8

Plant Plasma Membrane H^+-ATPase in Adaptation of Plants to Abiotic Stresses

Małgorzata Janicka-Russak
Wrocław University, Institute of Plant Biology, Department of Plant Physiology
Poland

1. Introduction

H^+-ATPase is a major enzyme protein of the plant plasma membrane (PM). This protein belongs to a large superfamily of pumps termed P-type ATPases. A characteristic feature of P-ATPases is the formation of a phosphorylated intermediate during the catalytic cycle. P-type ATPase genes can be divided into ten phylogenetic branches. Six of them are found in plants (Axelsen & Palmgren, 2001). The plasma membrane proton pump belongs to the P_3-type ATPase family. The H^+-ATPase branch is subdivided into five subfamilies (Arango et al., 2003). Plasma membrane H^+-ATPase is a tightly bound and integral transmembrane protein. The enzyme is a single polypeptide of ~100 kDa. By the use of the chemical energy of ATP, plasma membrane connected ATPases extrude protons from cells of plants to generate electrochemical proton gradients. The generation of this gradient has a major role in providing the energy for secondary active transport across the plasma membrane. The plant plasma membrane H^+-ATPase is a proton pump which plays a central role in physiological functions such as nutrient uptake, intracellular pH regulation, stomatal opening and cell growth. Besides regulation of physiological processes, the plasma membrane proton pump also plays a role in adaptation of plants to changing conditions, especially stress conditions. Thus, H^+-ATPase can be a mutual element for resistance mechanisms that are activated in various stress conditions. Many studies have shown the changes of gene expression of the plasma membrane H^+-ATPase in response to a variety of environmental factors. Moreover, besides the genetic regulation of the proton pump, its activity may undergo fast post-translational modulation.

2. H^+-ATPase structure and H^+ transport

The enzyme is a functional single polypeptide chain with mass of about 100 kDa. The protein can oligomerize to form dimeric and hexameric complexes (Kanczewska et al., 2005). The H^+-ATPase has N- and C-terminal segments, which emerge into the cytoplasm (Duby & Boutry, 2009). The structure of plasma membrane H^+-ATPase consists of domains A, M, P, N, and R. The A-domain (actuator) consists of the N-terminal segment and small loop. The M-domain (membrane) corresponds to a transmembrane domain with ten helices, M1 to M10. The P-domain (phosphorylation) is located in the large loop. The N-domain (nucleotide binding) is located between two parts of the sequence forming the P-domain. The R-domain (regulatory) consists of the C-terminal fragment of the protein which acts as

an autoinhibitory domain (Pedersen et al., 2007; Duby & Boutry, 2009). The plant plasma membrane H^+-ATPase is kept at a low activity level by its C-terminal domain, the inhibitory function of which is thought to be mediated by two regions (regions I and II) interacting with cytoplasmic domains essential for the catalytic cycle (Speth et al., 2010).

The catalytic cycle of H^+-ATPase is described by two main conformational states, E_1 and E_2. In the E_1 conformation, the transmembrane binding site has high affinity for the proton and for ATP, whereas in E_2 the same site has low affinity for both ligands. The states E_1 and E_2 alternate during transport (Buch-Pedersen et al., 2009). The cytoplasmically positioned N, P and A domains are in charge of ATP hydrolysis. Conformational changes in these domains during catalysis lead to simultaneous movements in the membrane-embedded part that directs the proton transport. The transporting unit of plasma membrane proton pump is defined by a centrally located proton acceptor/donor – a single protonable aspartic acid residue (Asp684), an asparagine residue (Asn106), an arginine amino acid residue (Arg655), and a large central cavity likely to be filled with water (Buch-Pedersen et al., 2009). The Asp684 is in close contact with Asn106. In the E_1P structure protonation of Asp684 is believed to facilitate hydrogen bond formation between these two. Phosphorylation leads from E_1P to E_2P conformational changes and proton unloading from Asp684. Arg655 is suggested to play an important role in proton release and proton pumping against high membrane potentials. The positive charge of Arg655 approaching Asp684 will favour proton release from Asp684 and inhibit reprotonation of Asp684 with an extracellular proton (Buch-Pedersen et al., 2009). In plasma membrane H^+-ATPases, a single proton is believed to be transported per hydrolysed ATP (Palmgren, 2001). However, partial uncoupling between ATP hydrolysis and proton transport has been suggested (Buch-Pedersen et al., 2006). The plant plasma membrane H^+-ATPase is stimulated by potassium (Palmgren, 2001). K^+ is bound to the proton pump in the cytoplasmic phosphorylation domain (P-domain). Binding of K^+ promotes dephosphorylation of the phosphorylated E_1P reaction cycle and it controls the H^+/ATP coupling ratio. It was suggested that potassium acts as an intrinsic uncoupler of the plasma membrane H^+-ATPase (Buch-Pedersen et al., 2006).

3. Transcriptional regulation of plant plasma membrane H^+-ATPase

The molecular study of plant H^+-ATPase has shown that this enzyme is encoded by a multigene family. The genes have been identified in: *Arabidopsis thaliana* 12 genes (Palmgren, 2001), *Lycopersicon esculentum* 10-12 genes (Kalampanayil & Wimmers, 2001), *Oryza sativa* 10 genes (Baxter et al., 2003), *Cucumis sativus* 10 genes (Wdowikowska, data unpublished), *Nicotiana plumbaginifolia* 9 genes (Oufattole et al., 2000), *Vicia faba* 5 genes (Nakajima et al., 1995), and *Zea mays* 4 genes (Santi et al., 2003). Phylogenetic and gene structure analysis of plant H^+-ATPases divided them into five subfamilies (Arango et al., 2003). Expression of H^+-ATPase subfamilies I and II is not restricted to particular organs. These subfamilies are highly expressed in many cell types. In *A. thaliana* two genes, *AHA1* and *AHA2*, are expressed in all tissues and organs. *AHA1* is predominantly expressed in shoots, *AHA2* in roots. In *N. plumbaginifolia*, *pma4* was highly expressed in several cell types, including meristematic tissues, root epidermis, hairs, phloem, and guard cells (Moriau et al., 1999). In maize, *MHA2* was expressed in the same set of cells as *PMA4* (Frias et al., 1996). Conversely, expression of genes belonging to subfamilies III, IV, and V is limited to specific organs or cell types (Arango et al., 2003). In *A. thaliana*, *AHA6* and *AHA9* transcripts are present

mainly in anthers, *AHA10* in the endothelium of the developing seed coat, and *AHA7* and *AHA8* in pollen (Gaxiola et al., 2007). It has been shown that various genes are expressed in the same organ. Moreover, even within the same cell type at the same developmental stage, at least two H^+-ATPase genes are expressed (Harms et al., 1994; Hentzen et al., 1996; Moriau et al., 1999). In *N. plumbaginifolia* two different plasma membrane H^+-ATPase genes, *PMA2* and *PMA4*, are expressed in guard cells (Moriau et al., 1999). This observation suggests that isoforms with distinct kinetics might co-exist in the same cell.

In addition to tissue-specific expression, the plasma membrane H^+-ATPases are differentially expressed according to environmental factors. Several studies have indicated that the H^+-ATPase genes might be activated by various abiotic and biotic stresses. With such a phenomenon the amount of H^+-ATPase might be increased under conditions requiring greater transport activity. The external signals result in changes in plant plasma membrane H^+-ATPase gene expression, include salt (Niu et al., 1993; Binzel, 1995; Janicka-Russak & Kłobus, 2007), low temperature (Ahn et al., 1999, 2000), heavy metals (Janicka-Russak et al., 2008), dehydration (Surowy et al., 1991), light conditions (Harms et al., 1994), mechanical stress (Oufattole et al., 2000) and externally applied hormones (Frías et al., 1996).

4. Post-translational regulation of plant plasma membrane H^+-ATPase

Plant plasma membrane H^+-ATPase is involved in many different physiological roles and what is more its activity is changed by a large number of physiological factors. Therefore, it can be assumed that there are multiple regulatory features that integrate signals from the environment. As to post-translational regulation, the best known mechanism described to date involves the autoinhibitory action of the C-terminal domain (approximately 100 amino acids) of the enzyme protein. Deletion of the carboxyl terminus by trypsin treatment or genetic engineering results in constitutively activated enzyme. Although it is clear that the carboxyl terminus is the main regulatory domain involved in activation of the H^+-ATPase, recent results suggest that the N-terminus may also play a role in modification of plasma membrane proton pump activity.

4.1 Regulation by phosphorylation

Phosphorylation and dephosphorylation of proteins is a very common example of post-translational modification that has the potential to alter protein activity. The activity of the enzyme is well known to be regulated by 14-3-3 proteins, the association of which requires phosphorylation of the penultimate H^+-ATPase residues of Thr 947 (Svennelid et al., 1999). The binding of 14-3-3 regulatory protein displaces the inhibitory R-domain, activating the enzyme. R-domains contains two regions (I and II), of about 20 residues each, which contribute to keeping the enzyme at a low activity level. Mutagenesis of these regions abolishes the inhibitory effect of the C-terminus (Morssome et al., 1998; Axelsen et al., 1999;). 14-3-3 binding to H^+-ATPase is stabilized by the fungal toxin fusicoccin, which decreases the dissociation rate. One 14-3-3 protein dimer binds two C-terminal polypeptides simultaneously, so a high activity state of H^+-ATPase could involve formation of dimers or multimeric complexes. An analysis with cryo-electron microscopy showed that PMA2-14-3-3 complex is a wheel-like structure with 6-fold symmetry, suggesting that the activated complex consists of six H^+-ATPase molecules and six 14-3-3 molecules (Kanczewska et al., 2005).

Activation of plasma membrane H^+-ATPase involves protein kinase mediated phosphorylation of penultimate Thr in the C-terminus (region II) of the enzyme protein. Which specific kinases catalyse the reaction is an unresolved question. The protein kinase responsible for this phosphorylation has not yet been identified. Recently, it was reported that calcium-dependent protein kinase (CDPK) stimulated by abscisic acid leads to phosphorylation-dependent activation of H^+-ATPase (Yu et al., 2006). In rice, a 55 kDa calcium-dependent protein kinase was shown to phosphorylate two Thr residues from the autoregulatory domain (region I) of the plasma membrane proton pump (Ookura et al., 2005).

