perception (Wrzaczek et al., 2009a; Wrzaczek et al., 2009b). A peptide derived from GRI can induce cell death in plants in the presence of superoxide. Interestingly cell death induced by GRI-peptide is dependent on superoxide produced by AtRBOHD but not AtRBOHF which could point to different timing of ROS production by different NADPH oxidases and different functions. However, while evidence could support a role for CRKs and GRI in ROS perception, this hypothesis has yet to be experimentally tested.

The intracellular redox status is sensed also by transcription factors. Interestingly, in yeast and bacteria redox-sensitive transcription factors are involved in the transcriptional regulation of genes encoding for antioxidant enzymes (Georgiou, 2002). However, only few studies have reported the presence of such sensors in plants. During plant immunity, NPR1 plays a critical role in the activation of defence related gene expression, such as *PATHOGENESIS-RELATED 1* (*PR1*). The monomerization of NPR1 occurred upon redox state changes, allowing the translocation of the protein to the nucleus, thereby enhanced the

transcription of defence genes after interaction with TGAs (TGA2). The conformation changes of NPR1 have been demonstrated to result from thioredoxin activity and S-nitrosylation (Tada et al., 2008). Recently, the use of cytosolic *ascorbate peroxidase1* (*apx1*) mutants, *Catalase* (*Cat*) antisense lines and pharmacological approach demonstrated that cytosolic H_2O_2 accumulation prevents the translocation of NPR1 protein to the nucleus (Peleg-Grossman et al., 2010), suggesting the important role of NPR1 in the sensing of redox state changes which occur in the cell. Based on the literature in mammals and yeast, other transcription factors, such as heat shock transcription factors have been suggested to act as direct H_2O_2 sensors (Miller & Mittler, 2006).

Another indirect mechanism through which ROS are perceived is *via* the oxidatively modified molecules that are produced by the action of ROS. In principle any oxidatively damaged biomolecule has the potential to act as a signal. In particular the lipids represent a rich source of potential ROS dependant signals. Oxidative membrane damage, especially the process of membrane lipid peroxidation chain reactions are a common and very well documented consequence of oxidative stress. Oxidized lipids are generally themselves highly reactive and toxic; however, many have demonstrated biological activity, especially at low concentrations (Mueller & Berger, 2009). Reactive oxylipins are thiol reactive and able to modify thiol groups on a large number of proteins. Accordingly, similar sets of genes are regulated in transcriptomics experiments by reactive oxylipins as are by other thiol active compounds such as ROS and reactive nitrogen species (RNS) (Mueller & Berger, 2009). Oxylipins represent good example of how oxidized lipids can act as signal molecules. 12-oxo-phytodienoic acid (12OPDA) is a cyclopentone oxylipin intermediate on the jasmonic acid biosynthesis pathway. Interestingly, 12OPDA can be produced both enzymatically and non-enzymatically *via* a free radical catalyzed peroxidation pathway. 12OPDA induces physiological responses similar to those of jasmonates including upregulation of stress and general detoxification pathways.

6. Antioxidant systems

As described above, ROS are actively produced and used as signalling molecules by cells in response to most abiotic stresses. In addition, ROS are continuously produced as by-products during different metabolic pathways in plants. Due to the highly reactive nature of ROS their production and detoxification needs to be strictly controlled. ROS production occurs in virtually all cell compartments; but most notably, in different organelles including mitochondria, chloroplasts and peroxisomes, due to their highly oxidizing metabolic activity, and also in the apoplast.

Plants have developed various antioxidant systems which are specifically localized to different subcellular loci and can be induced upon a stimulus. Diffusion of ROS is typically limited due to their high reactivity. This property requires ROS scavenging and detoxification to take place at or close to the location of ROS production. The ubiquitous presence of the antioxidant system is critical in order to prevent and survive oxidative stress. However, due to its presence and flexibility, the antioxidant systems could also present an efficient means to sense ROS through the antioxidant status of the cell.

Oxidative stress is defined as a disturbance in the equilibrium status of oxidants and antioxidants. Most of the antioxidant components act as free radical scavengers. By binding and inactivating the free radicals, antioxidants protect against oxidative stress. The tight cooperation between enzymatic and non-enzymatic antioxidant systems provides to the cell

an elaborated and efficient system to regulate ROS levels (De Gara et al., 2010; Foyer & Noctor, 2009; Miller et al., 2010; Shao et al., 2008).

