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# Post-Translational Modifications of Nuclear Proteins in the Response of Plant Cells to Abiotic Stresses

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## 1. Introduction

For a long time, in plant cells as in animal cells, the nucleus was only considered as the organelle in which fundamental mechanisms such as replication and transcription occurred. While strong efforts were deployed in order to identify important families of transcription factors such as MYB, WRKY or TGA families (Dubos *et al.*, 2010; Rushton *et al.*, 2010), a few attention was devoted to our lack of knowledge about their regulation in regard to the physiological conditions of the plant cells. Whereas the major importance of post-translational modification of proteins is well established for several decades regarding cytosolic proteins, the last years have been characterized by the discovery that the plant cell nucleus also contains all the enzymes necessary to assume these fundamental reactions in terms of signal transduction. For example, Mitogen-Activated Protein Kinases (MAPK) are well known protein kinases (PKs) involved in response to both biotic and abiotic stresses (for review see Dahan *et al.*, 2009). These MAPKs play a crucial role in the regulation of specific gene expression by phosphorylating particular transcription factors. However, while they are well described in the cytosol, only recently researchers focused on their presence and involvement in the nucleus of plant cells challenged by abiotic stresses (for example, Ahlfors *et al.*, 2004). Unfortunately, these authors like the other ones involved in plant cell nucleus studies did not try to identify the targets of these MAPK. This example highlights the fact that our knowledge of the incidence of protein posttranslational modifications regarding the cellular activities is still poorly rudimental, and particularly in the field of abiotic stress responses.

Amongst the targets of these post-translational modifications, histones will be a piece of choice, being one of the favourite substrates for acetylation or methylation for example. Histones are small basic protein associated with DNA to form the chromatin. Chromatin

contains histone octamere composed by two copies of each histone H2A, H2B, H3 and H4 to form the histone core. Histones composing the histone core are extremely conserved in the different kingdoms. For example, histone H3 differs only by two amino acids in its sequence in rat and pea. The histone core is rolled by approximately 146 bps of DNA to form a nucleosome, the repeating unit of chromatin which provided a first level of DNA compaction. Association of nucleosome with other protein like histone H1 creates a structure named 30 nm chromatin fiber (Kornberg and Lorch, 1999; Hayes and Hansen, 2001). This fiber can be unfold by several protein grouped under the term chromatin remodeling complex to generate a 11 nm fiber, the template for transcription. The 11 nm fiber can also be repressive to transcription process but different types of protein complexes can affect the chromatin to modulate DNA accessibility to transcriptional machinery and at the end gene transcription. Histone tails and globular domains are subjected to a variety of posttranslational modifications such as acetylation, methylation, phosphorylation, ubiquitination, sumoylation, ADP ribosylation, deimination and proline isomerization. These covalent modifications of histones are important in chromatin dynamics (Kouzarides, 2007). It has been proposed that all the histone postranslational modifications constitute a code, “the histone code” associating to all the possible combinations of modification a particular state allowing biological process such as transcription of gene. This code is written by particular proteins: “the writers”, interpreted by other proteins: “the readers” and erased by a last class of protein, “the erasers” (Figure 1). Readers could also be able to modify histones or to recruit other protein act on chromatin (Strahl and Allis, 2000).

The goal of this book chapter is to summarize our current knowledge of the molecular actors and their regulations that lead to posttranslational modifications of nuclear proteins, and *in fine* to the regulation of specific target gene expression. For this purpose, a large number of nuclear enzymes that are involved in (de)phosphorylation, (de)acetylation, and (de)methylation of nuclear proteins, but also in nuclear protein degradation pathway associated with sumoylation and ubiquitination, and in changes of the redox state of the nuclear proteins will be presented and their roles illustrated by various but non exhaustive cell responses to abiotic stresses.