Many reports indicate that the phosphorylation of amino acid residues at the C-terminus of the protein leads not only to raised enzyme activity but also to its inhibition (Vera- Estrella et al., 1994; Xing et al., 1996; Lino et al., 1998; Schaller & Oecking, 1999). A number of conserved serine and threonine residues found in the C-terminal regulatory domain serve as candidate residues for negative phosphorylation (Nühse et al., 2003). Some phospho-residues are close to each other and might influence the phosphorylation status of their neighbours (Duby & Boutry, 2009). In *Nicotiana tabacum* two new phosphorylation sites, Thr931 and Ser938, in the C-terminus of H^+-ATPase, were identified. Their mutation suggests that phosphorylation of Thr931 or Ser938 prevents 14-3-3 protein binding, although the penultimate Thr955 was still phosphorylated, and prevented full activation of the enzyme (Duby et al., 2009). PKS5, a Ser/Thr protein kinase, is a negative regulator of the plasma membrane proton pump. In *A. thaliana* this kinase phosphorylates the enzyme (AHA2) at Ser931 in the C-terminus. Phosphorylation at this site inhibits interaction between H^+-ATPase and 14-3-3 protein (Fuglsang et al., 2007). PKS5 is a salt overly sensitive (SOS) 2–like protein and interacts with the calcium-binding protein ScaBP1 (Fuglsang et al., 2007). During salt stress in *A. thaliana*, the calcium sensor Salt Overly Sensitive 3 (SOS3) binds to and activates the Ser/Thr protein kinase SOS2. The Ca^{2+}-SOS3-SOS2 complex phosphorylates and activates the Na^+/H^+ antiporter SOS1, resulting in regulation of Na^+ homeostasis and salt tolerance (Zhu, 2002). In *Arabidopsis*, a chaperone, J3 (DnaJ homolog 3, heat shock protein 40-like) activates plasma membrane H^+-ATPase activity by physically interacting with PKS5 kinase (Yang et al., 2010).

Two extensively expressed plasma membrane H^+-ATPase isoforms of *Nicotiana tabacum* (PMA2 and PMA4) are differentially regulated by phosphorylation of their penultimate threonine. Cold stress reduced the Thr phosphorylation of PMA2, whereas no significant changes in Thr phosphorylation of PMA4 were observed (Bobik et al., 2010a).

A phosphorylation event requires action of a protein phosphatases to make regulation reversible. Phosphatase 2A (PP2A) competes with binding of 14-3-3 protein to the C-terminus of H^+-ATPase (Fuglsang et al., 2006). Inhibition of phosphatase activity by administration of okadaic acid (inhibitor of phosphatase PP2A) to plants (maize roots) increased the bound level of 14-3-3 proteins and activity of H^+-ATPase (Camoni et al., 2000).

A novel interactor of the plant plasma membrane proton pump was identified. This protein is named PPI1 (proton pump interactor, isoform 1). This interactor is able to modulate the plasma membrane H^+-ATPase activity by binding to a site different from the 14-3-3 binding site (Morandini et al., 2002). PPI1 can only hyper-activate H^+-ATPase molecules whose C-terminus has been displaced by other factor such as 14-3-3 protein (Viotti et al., 2005).

Recent studies have shown that the N-terminus of the plant plasma membrane H^+-ATPase directly participates in pump regulation (Morsomme et al., 1998; Ekberg et al., 2010). It was

suggested that transformation from low to high activity state of enzyme protein involves a structural rearrangement of both the C- and the N-terminus.

4.2 Regulation by membrane environment

The plant plasma membrane H^+-ATPase requires lipids for activity. This lipid dependency suggests a possible mode of regulation of the plasma membrane proton pump via modification of its lipid environment (Kasamo, 2003). Abiotic stresses lead to changes in the plasma membrane lipid composition altering the fluidity of the membrane. The modulation of the phospholipid environment of the plasma membrane regulates the activity of H^+-ATPase. This enzyme protein activity was abolished upon the removal of membrane lipids by detergents, but it was restored by exogenous addition of phospholipids (Kasamo & Nouchi, 1987, Kasamo 1990). The activation of H^+-ATPase is dependent on the degree of saturation or unsaturation of the fatty acyl chain and its length. The activity decreased with an increase in the length of the fatty acyl chain and in the degree of unsaturation of fatty acid (Hernandez et al., 2002; Kasamo, 2003, Martz et al., 2006).

Lysophosphatidylcholine (a natural detergent produced from phosphatidylcholine by phospholipase A_2) increased the plasma membrane H^+-ATPase activity (Pedechenko et al., 1990, Regenberg et al., 1995). It was found that lysophosphatidylcholine binds to the C-terminal region of the protein and by displacing the autoinhibitory domain leads to increase of ATPase activity.

5. Physiological roles

All living plant cells are thought to express a plasma membrane H^+-ATPase. However, it has been found that the abundance of this protein varies in different cell types and tissues. The main role of roots is uptake of nutrients from soil and translocation of those nutrients to the shoots of plants. In roots high amounts of immunodetectable H^+-ATPase antibodies were observed in epidermal cells, endodermis and phloem (Parets-Soler et al., 1990; Jahn et al., 1998). Because the plasma membrane H^+-ATPase is responsible for establishing the proton gradient involved in the membrane energization used for solute transport, this enzyme controls the major transport processes in the plant: root nutrient uptake, xylem and phloem loading.

In addition to its fundamental role in nutrient uptake, H^+-ATPase plays a major role in cell growth. The so-called "acid growth" theory suggests that protons extruded by an activated H^+-ATPase decrease the apoplastic pH and activate enzymes involved in cell wall loosening (Hager, 2003). It is well established that auxin activates the proton pump, resulting in loosening of the cell wall (Hager, 2003). In plants, an auxin increases membrane flow from the endoplasmic reticulum to the plasma membrane. Therefore it was assumed that this membrane flow could carry newly synthesized H^+-ATPase molecules to the PM. It was reported that IAA increased the amount of antibody-detectable H^+-ATPases in the PM (Hager et al., 1991). Besides, treatment of maize coleoptile segments with auxin resulted in increase of mRNA levels of plasma membrane H^+-ATPase, *MHA2* (Frias, et al., 1996). Recent evidence has shown that the PM H^+-ATPase appears to be a target of NO-mediated auxin action (Kolbert et al., 2008; Zandonadi et al., 2010).

This pump is also involved in intracellular pH regulation. Acidification of the cytosol activates the plasma membrane proton pump and enhances the extrusion of protons from

the cytosol to the apoplast. This contributes to alkalinization of the cytosol (Sanders et al., 1981). In *Nicotiana tabacum* acidification of the cytosol increased PMA2 phosphorylation at the penultimate Thr in the C-terminus (Bobik et al., 2010b).

Moreover, the plasma membrane proton pump is involved in other important physiological functions, such as stomatal aperture. Cell turgor changes promote modification of the stomatal aperture. Activation of H^+-ATPase leads to plasma membrane hyperpolarization and subsequent opening of K^+ channels. K^+ and anion influx lead to water uptake, turgor increase, and cell swelling. On the other hand, an elevation of cytosolic Ca^{2+}, inhibition of plasma membrane H^+-ATPase, an increase in pH, a reduction in K^+, Cl^-, and organic solute contents in both guard cells surrounding the stomatal pore, are downstream elements of ABA-induced stomatal closure (Zhang et al., 2001). The plant hormone abscisic acid (ABA) is a key signal molecule, mediating responses to various environmental stresses, and has been demonstrated to induce stomatal closure, thereby preventing water loss (Assmann & Shimazaki, 1999). The opening of stomata is mediated by an accumulation of K^+ in guard cells, and K+ accumulation is driven by an inside-negative electrical potential across the plasma membrane. The electrical potential is created by the plasma membrane H^+-ATPase in response to blue light (Schroeder et al., 2001). Blue light activates the H^+-ATPase through the phosphorylation of Thr residues in the C-terminus. Next, phosphorylation induces the binding of 14-3-3 to the penultimate residue of Thr, which acts as a positive regulator for the H^+-ATPase (Kinoshita & Shimazaki, 2002). Blue light receptors that mediate activation of the plasma membrane proton pump in stomatal guard cells are phototropins (Kinoshita et al., 2001). Phototropins are autophosphorylating Ser/Thr protein kinases (Brigg & Christie, 2002). The activated phototropins transmit the signal to plasma membrane H^+-ATPase for its activation (Christie, 2007). In addition, it was demonstrated that phosphatase 1 (PP1, Ser/Thr protein phosphatase) mediates the signal between phototropins and H^+-ATPase in guard cells (Takemiya et al., 2006). It is known that ABA inhibits blue light dependent proton pumping by plasma membrane H^+-ATPase (Zhang et al., 2004). Biochemical and genetic studies have demonstrated that H_2O_2 mediates inhibition of the plasma membrane proton pump by ABA (Zhang et al., 2001). In guard cells, ABA induces production of phosphatidic acid (PA). Because PA also interacts with PP1 and decreases its phosphatase activity, it seems that PA suppresses the blue light signalling of guard cells (Takemiya & Shimazaki, 2010). Studies have demonstrated that ABA induces NO synthesis through H_2O_2 (Bright et al., 2006) and that NO causes PA production in guard cells (Distéfano et al., 2008).