The non-enzymatic antioxidant system includes ascorbic acid (AsA), GSH and α-tocopherol. AsA and GSH, the most abundant soluble antioxidants in plants, play a key role in plant defence against oxidative stress (Foyer & Noctor, 2011). These antioxidants are present predominantly in the reduced form in the majority of subcellular compartments. In response to stress, GSH can be oxidized into its disulphide form, GSSG, which can accumulate to high levels in plant cells. Glutathione redox status (GSSG/GSH ratio) reflects the level of oxidative stress, therefore GSH is frequently considered to be a suitable oxidative stress marker (Foyer & Noctor, 2009; Foyer & Noctor, 2011). GSH is also able to react with nitrous acid to form S-nitrosothiols called S-nitrosoglutathione (GSNO), which constitute a nitric oxide (NO) reservoir and are emerging to play key role in NO signalling pathways in plants (Besson-Bard et al., 2008; Del Rio, 2011; Lindermayr et al., 2005). In addition, glutathionylation of proteins can modify their activity (Palmieri et al., 2010). GSH and AsA are thought to function in a coordinated manner to regulate redox homeostasis plants during development and environmental responses (Foyer & Noctor, 2005; Foyer & Noctor, 2009; Foyer & Noctor, 2011). α-tocopherol, an abundant vitamin E compound, is a lipid soluble antioxidant found in chloroplasts where it counteracts lipid peroxidation through scavenging of lipid peroxyl radicals and detoxifies singlet oxygen and hydroxyl radicals (Munné-Bosch, 2005).

The major elements of the enzymatic antioxidant system are summarized in the Table 1. SOD, APX and CAT are three main enzymes present ubiquitously permitting the tightly control of ROS levels by scavenging directly ROS and converting them into less reactive and less harmful species. They can be considered as intracellular ROS sensors due to their direct interaction with ROS. Another group of enzymes, monodehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR), is involved in the reduction of oxidized AsA or GSH, thus, balancing the redox status of the cell (Asada, 1999; Foyer & Noctor, 2011). Up-regulation of the enzymes involved in the antioxidant system both at the transcript and the protein levels in response to ROS accumulation has been shown for a variety of abiotic stresses (Gill & Tuteja, 2010).

The low molecular-weight antioxidants and the enzymatic antioxidant system constitute a complex and diversified antioxidant system which participates efficiently in all the different organelles of plant cells to maintain redox state. The antioxidant system is one of the first barriers against ROS overproduction during abiotic stresses. The ratios between the oxidized and the reduced forms of antioxidants have been suggested to play a key role in the oxidative stress response and the control of the antioxidant systems (Karpinski et al., 1997). Other studies have underlined the importance of low ascorbate levels and variations of GSH pools during pathogen response, cell death and dormancy (Barth et al., 2004; Gomez et al., 2004; Kranner et al., 2002; Kranner et al., 2006; Mou et al., 2003; Parisy et al., 2007; Pastori et al., 2003)

7. Beyond signal perception and ROS detoxification

So far this review has addressed the perception mechanisms of abiotic stress. However, after a given stress has been perceived the various signals need to be integrated and transmitted

into an appropriate response for adaptation. Protein kinases are important components of the signal transduction cascade that links abiotic stress perception to signal integration and transcriptional reprogramming of the cell (de la Fuente van Bentem et al., 2008; Nakagami et al., 2010; Sugiyama et al., 2008). MAPKs and phosphatases alongside with CPKs are prominent participants in the abiotic stress signalling network (Ichimura et al., 2000; Jonak et al., 2004; Mehlmer et al., 2010; Miller et al., 2008; Mizoguchi et al., 1997; Takahashi et al., 2011; Wurzinger et al., 2011; Yuasa et al., 2001).

Enzyme	Reaction catalyzed	Subcellular localization	References
Superoxide dismutase (SOD)	$O_{2^{\cdot-}} + O_{2^{\cdot-}} + 2H^+ = 2H_2O_2 + O_2$	cytosol (Cu/Zn-SOD) chloroplast (Cu/Zn-SOD, Fe-SOD) mitochondria and peroxisome (Mn-SOD)	(Alscher et al., 2002; Del Rio, 2011)
Catalase (CAT)	$H_2O_2 = H_2O + ½\ O_2$	peroxisome	(Mhamdi et al., 2010; Willekens et al., 1997)
Ascorbate peroxidase (APX)	H_2O_2 + AsA = H_2O + DHA	chloroplast, cytosol, mitochondria	(Santos et al., 1996)
Monodehydroascorbate reductase (MDHAR)	MDHA + NAD(P)H = AA + $NAD(P)^+$	chloroplast, mitochondria, cytosol	(Asada, 1999)
Dehydroascorbate reductase (DHAR)	DHA + 2GSH = AsA + GSSG	chloroplast, cytosol	(Urano et al., 2000)
Glutathione reductase (GR)	GSSG + NAD(P)H = 2GSH + $NAD(P)^+$	cytosol,peroxisomes (AtGR1) chloroplast, mitochondria (AtGR2)	(Kaur & Hu, 2009)

Table 1. Major enzymes involved in ROS detoxification in plants.