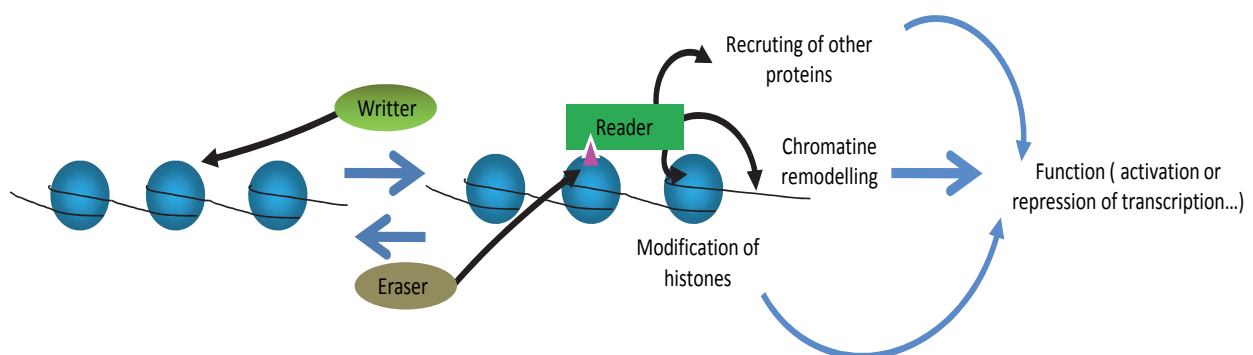


Fig. 1. Schematic representation of histone code. Writers can recognize chromatin area and add marks on histone (methylation, acetylation...). These labeling is dynamic because marks can be remove by erasers. They can also be recognized par readers, another group of proteins able to act directly or indirectly on chromatin structure. The final consequence can be a modification of the gene transcription in concerned loci.

## 2. Nuclear protein phosphorylation / dephosphorylation

Phosphorylation is probably the most prominent and major posttranslational modification in living organisms. This reversible modification consists on the covalent binding of a phosphate on aminoacids hydroxyl residues. In eukaryotes, phosphorylation occurs mainly on Ser, Thr and Tyr residues. This modification depends on the action of two types of enzymes with antagonistic activities: (i) PKs which phosphorylates and (ii) protein phosphatases (PPs) which remove phosphoryl groups from target proteins. The binding of the phosphoryl group alters the functional properties of target proteins in terms of activity, subcellular localization, protein-protein interactions or stability (Cohen, 2000). This versatility has made phosphorylation one of the major means for modulation of cellular activities, as phosphorylation status can be finely tuned as the result of the balance between PKs and PPs activities at a given time point on specific substrates. These enzymes are thus involved at every steps of signal transduction, from plasma membrane to final effectors. Although numerous studies like the ones regarding brassinosteroids, have investigated PKs, PPs and their targets in the plasma membrane and the cytoplasm (Li, 2005), only few ones has focused on those localized, temporarily or permanently, in the nuclear compartment, despite their involvement in critical processes for cell surviving (Dahan *et al.*, 2009). A recent phosphoproteomic analysis of the nuclear proteins from *Arabidopsis thaliana* showed that the identified phosphorylated proteins cover a wide range of nuclear activities, indicating an equal importance of phosphorylation in the modulation of nuclear activities as for the cytoplasmic ones (Jones *et al.*, 2009).

In plants, PKs constitute a superfamily of proteins, and according to their importance in cellular homeostasis, it was shown that around 4 % of *A. thaliana* genome encodes putative PKs (Champion *et al.*, 2004). According to their substrate specificities, PKs and PPs can be classified into three families: (i) Ser/Thr PKs/PPs, (ii) Tyr PKs/PPs and (iii) dual-specificity (Ser/Thr-Tyr) PKs/PPs. In plants, no functional Tyr PK has been described to date, although predicted (Miranda-Saavedra and Barton, 2007). Consistent with this, the relative abundance of phosphor-Ser, phosphor-Thr and phosphor-Tyr has been estimated in *A. thaliana* to 85 %, 11 % and 4 % respectively (Sugiyama *et al.*, 2008). Although Tyr (de)phosphorylation is thus accomplished through dual-specificity PKs/PPs, to date, the vast majority of studies have been focused on Ser/Thr PKs/PPs in plant.