6. H^+-ATPase in abiotic stress

The plant plasma membrane H^+-ATPase is an important functional protein, which plays a central role in plant physiology. PM H^+-ATPase couples ATP hydrolysis to proton transport out of the cell, and so establishes an electrochemical gradient across the plasma membrane, which is dissipated by secondary transporters using protons in symport or antiport. This enzyme controls the major transport processes in the plant, such as root nutrient uptake and xylem or phloem loading. Moreover, this pump has been proposed to be involved in other important physiological functions, such as stomata aperture, cell elongation, or cellular pH regulation. Generation of an electrochemical gradient across the membrane results in a proton-motive force that is used by secondary transport for assimilation of various nutrients, and also for releasing ions and toxic substances from cells. The plasma membrane proton pump is an enzyme whose activity is altered significantly in response to a number of

factors, such as light, temperature, hormones and presence of salt or heavy metals in the environment. Besides regulation of growth and development processes, the plasma membrane proton pump also plays a role in plastic adaptation of plants to changing conditions, especially conditions of stress. Adaptation is a complex process. Some of the modifications in plants subjected to abiotic stress are indicated to be adaptive. Physiological modifications caused by environmental stress and allowing continued plant functions are ascribed by plant physiologists as being adaptive.

6.1 Salt stress

Salt stress is a complex abiotic stress in which both ionic and osmotic components are involved (Alvarez et al., 2003). Under conditions of elevated NaCl levels outside the cell, sodium passively enters into the roots through non-selective cation channels and the low-affinity sodium transporter HKT1. Salinity tolerance of plants is a complex trait involving adaptation at the level of cells, organs and the whole plant. The key factor of salinity tolerance, beside osmotic adjustment, is the control of intracellular ion homeostasis (Niu et al., 1993). The excess of Cl^- is passively effluxed across the membrane down the $\Delta\mu H^+$ generated by plasma membrane H^+-ATPase. To prevent accumulation of toxic Na^+ amounts in the cytosol, active sodium efflux into the apoplast and its compartmentalization inside the vacuole occur. Since Na^+ pumps responsible for sodium extrusion in animals and microorganisms are absent in higher plant cells, secondary sodium/proton antiporters in both the plasma membrane and the tonoplast are needed to translocate sodium ions against their electrochemical gradients (Apse and Blumwald 2007). Molecular analyses in *Arabidopsis* led to the identification of a plasma membrane SOS1 (Salt Overly Sensitive 1) and vacuolar NHX1, Na^+/H^+ antiporters upregulated at the genetic level in response to NaCl (Apse et al. 1999; Gaxiola et al. 1999; Shi et al. 2000, 2003). These proton-coupled sodium transporters use the proton-motive force created by the specific proton pumps. The only pump which generates an electrochemical proton gradient across the plasma membrane is H^+-ATPase (Palmgren, 2001). For this reason, it is believed that plant plasma membrane H^+-ATPase plays a major role in salt stress tolerance. The importance of plant plasma membrane H^+-ATPase in salt tolerance is demonstrated by observations such as increase in its activity in halophytes (Braun et al., 1986; Niu et al., 1993; Vera-Estrella et al., 1994, Sahu & Shaw, 2009). In halophytes and salt-tolerant cultivars significantly greater activity of the enzyme is observed in normal conditions, without NaCl (Sahu & Shaw, 2009). Moreover, it has been well documented that salt treatment of plants induces the activities of the plasma membrane proton pumps both in halophytes and glycophytes (Niu et al., 1993; Perez-Prat et al., 1994; Binzel, 1995; Kłobus and Janicka-Russak, 2004, Sahu & Shaw, 2009; Lopez-Perez et al., 2009; Shen et al., 2011). However, there are few reports about the inhibition or no effect of NaCl on the plasma membrane H^+-ATPase in leaves (Chelysheva et al., 2001; Zörb et al., 2005; Pitann et al., 2009; Wakeel et al., 2010). The authors observed an increase of apoplastic pH in salt stress conditions. The salinity would thus limit leaf elongation.

The aforementioned salt-dependent activation of the plasma membrane proton pump encompasses the transcriptional as well as post-translational level. Accumulation of mRNAs of PM H^+-ATPase under NaCl stress and the positive correlation with salt tolerance are well documented (Niu et al., 1993; Perez-Prat et al., 1994; Janicka-Russak & Kłobus 2007; Sahu and Shaw, 2009). In *Suaeda maritima* (a natural halophyte) and *Oryza sativa* salt-tolerant

cultivar accumulation of PM H^+-ATPase gene transcript was greater than that in a non-tolerant cultivar of rice treated with NaCl (Sahu & Shaw, 2009). As mentioned earlier (subsection 11.3), plant plasma membrane ATPase is encoded by a large gene family. The existence of multiple isoforms of the enzyme creates the opportunity of their role in abiotic stress tolerance, particularly salt stress tolerance. In rice a new isoform of the enzyme (finding maximum homology with *OSA7*) in response to salt treatment was discovered. In the halophyte *Suaeda maritime* the related gene (*SM2*, which has 89% homology with the new isoform from rice) does not require the presence of salt for its expression. So the salt-inducible isoform of the plasma membrane H+-ATPase gene in rice remains constitutively expressed in the halophyte *S. maritime* (Sahu & Shaw, 2009). The isoform of PM H^+-ATPase from tomato *LHA8* is most closely related to *Nicotiana plumbaginifolia* gene *PMA6*. Both of these isoforms are specially induced by stress: *LHA8* by salt stress, *PMA6* by mechanical stress (Oufattole et al., 2000; Kalampanayil & Wimmers, 2001).

A direct role of H^+-ATPase in salt tolerance was confirmed by studies with transgenic tobacco, using a PMA4 mutant, lacking the autoinhibitory domain (ΔPMA4). In the mutant a constitutively activated PMA4 H^+-ATPase isoform was present. The ΔPMA4 plant roots showed better growth in saline conditions than those of untransformed plants (Gévaudant et al., 2007).

In rice phospholipase Dα (PLDα) is involved in salt tolerance by the mediation of H^+-ATPase activity and transcription (Shen et al., 2011). When rice suspension-cultured cells were treated with 100 mM NaCl, PLDα activity increased. The knockdown of OsPLDα1 prevented NaCl-induced increase in transcript levels of OSA2 (which encodes PM H^+-ATPase) as well as ATPase activity.

Recently evidence has been presented that NaCl also causes a rapid modulation of proton pumps, which is due to the reversible phosphorylation of enzyme proteins (Kerkeb et al., 2002; Kłobus and Janicka-Russak, 2004). In many plant tissues a salt-inducible shift in the cytoplasmic calcium level was observed (Heterington and Quatrano, 1991; Rock and Quatrano, 1995; Danielsson et al., 1996; Knight et al., 1997; Blumwald et al., 2000; Netting, 2000; Xiong et al., 2002), suggesting its involvement in the signalling pathway target under NaCl stress conditions. An SOS (salt overly sensitive) network exists in plants exposed to salt stress. SOS1, antiporter Na^+/H^+, enables Na^+ efflux across the plasma membrane and controls long-distance Na^+ transport between roots and leaves through loading and unloading of Na^+ in the xylem (Shi et al. 2002). Sodium efflux through SOS1 is mediated by SOS3-SOS2 complex (Qiu et al. 2002). Perception of salt stress induces a cytosolic calcium signal activating the calcium sensor, myristoylated protein SOS3. After binding with Ca^{2+}, SOS3 changes its conformation and interacts with the FISL motif of SOS2, a Ser/Thr protein kinase, and activates its substrate phosphorylation. The activated SOS3-SOS2 complex then phosphorylates SOS1 and activates its antiporter activity (Chinnusamy et al. 2005).

Evidence has also been presented that in the plasma membrane ATPase phosphorylation, as a target of activation by NaCl, a calcium/calmodulin-dependent protein kinase sensitive to staurosporine, is involved (Kłobus and Janicka-Russak, 2004).

Transient increases in cytosolic Ca^{2+} can induce the phosphorylation of different proteins in cells, improving the salt tolerance (Hasegawa et al. 2000). Evidence suggests that the major role in coupling the calcium signal to specific protein phosphorylation cascade(s) is played by the Ca^{2+}/calmodulin-dependent protein kinases (CDPKs) and the SOS3 family of Ca^{2+} sensors (Xiong et al. 2002, Zhu 2002). The results of Urao et al. (1994) and Saijo et al. (2000)

demonstrated that NaCl rapidly induced CDPK in different plant tissues. Furthermore, evidence has been presented that Ca^{2+}/calmodulin-dependent protein kinases are responsible for the phosphorylation of the plasma membrane H^+-ATPase protein (Van der Hoeven et al. 1996, Camoni et al., 2000).

Ca^{2+} has been identified as a possible mediator of ABA-induced stimulus-response coupling (Netting, 2000). Abscisic acid is known as a stress hormone, which mediates responses to a variety of stresses, including water and salt stress (Skriver and Mundy, 1990; Tan et al., 1994; Jia et al., 2001). The endogenous level of ABA increases when plants are stressed with drought or NaCl, and application of ABA to unstressed plants results in the induction of numerous water-deficit-related activities (La Rosa et al., 1985; 1987; Skriver and Mundy, 1990; Kefu et al., 1991; Cowan et al., 1997; Barkla, 1999). They include triggering of stomatal closure to reduce transpirational water loss by post-translational modulation of ion channels in guard cells (Grabov and Blatt, 1998), and alterations in gene expression through induction of ABA-responsive genes coding for structural, metabolic or transport proteins (Ingram and Bartels, 1996; Shinozaki and Yamaguchi-Shinozaki, 1996; Barkla et al., 1999).

It was reported that ABA treatment of cucumber plants, as well as NaCl treatment, increased activity of plasma membrane H^+-ATPases. ABA treatment of seedlings elevated the level of plasma membrane H^+-ATPase transcript (Janicka-Russak & Kłobus, 2007). Thus activation of this proton pump by salt and abscisic acid seems to involve the genetic level.