Also forward genetic screens have yielded significant insight into the metabolism and signalling in response to abiotic stress and in ROS signalling. Paraquat (methyl viologen) and ozone (O_3) are two of the most commonly used stress inducers in these screens. Paraquat leads to ROS production in the chloroplast as it unlinks the electron transport chain in PSI and is used as a model to address the role and metabolism of chloroplastic ROS. A large-scale screen has identified several new proteins of mostly unknown function involved in the response to oxidative stress (Luhua et al., 2008). O_3 breaks down in the leaf apoplastic space to form secondary ROS that both mimic and induce an apoplastic oxidative burst similar to that of other stresses, most notably the pathogen response. Therefore O_3 is used as a model to investigate the signalling processes associated with apoplastic ROS. Many mutants isolated in screens for O_3-sensitivity are related to antioxidants (Conklin et al., 1996; Conklin & Last, 1995), stomatal biology (Vahisalu et al., 2008) and stress hormones (Ahlfors et al., 2008; Mahalingam et al., 2003; Vahala et al., 2003a; Vahala et al., 2003b), which are covered elsewhere in this chapter or have been previously reviewed (Overmyer et al., 2003). Some mutants have helped to define novel ROS signalling pathways; such as the *rcd1* mutant. The *rcd1* mutant was originally identified in a screen for O_3-sensitivity (Overmyer et al., 2000). The *RCD1* gene is also highly induced during high light stress

(Bechtold et al., 2008) providing a link to light induced chloroplastic ROS signalling. Intriguingly *rcd1* shows enhanced tolerance to paraquat (Ahlfors et al., 2004; Overmyer et al., 2000). RCD1 also shows a subtle salt-sensitive phenotype and is able to interact with the Na^+/H^+ antiporter SOS1 in yeast 2-hybrid (Katiyar-Agarwal et al., 2006). SOS1 is crucial for salt stress tolerance and *sos1* mutants are hypersensitive to salt stress, thus the interaction with RCD1 provides one more link between salt stress and ROS signalling. RCD1 is able to interact with several transcription factors in yeast 2-hybrid analysis (Jaspers et al., 2009; Jaspers et al., 2010b). This together with physiological data makes RCD1 a promising candidate as a central integration node for ROS signalling and indicates that highly divergent perception mechanisms, such as those described here for highlight, salt, dehydration (stomatal), and herbicide induced stresses, all converge into a common pathway (Jaspers et al., 2009; Jaspers et al., 2010a; Jaspers & Kangasjärvi, 2010).

8. Conclusions

The signalling pathways leading to an appropriate and coordinated response to abiotic stress have been the target of intensive research in the past decades. Global warming and intensive farming make it necessary to understand the underlying mechanisms and modify plant stress tolerance through selective breeding or genetic modification. However, with the exception of light perception, relatively little is known about the mechanisms of abiotic stress sensing. Recent research has identified several potential candidates as sensors for salt and heavy metals but a final proof of their function as true receptors is still needed. Similarly to biotic interactions, the production of ROS in abiotic stress has been well established in the last years. Increasing amount of evidence suggests that the generation of specific types of ROS in defined subcellular compartments is an important component of the stress response. Rather than being just cytotoxic by-products of biochemical processes ROS are likely to play central roles as regulators of stress adaptation, PCD, and even plant development (Apel & Hirt, 2004; Jaspers & Kangasjärvi, 2010; Miller et al., 2008). While ROS are biochemically simple molecules the intricate specificity observed during ROS signalling is still insufficiently understood (Gadjev et al., 2006). Some components of ROS perception inside the cell through modification of transcription factors and monitoring of the oxidative potential by means of ROS scavengers have been identified. However these do not explain the high specificity of transcriptional reprogramming induced by production of different ROS in specific subcellular locations.

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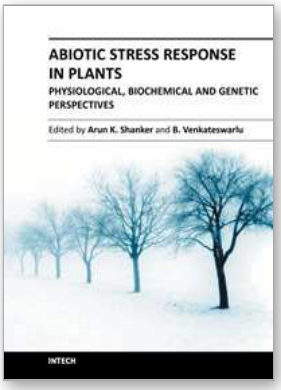

Abiotic Stress Response in Plants - Physiological, Biochemical and Genetic Perspectives

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

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