More than half of the putative PKs from the *A. thaliana* genome fall in the clade of the so-called Receptor-Like protein Kinases (RLKs), which are transmembrane proteins probably acting as receptors of environmental stimuli (Tör *et al.*, 2009). The other part of plant PKs, which is of interest in this article, constitutes the clade of the “soluble” ones, and concerns all PKs found in the cytoplasm and the nucleus. This clade can be divided into numerous families and subfamilies, based on sequence similarities of the kinase domain and features of flanking sequences determining regulation properties (Hanks and Hunter, 1995; Champion *et al.*, 2004; Miranda-Saavedra and Barton, 2007); readers are invited to report to these works for more details). Although for a large part studied in the cytoplasm or at the plasma membrane level, members from almost all families have been found in the nuclear compartment (for a detailed review, see Dahan *et al.*, 2010). The majority of the available data on these nuclear PKs comes from subcellular distribution studies. Indeed for most of them their nuclear localization has been investigated using chimerical PKs fused to a fluorescent reporter, or immunolocalization studies based on specific antibodies. The

activity of the PKs in the nucleus has only been assessed in rare cases, impairing our understanding of their roles and functionality.

While the core catalytic domain of PKs derived from a single ancestor (Hanks and Hunter, 1995), PPs origins are more diversified (Moorhead *et al.*, 2009). In plants, around 160 sequences coding for putative catalytic subunit of PPs have been retrieved (Kerk *et al.*, 2002). They can be divided in three main families, based on catalytic domain sequences and enzymatic features: (i) the PPP (phosphoprotein phosphatase) family, (ii) the PPM (metalloindependent protein phosphatase) family, and (iii) the PTP (phosphotyrosine phosphatase) including the DSP (dual-specificity phosphatase). Readers are invited to refer to other reviews that detailed the features of these families (Kerk *et al.*, 2002; Luan, 2003; Moorhead *et al.*, 2009). As for plant PKs, PP functionalities in the nucleus have been poorly studied.

The role of several nuclear PKs in response to different abiotic stresses has been investigated in different model plants. To date, and despite the great diversity of PKs, only a few families have been shown to be involved in these signaling pathways at a nuclear level. Among them, the MAPK family is certainly the most studied family of PKs in the nucleus. MAPK is the last component of a cascade of three PKs, which are sequentially activated (Widmann *et al.*, 1999). The perception of an environmental stimulus drives the activation of the first PK of this transduction module, namely MAPKKK (MAPK kinase kinase). MAPKKK in turn activates by phosphorylation on a specific motif a MAPKK (MAPK kinase), which phosphorylates MAPK, the final effector, on conserved residues. This chain of phosphorylation is thought to take place in the cytoplasm, and the MAPK is then translocated upon activation by phosphorylation into the nucleus, where it modulates gene expression by acting on transcription factors. However the presence of MAPKK and MAPKKK in the nucleus was already reported (Dahan *et al.*, 2009).