Nitric oxide (NO) and hydrogen peroxide (H_2O_2) function as signal molecules in plants subjected to abiotic stresses. In plants, the generation of H_2O_2 seems to be mediated by a plasma membrane bound NADPH oxidase complex (Yang et al., 2007; Lherminier et al., 2009). NO is synthesized via nitric oxide synthase (NOS) and nitrate reductase (Yamasaki & Sakihama, 2000). NO and H_2O_2 interact as signalling molecules in plants (Zhang et al., 2007). Under salt stress, both NO and H_2O_2 are produced. Treatment of plants with NO increased the activity of plasma membrane NADPH oxidase and thus the generation of hydrogen peroxide. Both these molecules stimulated the activity, as well as the expression of plasma membrane H^+-ATPase in *Populus euphratica* (Zhang et al., 2007). However, the increase of proton pump activity is induced by NO possibly via the regulation of PM NADPH oxidase. Additionally, activity of PM H^+-ATPase may depend on the membrane redox state. Plasma membrane oxidoreductase can modify activity of the PM H^+-ATPase proton pump (Kłobus and Buczek 1995). PM oxidoreductase, by transporting electrons across the PM, simultaneously acidifies the cytoplasm (Lüthje et al. 1997). Low pH of the cytoplasm and membrane depolarization stimulate the activity of PM H^+-ATPase (Hager and Moser 1985; Rubinstein and Stern 1986; Kłobus 1995).

Plants can increase salinity tolerance by modifying the biosynthesis of polyamines. In cucumber the level of polyamines decreased when the concentration of Na^+ in the cytosol increased, so the action of polyamines contributes to ionic equilibrium (Janicka-Russak et al., 2010). Moreover, it was found that polyamines decreased activity of the plasma membrane proton pump in cucumber. So a decrease in their biosynthesis under salinity seems to be beneficial in stress tolerance.

Fatty acids, as the main component of membrane lipids, are considered to be important in salt tolerance of plants. Salt-tolerant plants showed an increase of unsaturated fatty acids (Lin & Wu, 1996). In broccoli plants a high degree of unsaturation in the plasma membrane of roots was observed (López-Pérez et al., 2009). The activity of plant plasma membrane H^+-ATPase increased with an increase in the degree of unsaturation of fatty acid (Kasamo, 2003,

Martz et al., 2006). Non-tolerant plants subjected to salt stress commonly show decreased levels of 18:3 in their membranes (Upchurch, 2008). A study with transgenic tobacco showed that overexpression of ω-3 desaturases, which increases 18:3, elevated tolerance to salt stress (Zhang et al., 2005).

In potato the mRNA level of *StPPI1*, a homologue of the *A. thaliana* PPI1 (proton pump interactor isoform 1), increased under salt and cold stress conditions. StPP1 increases PM H^+-ATPase activity by hyperactivation of H^+-ATPase whose C-terminus has been displaced earlier by 14-3-3 protein (García et al., 2011).

6.2 Heavy metals

An increase in permeability related to membrane damage is observed in plants that have been subjected to heavy metal stress. It is well known that metal ions are easily bound to both the sulfhydryl groups of proteins and hydroxyl groups of phospholipids (Devi and Prasad, 1999). They can also replace the calcium ions at essential sites of cell membranes (Breckle and Kahle, 1991). All these events result in disruption of membrane integrity and ionic homeostasis of cells. Maintaining ionic balance and replenishing the loss of essential substances in repair processes is an important issue under such conditions. Support of active transport of ions and organic compounds through the plasma membrane requires increased generation of a proton gradient by PM H^+-ATPase. Generation of an electrochemical gradient across the membrane results in a proton-motive force that is used by passive transport for assimilation of various nutrients, as well as for releasing ions and toxic substances from cells.

To date, data concerning the action of heavy metals on plasma membrane H^+-ATPase are limited. A few observations have indicated that enzyme activity was changed under heavy metal (Cd, Cu, Ni, Al) stresses (Lindberg & Wingstrand, 1985; Kennedy and Gonsalves, 1989; Ros et al., 1992 a,b; Fodor et al., 1995; Demidchik et al., 1997; Astolfi et al., 2003; Burzyński & Kolano, 2003; Astolfi et al., 2005; Shen et al., 2005; Janicka-Russak et al., 2008; Kabała et al., 2008). The effect of metals on plasma membrane H^+-ATPase activity depends on time of exposure of plants to heavy metals, kind and concentration of heavy metal or plant species. In cucumber seedling roots, brief treatment of plants with Cd and Cu leads to inhibition of plasma membrane H^+-ATPase activity (Janicka-Russak et al., 2008, Kabała et al., 2008). The inhibition of the enzyme was partially diminished in the presence of cantharidin, a specific inhibitor of PP2A and PP1 phosphatases. Moreover, Western blot analysis with an antibody against phosphothreonine confirmed that decreased activity of plasma membrane H^+-ATPase in a short time (2 hours, 10 and 100 μM Cd or Cu) resulted from dephosphorylation of the enzyme protein (Janicka-Russak et al., 2008). However, longer time of treatment of cucumber roots with those heavy metals (6 days, 10 μM Cd or Cu) leads to increased activity of the enzyme measured both as hydrolysis of ATP and proton transport across the plasma membrane (Janicka-Russak, data unpublished). The same effect was observed in cucumber plants treated for 18 hours with 100 μM Cd and in maize with 100 μM both Cd and Cu (Burzyński & Kolano, 2003). In rice treated for 5 or 10 days with 100 and 500 μM Cd increased proton pump activity was observed (Ros et al., 1992a). On the other hand, in oat roots treated long term (7 and 21 days) with 100 μM Cd plasma membrane proton pump activity was inhibited (Astolfi et al., 2003). The same effect was observed in maize subjected for 4 days to cadmium (Astolfi et al., 2005). When plants were treated for 5 or 10 days with nickel, stimulation of H^+-ATPase in rice shoots' plasma

membrane was observed both in 100 and 500 μM concentration. But in rice roots only 100 μM concentrations of Ni lead to stimulation of the enzyme protein (Ros et al., 1992a). The increase of ATPase activity in conditions of Ni and Cd metal stress was observed simultaneously with decrease in the degree of unsaturation and length of the phospholipid fatty acyl chain (Ros et al., 1992b). In contrast, Hernandez & Cook (1997) observed an increased degree of unsaturation of phospholipid-associated fatty acid in pea root plasma membrane as a result of 10-day cadmium treatment of plants. A similar effect was observed in the case of Cu in tomato membrane lipids as a result of 7 days' stress (Ouariti et al., 1997). It is known that PM H^+-ATPase is stimulated when the degree of unsaturation of fatty acids is increased (Hernandez et al., 2002). In soybean root, under aluminium stress, up-regulation of transcript, translation and threonine-oriented phosphorylation of plasma membrane H^+-ATPase was observed (Shen et al., 2005).

6.3 Low temperature

An increase in membrane permeability and a change in its viscosity and fluidity result in a decrease of cell turgor due to low temperature (Guy 1990). Membrane changes at low temperature concern positional redistribution of saturated and unsaturated fatty acids (Hughes and Dunn 1996). Probably the change in membrane fluidity in cold-sensitive species initiates a signal chain reaction that leads to acclimation to cold stress by increasing the expression of certain genes, for example genes encoding desaturases (Xiong and Zhu 2001; Chinnusamy et al. 2006). An increase in permeability related to membrane damage is observed in plants that have been subjected to low temperature. Maintaining ionic balance and replenishing the loss of essential substances in repair processes is an important issue under such conditions. Support of active transport of ions and organic compounds through the PM requires increased generation of a proton gradient by PM H^+-ATPase. Generation of an electrochemical gradient across the membrane results in a proton-motive force that is used by active transport for assimilation of various nutrients. Published data indicate that activity of PM H^+-ATPase is modulated under low temperature by changes in lipids associated with the PM proton pump (Lindberg et al. 2005; Martz et al. 2006). Plants capable of cold acclimation accumulate polyunsaturates during cold stress (Vega et al., 2004; Upchurch et al., 2008). In *Pinus resinosa* the activity of plasma membrane H^+-ATPase increased more than twofold following cold acclimation (Martz et al., 2006). In winter hardy tree species seasonal changes in PM H+-ATPase activity and fatty acid composition occur during cold acclimation and de-acclimation under natural conditions. Fatty acid-regulated plasma membrane proton pump activity is involved in the cellular response underlying cold acclimation and de-acclimation (Martz et al., 2006). Similarly, in rye roots H^+-ATPase activity increases during acclimation to low temperature, following increases in fatty acid unsaturation, particularly linoleic acid (White et al., 1990). An increase in plasma membrane H+-ATPase at low temperature (5 ^oC) was also observed in cells of winter wheat seedlings which were hardened earlier. In non-hardened tissues such an increase of enzyme activity was not observed (Ling-Cheng et al., 1982). In *Oryza sativa* plasma membrane H^+-ATPase activity increased at low temperature in chilling-insensitive plants whereas in chilling-sensitive plants a slight decrease in enzyme activity was observed (Kasamo, 1988). The length of plants' exposure to the low temperature affects activity of the PM proton pump in various ways. Brief (1 or 3 days) exposure of cucumber seedlings to low temperature inhibits hydrolytic and transport activity of H^+-ATPase (Lee et al., 2004, Janicka-Russak,

data unpublished). However, stimulation of activity was observed after treating plants with a low temperature (10 ^{o}C) for 6 days (Janicka-Russak, data unpublished). On the other hand, Ahn and coworkers (2000), despite using the same plant species, cucumber, observed different results. The increase in H^+-ATPase activity after 1 day of low temperature treatment was reversed and gradually diminished as root temperatures of 10 ^{o}C continued for the next 6 days.

It was shown that regulation of the plasma membrane proton pump may be based on the interaction of H^+-ATPase and 14-3-3 protein. Rapid cooling of protoplasts derived from sugar beet cells results in activation of the proton pump. Moreover, cytoplasmic 14-3-3 protein associated with plasma membrane and thus the amount of ATPase-14-3-3 complexes increased (Chelsyheva et al., 1999).

The activity changes of PM H^+-ATPase may partly result from changes in the pattern of expression of PM H^+-ATPase genes (Ahn et al., 1999, 2000; Janicka-Russak, data unpublished).

7. Conclusion

According to the above information, we can conclude that plant plasma membrane H^+-ATPase is an important functional protein, which plays a central role in plant physiology in normal growth conditions and under abiotic stresses. In plants exposed to different abiotic stresses an increase in permeability related to membrane damage is observed. Maintaining ionic balance and replenishing the loss of essential substances in repair processes is an important issue under such conditions. Support of active transport of ions and organic compounds through the plasma membrane requires increased generation of a proton gradient by PM H^+-ATPase. In addition, stress conditions such as salinity or heavy metals leads to accumulation of a toxic excess of certain ions. Generation of an electrochemical gradient across the membrane results in a proton-motive force that is used by active transport for assimilation of various nutrients, as well as for releasing ions and toxic substances from cells. Thus, plasma membrane H^+-ATPase can be a mutual element for resistance mechanisms that are activated in various stress conditions.

8. References

Ahn, S.; Im, Y.; Chung, G. & Cho, B. (1999). Inducible expression of plasma membrane H^+-ATPase in the roots of figleaf gourd plants under chilling root temperature. *Physiologia Plantarum*, Vol.106, pp.35-40

Ahn, S.; Im, Y.; Chung, G.; Seong, K. & Cho, B. (2000). Sensitivity of plasma membrane H^+-ATPase of cucumber root system in response to low root temperature. *Plant Cell Reports*, Vol.19, pp. 831-835

Alvarez, I.; Tomaro, M. & Benavides M. (2003). Changes in polyamines, proline and ethylene in sunflower calluses treated with NaCl. I. *Plant Cell Tissue Organ Cult,* Vol.74, No.1, pp. 51-59

Apse, M.; Aharon, G.; Snedden, W. & Blumwald, E. (1999). Overexpression of a vacuolar Na^+/H^+ antiport confers salt tolerance in *Arabidopsis*. *Science*, Vol.285, pp. 1256-1258

Apse, M. & Blumwald, E. (2007). Na^+ transport in plants. FEBS Letters, Vol.581, pp. 2247-2254

Arango, M. ; Gevaudant, F. ; Oufattole, M. & Boutry, M.(2003). The plasma membrane proton pump ATPase : the significance of gene subfamilies. *Planta*, Vol.216, pp. 355-365

Assmann, S. & Schimazaki, K. (1999). The multisensory guard cell : stomatal responses to blue light and abscisic acid. *Plant Physiology*, 119, pp. 809-815

Astolfi, S. ; Zuchi, S. ; Chiani, A. & Passera, C. (2003). *In vivo* and *in vitro* effects of cadmium on H+-ATPase activity of plasma membrane vesicles from oat (*Avena sativa* L.) roots. *Journal of Plant Physiology*, Vol.160, pp. 387-393

Astolfi, S. ; Zuchi, S. Passera, C. (2005). Effect of cadmium on H^+-ATPase activity of plasma memebrane vesicles isolated from roots of different S-supplied maize (*Zea mays* L.) plants. *Plant Science*, Vol.169, pp. 361-368

Axelsen, K. & Palmgren, M. (2001). Inventory of the superfamily of P-type ion pumps in Arabidopsis. *Plant Physiology*, vol. 126, (June 2001), pp. 696-706

Barkla, B.; Vera-Estrella, R.; Maldonado-Gama, M. & Pantoja, O. (1999). Abscisic acid induction of vacuolar H^+-ATPase activity in *Mesembryanthemum crystallinum* is developmentally regulated. Plant Physiology, Vol.120, pp. 811-819

Baxter, I.; Tchieu, J.; Sussman, M.; Boutry, M.; Palmgren, M.; Gribskov, M.; Harper, J. & Axelsen, K. (2003). Genomic comparison of P-type ATPase ion pumps in Arabidopsis and rice. *Plant Physiology*, Vol.132, pp. 618-828

Binzel, M. (1995). NaCl induced accumulation of tonoplast and plasma membrane H^+-ATPase message in tomato. *Physiol Plantarum*, Vol.94, pp.722-728

Bobik, K.; Duby, G.; Nizet, Y.; Vandermeeren, C.; Stiernet, P., Kanczewska, J. & Boutry, M. (2010a). Two wdely espressed plasma membrane H+-ATPase isoforms of *Nicotiana tabacum* are differentially regulated by phosphorylation of their penultimate threonine. *The Plant Journal*, Vol.62, pp. 291-301

Bobik, K.; Boutry, M. & Duby, G. (2010b). Activation of the plasma membrane H^+-ATPase by acid stress. *Plant Signaling & Behavior*, Vol.5, No.6, (June) pp. 681-683

Braun, Y.; Hassidini, N.; Lerner, H. & Reinhold, L. (1986). Studies on H^+ translocating ATPases in plants of varying resistance to salinity. *Plant Physiology,* Vol.81, pp. 1050-1056.

Briggs,, W. & Christie, J. (2002). Phototropins 1 and 2: versatile plant blue-light receptors. *Trends in Plant Science*, Vol. 7, pp. 204-2010

Bright, J.; Desikaan, R.; Hancock, J.; Weir, I. & Neill, S. (2006). ABA-induced NO generation and stomatal closure in Arabidopsis are dependent on H_2O_2 synthesis. *Plant Journal*, Vol.45, pp. 113-122

Buch-Pedersen, M. ; Rudashevskaya, E. ; Berner, T. ; Venema, K. & Palmgren, M. (2006). Potassium as an intrinsic uncoupler of the plasma membrane H^+-ATPase. *The Journal of Biological Chemistry*, Vol.281, No.50, (December 15), pp. 38285-38292

Buch-Pedersen, M. ; Pedersen, P. ; Veierskov, B. ; Nissen, P. & Palmgren, M. (2009). Protons how they are transported by proton pumps. *Pflugers Archiv. European Journal of Physiology*, Vol.457, pp. 573-579

Burzyński, M. & Kolano, E. (2003). *In vivo* and *in vitro* effects of copper and cadmium on the plasma membrane H^+-ATPase from cucumber (*Cucumis sativus* L.) and maize (*Zea mays* L.) roots. *Acta Physiologiae Plantarum*, Vol.25, pp. 39-45

Camoni, L. ; Iori, V. ; Marra, M. & Aducci, P. (2000). Phosphorylation-dependent interaction between plant plasma membrane H^+-ATPase and 14-3-3 proteins. *Journal of Biological Chemistry*, Vol. 275, pp. 9919-9923

Chelysheva, V.; Smolenskaya, I.; Trofimova, M.; Babakov, A. & Muromtsev, G. (1999). Role of the 14-3-3 proteins in the regulation of H^+-ATPase activity in the plasma membrane of suspension cultured sugar beet cells under cold stress. *FEBS Letters,* Vol.456, pp. 22-26

Chelysheva, V. ; Zorinyants, S. ; Smolenskaya, I. & Babakov, A. (2001). Regulation of H+ pumping By plants plasmalemma under osmotic stress : The role of 14-3-3 proteins. *Russian Journal of Plant Physiology*, Vol.48, pp. 271-180

Chinnusamy, V.; Jagendorf, A. & Zhu, J. (2005). Understanding and improving salt tolerance in plants. *Crop Science*, Vol. 45, pp.437-448

Chinnusamy, V.; Zhu, J. & Zhu, J. (2006). Gene regulation during cold acclimation in plants. *Physiologia Plantarum*, Vol.126, pp. 52-61

Christie, J. (2007). Phototropin blue-light receptors. *Annual Review of Plant Biology*, Vol.58, pp. 21-45

Cowan, A.; Richardson, G. & Maurel, J. (1997). Stress-induced abscisic acid transients and stimulus-response- coupling. *Physiologia Plantarum*, Vol.100, pp. 491-499

Danielsson, A.; Larsson, C.; Larsson, K.; Gustafsson, L. & Adler, L. (1996) A genetic analysis of the role of calcineurin and calmodulin in Ca^{2+} dependent improvement of NaCl tolerance of *Saccharomyces cerevisiae. Current Genetics*, Vol. 30, pp.476-484

Demidchik, V.; Sokolik, A. & Yurin, V. (1997). The effect of Cu^{2+}on ion transport systems of the plant cell plasmalemma. *Plant Physiology*, Vol.114, pp. 1313-1325

Devi, S. & Prasad, M. (1999). Membrane lipid alterations in heavy metal exposed plants. In: Prasad MNV, Hagemeyer J, eds. *Heavy metal stress in plants. From molecules to ecosystems.* Berlin: Springer, pp. 99-116

Diestéfano, A. ; Garcia-Mata, C. ; Lamattina, L. & Laxalt, A. (20080. Nitric oxide- induced phosphatidic acid accumulation : a role for phospholipases C and D in stomatal closure. *Plant Cell Environment*, Vol.31, pp. 187-194

Duby, G. & Boutry, M. (2009). The plant plasma membrane proton pump ATPase: a highly regulated P-type ATPase with multiple physiological roles. *Pflugers Archiv. European Journal of Physiology*, Vol.457, pp. 645-655

Duby, G. ; Poręba, W. ; Piotrowiak, D. ; Bobik, K. ; Gerua, R. ; Waelkens, E. Boutry, M. (2009). Activation of plant plasma mmebrane H_-ATPase by 14-3-3 proteins is negatively controlled by two phosphorylation sites within the H+-ATPase C-terminal region. *The Journal of Biological Chemistry*, Vol.284, No. 7,(February 13), pp. 4213-4221

Ekberg, K. ; Palmgren, M. ; Veierskov, B. & Buch-Pedersen, M (2010). A novel mechanism of P-type ATPase autoinhibition involving both termini of the protein. *The journal of Biological Chemistry*, Vol.285, No.10, (March 5) pp. 7344-7350

Fodor, E. ; Szabo-Nagy, A. & Erdei L. (1995). The effects of cadmium on the fluidity and H^+-ATPase activity of plasma membrane from sunflower and wheat roots. *Journal of Plant Physiology*, Vol.147, pp. 87-92