Figure 2 illustrates, although partially, the known nuclear PKs that were shown to be involved in response to various abiotic stresses. Even though MAPK was involved in the response to many abiotic stresses on the basis of their activation in the cytosol, few of them have been demonstrated to localize and to act in the nuclear compartment. In fact in the context of abiotic stresses only one study showed the translocation in *A. thaliana* of two MAPKs, AtMPK3 and AtMPK6, following ozone exposure and using immunolocalization of the native protein (Ahlfors *et al.*, 2004). However contradictory results were obtained when these two MAPKs were expressed fused to GFP, and showed a constitutive nuclear and cytoplasmic localization (Yoo *et al.*, 2008). In addition to ozone exposure, these two MAPKs are furthermore activated in response to several abiotic stresses, such as cold, salt, drought, wounding and touch for AtMPK6 (Ichimura *et al.*, 2000) and osmotic stress for AtMPK3 (Droillard *et al.*, 2002). The orthologs of AtMPK3 and AtMPK6 in tobacco, respectively WIPK (Wounding-Induced Protein Kinase) and SIPK (Salicylic acid-Induced Protein Kinase), are also activated in response to several environmental cues, such as high salinity and osmotic stresses, wounding and ozone exposure (Zhang and Klessig, 1998; Mikołajczyk *et al.*, 2000; Samuel and Ellis, 2002). They were shown to be nuclear, independently of any stimuli when fused to GFP (Menke *et al.*, 2005; Yap *et al.*, 2005), and the activity of SIPK could be retrieved in nuclear extracts of osmotically stressed tobacco cells (Dahan *et al.*, 2009), demonstrating its functionality in the nuclear compartment in response to environmental stresses. A few substrates of MAPKs have been identified, and so their precise roles in response to abiotic stresses remain elusive. For the most part, their known targets are transcription factors. For example, SIPK was shown to phosphorylate *in vitro* the transcription factor WRKY1, involved in the expression of defense-related genes (Menke *et al.*, 2005). This suggests that



MAPKs, in response to different abiotic stresses, could be involved in the reprogramming of transcription patterns to allow the plant to cope with the perceived stresses. Given that, the overexpression or knock-out of several MAPKs impairs the outcome of the response to some abiotic stresses. The extinction of *Atmpk6* expression using RNAi and a loss-of-function mutation of *Atmpk3* both generate increased sensitivity to ozone leading to cell death, implying that these MAPK play an important role in the management of ozone stress by *A. thaliana* (Ahlfors *et al.*, 2004). Another *A. thaliana* MAPK, AtMPK4, has been shown to reside permanently in the nucleus along with the cytoplasm (Andreasson *et al.*, 2005; Kosetsu *et al.*, 2010). Although more studied for its potential role in cytokinesis (Kosetsu *et al.*, 2010) and its involvement in plant defense reactions (Andreasson *et al.*, 2005; Gao *et al.*, 2008), its activity is observed upon application of stresses such as cold, salt and osmotic stresses (Droillard *et al.*, 2004; Teige *et al.*, 2004). One substrate for this MAPK has been described in vitro: MKS1, which is a protein interacting with two WRKY transcription factors (Andreasson *et al.*, 2005). The phosphorylation of MKS1 by AtMPK4 is thought to result in the release of the WRKY33, which could then play its role as a transcriptional regulator (Qiu *et al.*, 2008). However, this interaction takes place in the context of defense reaction, and no data is available regarding functionality of AtMPK4 in response to abiotic stresses.

Stress	Kinase/phosphatase	HDAC/HAT
Cold	MPK6 (Ichimura <i>et al.</i> , 2000) MPK4 (Droillard <i>et al.</i> , 2004; Teige <i>et al.</i> , 2004)	AtGCN5/HAG1 (Servet <i>et al.</i> , 2010) HDA18, HDA19 (Alinsug <i>et al.</i> , 2009) SIR2 (Bond <i>et al.</i> , 2009)
Heat		HDA7 (Alinsug <i>et al.</i> , 2009)
Salt	MPK6 (Ichimura <i>et al.</i> , 2000) SnRK2 (Halford and Hey, 2009) MPK4 (Droillard <i>et al.</i> , 2004; Teige <i>et al.</i> , 2004)	HDA6 (Chen <i>et al.</i> , 2010) HDA19 (Chen and Wu, 2010) HDA2, HDA14 (Alinsug <i>et al.</i> , 2009) HD2C (Sridha and Wu, 2006)
Osmotic	MPK3 (Droillard <i>et al.</i> , 2002) MPK4 (Droillard <i>et al.</i> , 2004; Teige <i>et al.</i> , 2004) SnRK2 (Halford and Hey, 2009)	
Drought	MPK6 (Ichimura <i>et al.</i> , 2000) SnRK2 (Halford and Hey, 2009)	
Light		HDA19 (Tian <i>et al.</i> , 2003) HDA7 (Alinsug <i>et al.</i> , 2009) GCN5 (Benhamed <i>et al.</i> , 2006)
Ozone	MPK3, MPK6 (Ahlfors <i>et al.</i> , 2004)	
Wounding	MPK6 (Ichimura <i>et al.</i> , 2000)	HDA19 (Zhou <i>et al.</i> , 2005)