Frías, I.; Caldeira, M.; Pérez-Castiiieira, J.; Navarro-Aviiió, J.; Culiaiiez-Macia, F. ; Kuppinger, O.; Stransky, H. ; Pagés, M. ; Hager, A. & Serrano, R. (1996). A Major

isoform of the Maize Plasma embrane H+-ATPase: Characterization and induction by Auxin in Coleoptiles. *The Plant Cell*, Vol.8, pp. 1533-1544

Fugslang, A,; Tulinius, G.; Ciu, N. & Palmgren, M. (2006). Protein phosphatases 2A scaffolding subunit A interacts with plasma membrane H+-ATPase C-terminus in the same region as 14-3-3 protein. *Physiologia Plantarum*, Vol. 128, pp. 334-340

Fuglsang, A.; Guo, Y.; Cuin, T.; Qiu, Q.; Song, C.; Kristiansen, K.; Bych, K.; Schulz, A.; Shabala, S.; Schumaker, K.; Palmgren, M. & Zhu, M. (2007). *Arabidopsis* protein kinase PKS5 inhibits the plasma membrane H+-ATPase by preventing interaction with 14-3-3 protein. *The Plant Cell*, Vol.19, (May), pp. 17-17-1634

García, M.; País, S.; Téllez-Iñón, M. & Capiati, D. (2011). Characterization od StPPI1, a proton pump interactor from *Solanum tuberosum* L. that is up-regulated during tuber development and by abiotic stress. *Planta* , Vol.233, pp. 661-674

Gaxiola, R.; Rao, R.; Sherman, A.; Grisafi, P.; Alper, S. & Fink, G. (1999). The *Arabidopsis thaliana* proton transporters, AtNhx1 and Avp1, can function in cation detoxification in yeast. *PNAS*, Vol.96, pp. 1480-1485

Gaxiola, R.; Palmgren, M. & Schumacher, K. (2007). Plant proton pumps. *FEBS Letters*, Vol.581, pp. 2204-2214

Géwaudant, F.; Duby, G.; Stedingk, E. Zhao, R. (2007). Expression of a constitutively activated plasma membrane H+-ATPase alters plant development and increases salt tolerance. *Plant Physiology*, Vol.144, (August), pp. 1763-1776

Grabov, A. & Blatt, M. (1998). Co-ordination of signaling elements in guard cell ion channel control. *Journal of Experimental Botany*, Vol.49, pp. 351-360

Guy, C. (1990). Cold acclimation and freezing stress tolerance: role of protein metabolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.41, pp.187-223

Hager, A. (2003). Role of the plasma membrane H+-ATPase in auxin induced elongation growth: historical and new aspects. *Journal of Plant Research*, Vol.116, pp. 483-505

Hager, A. & Moser, I. (1985). Acetic acid esters and permeable weak acids induce active proton extrusion and extension growth of coleoptile segments by lowering the cytoplasmic pH. *Planta*, Vol.163, pp. 391-400

Hager, A.; Debus, G.; Edel, H.; Stransky, H. & Serrano, R. (1991). Auxin induced exocytosis and the rapid synthesis of a high-turnover pool of plasma membrane H+-ATPase. *Planta*, Vol. 185, pp. 527-537

Harms, K.; Wohner, R.; Schulz, B. & Frommer, W. (1994). Isolation and characterization of P-type H+-ATPase genes from potato. *Plant Molecular Biology*, Vol.26, pp. 978-988

Hasegawa, P.; Bressan, R.; Zhu, J. & Bohnert, H. (2000). Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol. 51, pp.463-499

Hentzen, A.; Smart, L.; Wimmers, L.; Fang, H.; Schroeder, J. & Bennett, A. (1996). Two plasma membrane H+-ATPase genes expressed in guard cells of *Vicia faba* are also expressed throughout the plant. *Plant and Cell Physiology*, Vol. 37, pp. 650-659

Hernandez, L. & Cook, D. (1997). Modification of the root plasma membrane lipid composition of cadmium treated *Pisum sativim. Journal of Experimental Botany*, Vol.48, pp. 1375-1381

Hernandez, A.; Cooke, D. & Clarkson, D. (2002). *In vivo* activation of plasma membrane H+-ATPase hydrolytic activity by complex lipid-bound unsaturated fatty acids in *Ustilago maydis. European Journal of Biochemistry*, Vol.269, pp. 1006-1011

Hetherington, A. & Quatrano, R. (1991). Mechanisms of action of abscisic acid at the cellular level. *New Phytologist*, Vol.119, pp. 9-32

Hughes, M. & Dunn, M. (1996). The molecular biology of plant acclimation to low temperature. *Journal of Experimental Botany*, Vol.47, pp. 291-305

Ingram, J. & Bartels, D. (1996). The molecular basis of dehydration tolerance in plants. *Annual Review of Plant Physiology and Molecular Biology*, Vol.47, pp. 377-403

Jahn, T.; Baluska, F.; Michalke, W.; Harper, J. & Volkmann, D. (1998). Plasma membrane H+-ATPase in the root apex: evidence for strong expression in xylem parenchyma and asymetric localization within cortical and epidermal cells.*Physiologia Plantarum*, Vol.104, pp. 311-316

Jang, Y.; Qin, Y.; Xie,, C.; Zhao, F.; Zhao, J.; Liu, D.; Chen, S.; Fuglsang, A.; Palmgren, M.; Schumaker, K.; Deng,X. & Guo, Y. (2010). The *Arabidopsis* chaperone J3 regulates the plasma membrane H^+-ATPase through interaction with the PKS5 kinase. *The Plant Cell*, Vol.22, pp.1313-1332

Janicka-Russak, M. & Kłobus, G. (2007). Modification of plasma membrane and vacuolar H^+-ATPase in response to NaCl and ABA. *Journal of Plant Physiology*, Vol.164, pp. 295-302

Janicka-Russak, M.; Kabała, K.; Burzyński, M. & Kłobus, G. (2008). Response of plasma membrane H^+-ATPase to heavy metal stress in *Cucumis sativus* roots. *Journal of Experimental Botany*, Vol.59, pp. 3721-3728

Janicka-Russak, M.; Kabała, K.; Młodzińska, E. & Kłobus, G. (2010). The role of polyamines in the regulation of the plasma membrane and the tonoplast proton pumps under salt stress. *Journal of Plant Physiology*, Vol.167, pp. 261-269

Jia, W.; Zhang, J. & Liang J. (2001). Initiation and regulation of water deficit-induced abscisic acid accumulaiton in maize leaves and roots: cellular volume and water relations. *Journal of Experimental Botany*, Vol.52, pp. 295–300

Kabała, K.; Janicka-Russak, M.; Burzyński, M. & Kłobus, G. (2008). Comparison of heavy metal effect on the proton pumps of plasma membrane and tonoplast in cucumber root cells. *Journal of Plant Physiology*, Vol.165, pp. 278-288

Kalampanayil, B. & Wimmers, L. (2001). Identification and characterization of a salt-stressed-induced plasma membrane H^+ATPase in tomato. *Plant Cell Environment*, Vol.24, pp. 999-1005

Kanczewska, J. ; Marco, S. ; Vandermeeren, C. ; Maudoux, O. ; Rigaud, J. & Boutry, M. (2005). Activation of the plant plasma membrane H^+-ATPase by phosphorylation and binding of 14-3-3 proteins convert a dimer into a hexamer. *PNAS*, Vol.102, No.33, (August 16), pp. 11675-11680

Kasamo, K. (1988). Response of tonoplast and plasma membrane ATPase in chilling sensitive and insensitive rice (Oryza sativa L.) culture cells to low temperature. Plant and Cell Physiology, Vol. 29, No.7, pp. 1085-1094.

Kasamo, K. (1990). Mechanism for activation of plasma membrane H+-ATPase from rice (*Oryza sativa*) culture cells by molecular species of a phospholipid. *Plant Physiology*, Vol.93, pp. 1049-1052

Kasamo, K. (2003). Regulation of plasma membrane H^+-ATPase activity by the membrane environment. *Journal of Plant Research*, Vol.116, pp. 517-523

Kasamo, K. & Nouchi, I. (1987). The role of phospholipids in plasma membrane ATPase activity in *Vagina radiata* L. (Mung bean) roots and hypocotyls. *Plant Physiology*, Vol.83, pp. 323-328

Kennedy, C. & Gonsalves, F. (1989). The action of divalent Zn, Cd, Hg, Cu and Pb ions on the ATPase activity of plasma membrane fraction isolated from roots of *Zea mays*. *Plant and Soil*, Vol.117, pp. 167-175

Kerkeb, L. ; Venema, K. ; Donaire, J. & Rodriguez-Rozales, M. (2002). Enhanced H^+/ATP coupling ratio of H^+-ATPase and increased 14-3-3 protein content in plasma membrane of tomato cells upon osmotic shock. *Physiologia Plantarum*, Vol.16, pp. 37-41

Kinoshita, T. & Shimazaki, K. (2001). Analysis of the phosphorylation level in guard-cell plasma membrane H+-ATPase in response to fusicoccin. *Plant Cell Physiology*, Vol.42, pp. 424-432

Kinoshita, T. & Shimazaki, K. (2002). Biochemical evidence for the requirement of 14-3-3 protein binding in activation of the guard-cell plasma membrane H+-ATPase by blue light. *Plant Cell Physiology*, Vol.43, pp. 1359-1365

Kłobus, G. & Janicka-Russak, M. (2004). Modulation by cytosolic components of proton pump activities in plasma membrane and tonoplast from *Cucumis sativus* roots during salt stress. *Physiologia Plantarum*, Vol.121, pp. 84-92

Kłobus, G. & Buczek, J. (1995). The role of plasma membrane oxidoreductase activity in proton transport. *Plant Physiology*, Vol.146, pp. 103-107

Knight, H.; Trewavas, A. & Knight, M. (1997). Calcium signalling in *Arabidopsis thaliana* responding to drought and salinity. *Plant Journal*, Vol.12, pp. 1067- 1078

Kolbert, Z. ; Bartha, B. & Erdei, L. (2008). Osmotic stress- and indolile-3-butyric acid-induced NO generation are partially distinct processes in root growth and development in *Pisum sativum*. *Physiologia Plantarum*, Vol.133, pp. 406-416

La Rosa, P.; Handa, A.; Hasegawa, P. & Bressan, R. (1985). Abscisic acid accelerates adaptation of cultured tobacco cells to salt. *Plant Physiology*, Vol.79, pp. 138-142.

La Rosa, P.; Hasegawa, P.; Rhodes, D. & Clithero, J. (1987). Abscisic acid stimulated osmotic adjustment and its involvement in adaptation of tobacco cells to NaCl. *Plant Physiology*, Vol. 85, pp. 174-185

Lee, S.; Singh, A.; Chung, G.; Ahn, S.; Noh, E. & Steudle, E. (2004) Exposure of roots of cucumber (Cucumis sativus) to low temperature severely reduces root pressure, hydraulic conductivity and active transport nutrients. *Physiologia Plantarum*, Vol.120, pp. 413-420

Lherminier, J.; Elmayan, T.; Fromentin, J.; Ekaraqui, K.; Vesa, S.; Morel, J.; Verrier, J.; Cailleteau, B.; Blein, J. & Simon-Plas, F. (2009). NADPH oxidase mediated reactive oxygen species production: subcellular localization and reassessment of its role in plant defence. *Molecular Plant Microbe Interaction*, Vol.22, No.7, pp. 868-881

Lin, H. & Wu, L. (1996). Effects of salt stress on root plasma memebrane characteristics of salt-tolerant and salt-sensitive buffalograss clones. *Environmental and Experimental Botany*, Vol.36, pp. 239-254

Linndberg, S. & Wingstrand, G. (1985). Mechanism for Cd^{2+} inhibition of (K^+ + Mg^{2+}) ATPase activity and K^+ ($^{86}Rb^+$) uptake join roots of sugar beet (*Beta vulgaris*). *Physiologia Plantarum*, Vol.63, pp. 181-186

Lindberg, S.; Banaś, A. & Stymne, S. (2005). Effects of different cultivation temperatures on plasma membrane ATPase activity and lipid composition of sugar beet roots. *Plant Physiology and Biochemistry*, Vol.43, pp. 261-268

Ling-Cheng, J.; Sun, L. & Dong, H. (1982). Adaptive changes in ATPase activity in the cells of winter wheat seedlings during cold hardening. *Plant Physiology*, Vol.70, pp. 127-131

Lino, B. ; Baizabal-Aguirre, V. & González de la Vara, L. (1998). The plasma H+-ATPase from beet root is inhibited by calcium-dependent phosphorylation. *Planta*, Vol.204, pp. 352-359

López-Pérez, L.; Martínez Ballesta, M.; Maurel, C. & Carvajal, M. (2009). Changes in plasma membrane lipids, aquaporins and proton pump of broccoli roots, as an adaptation mechanism to salinity. *Phytochemistry*, Vol.70, pp. 492-500

Lüthje, S.; Döring, O.; Heuer, S.; Lüthen, H. & Böttger, M. (1997). Oxidoreductases in plant plasma membranes. *Biochimica et Biophysica Acta*, Vol.1331, pp. 81-102

Martz, F.; Sutinen, M.; Kiviniemi, S. & Palta, J. (2006). Changes in freezing tolerance, plasma membrane H^+-ATPase activity and fatty acid composition in *Pinus resinosa* needles during cold acclimation and de-acclimation. *Tree Physiology,* Vol. 26, pp. 783-790

Morandini, P. ; Valera, M. ; Albumi, C. ; Bonza, M. ; Giacometti, S. ; Ravera, G. ; Murgia, I. ; Soave, C. & De Michelis, M. (2002). A nivel interaction partner for C-terminus of *Arabidopsis thaliana* plasma memebrane H+-ATPase (AHA1 isoform) : site and mechanism of action on H+-ATPase activity differ from those of 14-3-3 proteins. *The Plant Journal*, VOL.31, No.4, pp. 487-497

Moriau, L.; Michelet, B.; Bogaerts, P.; Lambert, L.; Michel, A.; Oufattole, M. & Boutry, M. (1999). Expression analysis of two gene subfamilies encoding the plasma membrane H^+-ATPase in *Nicotiana plumbaginifolia* reveals the major transport functions of this enzyme. *Plant Journal*, Vol.19, pp. 31–41

Morssome, P.; Dambly, S.; Maudoux, O. & Boutry, M. (1998). Single point mutations distributed in 10 soluble and mambrane regions of the Nicotiana plumbaginifolia plasma membrane PMA2 H^+-ATPase activate the enzyme and modify the structure of the C-terminal region. *Journal of Biological Chemistry*, Vol.273, pp. 34837-34842

Nakajima, N.; Saji, H.; Aono, M. & Kondo, N. (1996). Isolation of cDNA for a plasma membrane H^+-ATPase from guard cells of *Vicia faba* L. *Plant Cell Physiology*, Vol.36, pp. 919-924

Netting, A. (2000). pH, abscisic acid and the integration of metabolism in plants under stressed and non-stressed conditions: cellular responses to stress and their implication for plant water relations. *Journal of Experimental Botany*,Vol. 343, pp. 147-158

Niu, X.; Narasimhan, M. & Salzman, R. (1993). NaCl regulation of plasma membrane H+ATPase gene expression in *Glycophyte* and *Halophyte*. *Plant Physiology*, Vol.103, pp. 712-718

Nüchse, T.; Stensballe, A.; Jensen O. & Peck, S. (2003). Large-scale analysis of *in vivo* phosphotrylated membrane proteins by immobilized metal ion affinity. *Mollecular and Cellular Proteomics*, Vol. 1, pp. 1234-1243

Ookura, T.; Komatsu, S.; Kawamura, Y. & Kasamo, K. (2005). A 55-kDa calcium dependent protein kinase phosphorylated Thr residues from the auto-regulatory domain of plasma membrane H^+-ATPase in rice. *JARQ*, Vol.39, No2, pp. 99-104

Ouffatole, M.; Arango, M. & Boutry, M. (2000). Identification and expression of tree new *Nicotianaplumbaginifolia* genes which encode isoforms of a plasma-membrane H^{+}-ATPase, and one of which is induced by mechanical stress. *Planta*, Vol.210, pp. 715-722

Ouriti, O.; Boussama, N.; Zarrouk, M.; Cherif, A. & Ghorbal, M. (1997). Cadmium- and copper-induced changes in tomato membrane lipids. *Phytochemistry*, Vol.45, No.7, pp. 1343-1350

Qiu, Q.; Guo, Y.; Dietrich, M.; Schumaker, K. & Zhu, J. (2002). Regulation of SOS1, a plasma membrane Na^{+}/H^{+} exchanger in *Arabidopsis thaliana*, by SOS2 and SOS3. *PNAS*, Vol.99, pp. 8436-8441

Palmgren, M. (2001). Plant plasma membrane H^{+}-ATPase : powerhous for nutrient uptake. *Annual Review of Plant Physiology and Molecular Biology*, Vol.52, pp. 817-845

Pedechenko, V. ; Nasirova, G. & Palladina, T. (1990). Lysophosphatidylcholinespecifically stimulates plasma membrane H+-ATPase from corn roots. *FEBS Letters,* Vol.275, pp. 205-208

Perez-Prat, E. ; Narasimhan, M. ; Niu, X. ; Botella, M. ; Bressan, R. ; Valupesta, V. ; Hasegawa, P. & Binzel, M. (1994). Growth cycle stage dependent NaCl induction of plasma membrane H^{+}-ATPase mRNA accumulation in de-adapted tobacco cells. *Plant, Cell and Environment*,Vol.17, pp. 327-333

Peters-Soler, A. ; Prado, J. & Serrano, R. (1990). Immunocytolocalization of plasma membrane H^{+}-ATPase. *Plant Physiology*, Vol.93, pp. 1654-1658

Pitan , B. ; Schubert, S. & Mühling, K. (2009). Decline in leaf growth under salt stress is due to an inhibition of H^{+} pumping activity and increase in apoplastic pH of maize leaves. *Journal of Plant Nutrition and Soil Science*, Vol.172, pp. 535-43

Regenberg, B. ; Villalba, J. ; Lanfermeijer, F. & Palmgren, M. (1995). C-terminal deletion analysis of plant plasma membrane H+-ATPase : yeast as a model sysytem for solute transport across the plant plasma membrane. *Plant Cell*, Vol.7, pp. 1655-1666

Ros, R. ; Morales, A. ; Segura, J. & Picazo, I. (1992a). In vivo and in vitro effects of nickel and adcmium on the pasmalemma ATPase from rice (*Oryza sativa* L.) shoots and roots. *Plant Science*, Vol.83, pp. 1-6

Ros, R.; Cooke ,D.; Martinez-Cortina, C. & Picazo, I. (1992b). Nickel and cadmium related changes in growth, plasma membrane lipid composition, ATPase hydrolytic activity and proton-pumping of rice (*Oryza sativa* L. cv. Bahia) shoots. *Journal of Experimental Botany*, Vol.43, pp. 1475-1481

Rubinstein, B. & Stern, A. (1986). Relationship of transplasmalemma redox activity to proton and solute transport of Zea mays. *Plant Physiology*, Vol.80, pp. 805-811

Sahu, B. & Shaw, B. (2009). Salt-inducible isoform of plasma membrane H^{+}-ATPase gene in rice remains costitutively ezpressed in natural halophyte, *Suaeda maritima.Journal of Plant Physiology*, Vol. 166, pp. 1077-1089

Santi, S.; Locci, G.; Monte, R.; Pinton, R. & Varanini, Z. (2003). Induction of nitrate uptake in maize roots: expression of a putative high-affinity nitrate transporter and plasma membrane H^{+}-ATPase isoforms. *Journal of Experimental Botany*, Vol.54, pp. 1851-1864

Schaller, A. & Oecking, C. (1999). Modulation of plasma membrane H^{+}-ATPase activity differentially activates wound and pathogen defence responses in tomato plants. *Plant Cell,* Vol. 11, pp. 263-272