Fig. 2. An overview of nuclear enzymes involved in phosphorylation/ dephosphorylation or acetylation/ deacetylation processes in response to various abiotic stresses.

Not only MAPKs are the nuclear crossroads of abiotic stresses. Data that are piling up to put PKs and PPs at the centre of the regulation of the adaptative responses of plant cells to osmotic, saline and hydric stresses, in link with ABA (abscisic acid), point out the role of other nuclear PK. In particular SnRK2 (for Snf1-Related protein Kinase) family is constituted of PKs initially characterized as ABA signalling factors. They can be categorized into three subclasses, and subsequent studies on rice and *A. thaliana* PKs demonstrated that all of the subclasses could be activated in response to osmotic stress, with subclasses II and III being also responsive to ABA (Halford and Hey, 2009). ABA is a phytohormone essential for the establishment of adaptative responses to drought and salinity stresses. Its accumulation leads to expression of ABA-responsive genes helping cells to cope with hydric and osmotic variations (Hubbard *et al.*, 2010). It was recently shown that at the heart of its signalling pathway in *A. thaliana* is a core complex composed of three subclass III SnRK2 called SnRK2D, E and I, and their cognate PPs PP2C. Indeed SnRK2s are rendered active upon phosphorylation on two critical residues in their activation loop (Belin *et al.*, 2006; Burza *et al.*, 2006; Boudsocq *et al.*, 2007). Recently, several PPs from the PP2C family have been shown to dephosphorylate these residues, thus inactivating the PKs. These partners have been colocalized in the nuclear compartment, where they interact in permanence (Umezawa *et al.*, 2009). Interestingly, the same SnRK2s were also shown to associate in the nucleus with AREB1, a transcription factor whose expression occurs during drought (Fujii *et al.*, 2009). A triple mutant plant impaired in the expression of SnRK2D, E and I exhibited a strongly reduced tolerance to drought, comforting the involvement of these PKs in response to water shortage. Accordingly, drastic changes were observed in response to ABA, high salinity stress and drought at the transcriptional level, with down-regulation of ABA responsive-genes as compared to wild type plants (Fujita *et al.*, 2009). Upon perception, water and osmotic stresses lead to production of ABA which in turn activates the transduction module composed of the PP2Cs and the SnRK2s. The signaling pathway is then achieved by phosphorylation of specific transcription factors, controlling a set of stress and ABA-responsive genes. Likewise, other SnRK2s have been characterized in several plant species that can phosphorylate ABA-responsive transcription factors. In wheat, the SnRK2 PKABA1 has been shown to interact with and phosphorylate *in vitro* TaABF, an ortholog of AREB1 (Johnson *et al.*, 2002). Furthermore, three rice SnRK2s were found to phosphorylate and activate another ortholog of AREB1, TRAB1 (Kobayashi *et al.*, 2005). However in the last two cases, the subcellular partitioning of the PK was not investigated. Recent data suggest that the transduction module composed of the SnRK2 and PP2C could be directly activated in the nucleus, meaning that the ABA receptor is expected to translocate after binding to its ligand.