Schroeder, J.; Allen, G.; Hugouvieux, V.; Kwak, J. & Waner, D. (2001). Guard cell signal transduction. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.52, pp. 627-658

Shen, H.; He, L.; Sasaki, T.; Yamamoto, Y.; Zheng, S.; Ligaba, Z.; Yan, X.; Ahn, S.; Yamaguchi, M.; Sasakawa, H. & Matsumoto, H. (2005). Citrate secretion coupled with the modulation of soybean root tip under aluminium stress. Up-regulation of transcription, translation, and threonine-oriented phosphorylation of plasma membrane H+-ATPase. *Plant Physiology*, Vol.138, (May), pp. 287-296

Shen, P.; Wang, R. Zhang, W. (2011). Rice phospholipase Dα is involved in salt tolerance by the mediation of H+-ATPase activity and transcription. Journal of Integrative Plant Biology, Vol. 53, No.4, (April), pp. 289-299

Shi, H.; Ishitani, M.; Kim, C. & Zhu, J. (2000). The *Arabidopsis thaliana* salt tolerance gene *SOS1* encodes a putative Na^+/H^+ antiporter. *PNAS,* Vol.97, pp. 6896-6901

Shi, H.; Quintero, F.; Pardo, J. & Zhu, J. (2002). The putative plasma membrane Na^+/H^+ antyporter SOS1 controls long-distance Na^+ transport in plants. *Plant Cell*, Vol.14, pp. 465-477

Shi, H.; Lee, B.; Wu, S. & Zhu, J (2003). Overexpression of a plasma membrane Na^+/H^+ antiporter gene improves salt tolerance in *Arabidopsis thaliana*. *Nature Biotechnology*, Vol.21, pp. 81-85

Shinozaki, K. & Yamaguchi-Shinozaki, K. (1996). Molecular responses to drought and cold stress. *Current Opinion Biotechnology*, Vol. 7, pp. 161-167

Skriver, K. & Mundy, J. (1990). Gene expression in response to abscisic acid and osmotic stress. *Plant Cell*, Vol. 2, pp. 503-512

Speth, C. ; Jaspert, N. ; Marcon, C. & Oecking, C. (2010). Regulation of the plant plasma membrane H+-ATPase by its C-terminal domain : what we know for sure? *European Journal of Cell Biology*, Vol.89, pp. 145-151

Surowy, T. & Boyer J. (1991). Low water potentials affect expression of genes encoding vegetative storage proteins and plasma membrane proton ATPase in soybean. *Plant Molecular Biology*, Vol.16, pp. 252–262

Svennelid, F.; Olsson, A.; Piotrowski, M.; Rosenquist, M.; Ottman, C.; Larsson, C.; Oecking, C. & Sommarin, M. (1999). Phosphorylation of Thr-948 at the C-terminus of the plasma membrane H^+-ATPase creates a binding site for regulatory 14-3-3 protein. *Plant Cell*, Vol.11, pp. 2379-2391

Takemiya, A. & Schimazaki,, K. (2010). Phosphatidic acid inhibits blue light-induced stomatal opening via inhibition of protein phosphatases 1. *Plant Physiology*, Vol.153, (August) pp. 1555-1562

Takemiya, A.; Kinoshita, T, Asanuma, M. & Shimazaki, K. (2006). Protein phosphatases 1 positively regulates stomatal opening in response to blue light in *Vicia faba*. *Proceedings of the National Academy of Sciences USA*, Vol.103, pp. 13549-13554

Tan, B.; Schwartz, S.; Zeevaart, J. & Mc Carty, R. (1994). Genetic control of abscisic acid biosynthesis in maize. *Proceedings of the National Academy of Sciences USA,* Vol.94, pp. 12235-12240

Upchurch, R. (2008). Fatty acid unsaturation, mobilization, and regulation in the response of plants to stress. *Biotechnological Letters*, Vol.30, pp. 967-977

Van der Hoeven, P.; Siderius, M.; Korthout, H.; Drabkin, A. & De Boer, A. (1996). A calcium and free fatty acid modulated protein kinase as putative effector of the fussicoccin 14-3-3 receptor. *Plant Physiology*, Vol.111, pp. 857-865

Vega, S.: Del Rio, A.; Bamberg, J. & Palta J. (2004). Evidence for the up-regulation of stearoyl-ACP (D9) desaturase gene expression during cold acclimation. *American Journal of Potato Research*, Vol.81, pp. 125–135

Vera-Estrella, R.; Barkla, B. Higgins, V. & Blumwald E. (1994). Plant defense response to fungal pathogens (activation of host-plasma membrane H+-ATPase by elicitor-induced enzyme dephosphorylation). *Plant Physiology*, Vol.104, pp. 209-215

Viotti, C; Luoni, L.; Morandini, P. & De Michelis, M. (2005). Characterization of the interaction between the plasma membrane H+-ATPase of *Arabidopsis thaliana* and a novel interactor (PP1). *FEBS Journal*, Vol.272, pp. 5864-5871

Wakeel, A. Hanstein, S.; Pitann, B. & Schubert, S. (2010). Hydrolytic and pumping activity of H+-ATPase from leaves of sugar beet (*Beata vulgaris* L.) as affected by salt stress. *Journal of Plant Physiology*, Vol.167, pp. 725-731

White, F.; Cooke, D.; Earnshaw, M.; Clarkson, D. & Burden, R. (1990). Does plant growth temperature modulate the membrane composition and ATPase activities of tonoplast and plasma membranes fractions from rye roots? *Phytochemistry*, Vol.29, pp. 3385-3393

Xing, T.; Higgins, V. & Blumwald E. (1996). Regulation of plant defense response to fungal pathogens: Two types of protein kinases in the reversible phosphorylation of the host plasma membrane H^+-ATPase. *Plant Cell*, Vol.8, pp. 555-564

Xiong, L. & Zhu, J. (2001). Abiotic stress signal transduction in plants: Molecular and genetic perspectives. *Physiologia Plantarum*, Vol.112, pp. 152-166

Xiong, L.; Schumaker, K. & Zhu, J. (2002). Cell Signaling during Cold, Drought, and Salt Stress. *Plant Cell*,Vol.14, pp.165-183

Yamasaki, H. & Sakihama, Y. (2000). Simultaneous production of nitric oxide and peroxynitriteby plant nitrate reductase: in vitro evidence for the NR-dependent formation of active nitrogen species. *FEBS Letters*, Vol.468, pp. 98-92

Yang, Y.; Xu, S.; An, L. & Chen, N. (2007). NADPH oxidase dependent hydrogen peroxide production, induced by salinity stress, may be involved in the regulation of total calcium in roots of wheat. *Journal of Plant Physiology*, Vol.164, pp. 1429-1435

Yu, X.; Li, M.; Gao, G.; Feng, H.; Geng, X.; Peng, C.; Zhu, S.; Wang, X.; Shen, Y. & Zhang, D. (2006). Abscisic acid stimulates a calcium-dependent protein kinase in grape berry. *Plant Physiology*, Vol.140, pp.558-579

Zandonadi, D.; Santos, M.; Dobbss, L.; Olivares, F.; Canellas, LL.;, Binzel, M.; Okorokova-Façanha, A. & Façanha, A. (2010). Nitric oxide mediates humic acids-induced root development and plasma membrane H^+-ATPase activation. *Planta,* (2010). Vol.231, pp. 1025-1036

Zhang, X.; Zhang, L.; Dong, F.; Gao, J.; Galbraith, D. & Song, C. (2001). Hydrogen peroxide id involved in abscisic acid-induced stomatal closure in *Vicia faba*. *Plant Physiology*, Vol.126, (August), pp. 1438-1448

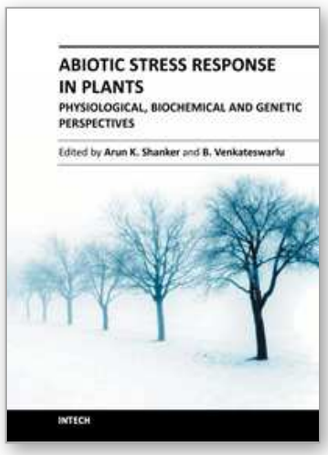
Zhang, X.; Wang, H.; Takemiya, A.; Song, C.; Kinoshita, T. & Shimazaki, K. (2004). Inhibition of blue light-dependent H^+ pumping by Abscisic acid through hydrogen peroxide-induced dephosphorylation of the plasma membrane H^+-ATPase in guard cell protoplasts. *Plant Physiology* , Vol.136, (December), pp. 4150-4158

Zhang , m.; Barg, R.; Yin, M.; Gueta-Dahan, Y.; Leikin-Frenkel, A.; Salts, Y.; Shabtai, S. & Ben-Hayyim, G. (2005). Modulated fatty acid desturation via over-expression of two distinct ω-3 desaturases differentially alters tolerance to various abiotic stresses in transgenic tobacco cells and plants. *Plant Journal*, Vol.44, pp. 361-371

Zhang, F.; Wang, Y. & Wang, D. (2007). Role of nitric oxide and hydrogen peroxide during the salt resistance response. *Plant Signaling & Behavior*, Vol.2, No.6, (November/December), pp. 473-474

Zhu, J. (2002). Salt and drought stress signal transduction in plants. *Annual Review of Plant Biology*, Vol.53, pp. 247-273

Zörb, C.; Stracke, B.; Tramnitz, B.; Denter, D.; Sümer, A.; et al. (2005). Does H^+ pumping by plasmalemma ATPase limit leaf growth of corn (*Zea mays* L.) during the first phase of salt stress? *Journal of Plant Nutrition and Soil Science*, Vol.168, pp. 550-557



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

Edited by Prof. Arun Shanker

ISBN 978-953-307-672-0
Hard cover, 346 pages
Publisher InTech
Published online 29, August, 2011
Published in print edition August, 2011

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.

InTech Europe
University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
Fax: +385 (51) 686 166
www.intechopen.com

InTech China
Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

IntechOpen