Calcium is a well recognized second messenger, and as such its variations in the cytosol specifically induced by many stimuli promote specific signal transduction through decoding by a panel of Ca<sup>2+</sup> sensor molecules (Kudla *et al.*, 2010). It is now well established that apart from the cytosol, nucleus is able to generate its own Ca<sup>2+</sup> signatures following diverse environmental cues (Mazars *et al.*, 2009). Accordingly, Ca<sup>2+</sup>-binding proteins have been localized in the nucleus, where they can decode Ca<sup>2+</sup> variations into an appropriate response, like modulation of the expression of specific set of genes (Xiong *et al.*, 2006). Accordingly, several PKs and PPs potentially regulated by Ca<sup>2+</sup> have been localized in the nucleus, where they are thought to decode nuclear Ca<sup>2+</sup> variations into modifications of phosphorylation state of specific target proteins. The concerned PKs are mainly CDPKs

(Ca<sup>2+</sup>-Dependent Protein Kinases) and CIPKs (Calcineurin B-like[CBL]-Interacting Protein Kinases). CDPKs are specific to plant and exhibit in their sequence a CaM-like domain with three to four EF-hand Ca<sup>2+</sup> binding motifs, rendering them directly dependent on Ca<sup>2+</sup> binding for their activities (Klimecka and Muszynska, 2007). A study on the subcellular targeting performed for 9 of the 34 putative CDPK in *A. thaliana* showed that two of them, AtCPK3 and AtCPK4 are constitutively cytosolic and nuclear (Dammann *et al.*, 2003). AtCPK3 has been shown to be activated at the plasma membrane level following a salt stress, and in accordance to this putative involvement knock-out *Atcpk3* mutant plant exhibited altered resistance to salt stress, whereas it was improved in *Atcpk3* overexpressor mutant line (Mehlmer *et al.*, 2010). Intriguingly, no transcriptional changes in the expression of traditionally salt-stress related genes were observed, raising the question of AtCPK3 nuclear role (Mehlmer *et al.*, 2010). Apart salt stress, another CDPK, AtCPK32, has been found to be involved in ABA signaling, through interaction and phosphorylation with an ABA-responsive transcription factors, ABF4. Interestingly these two proteins are colocalized in the nucleus (Choi *et al.*, 2005). Whereas most of the CDPK studied show a constitutive partitioning between different sublocation and the nucleus, two CDPK from different species are suggested to translocate from the plasma membrane to the nucleus upon stresses. McCPK1 from *Mesembryanthemum crystallinum* is transcriptionally induced following salt- or water deficit stresses and when fused to GFP, translocate from the plasma membrane to the nuclear compartment (Chehab *et al.*, 2004). However the mechanisms and the functions of this phenomenon are not explained to date. Even if CDPKs are thought to have their activities regulated by Ca<sup>2+</sup> concentrations in the cytosol (Harmon, 2003), recent data suggest that they could also be part of phosphorylation cascade, as for NtCDPK2 and NtCDPK3, complicating conventional signaling schemes (Witte *et al.*, 2010). Despite recent advances in the understanding of the functionality of Ca<sup>2+</sup> variations, the ion still constitute a missing when it comes down to evaluate its part in the activation of specific signaling pathways.

### 3. Nuclear protein acetylation / deacetylation

The first descriptions of a nuclear protein modification by the chemical binding of an acetyl group on the amine function of lysine residues was observed on histone proteins (Allfrey *et al.*, 1964), explaining why enzymes responsible for the acetylation and deacetylation processes were named histone acetyltransferases (HATs; Gallwitz, 1971) and histone deacetylases (HDACs; Inoue and Fujimoto, 1969), respectively. However, based on their ability to act on proteins unrelated to histone such as transcription factors or coregulators of gene transcription, HATs and HDACs are more generally considered as lysine acetyl transferases and lysine deacetylases (Chen and Tian, 2007). All these proteins were reported to be located, exclusively or not, into the nucleus of plant cell.

#### 3.1 Histone deacetylases (HDACs)

Concerning HDACs, plant genomes contain members that belong to two different families that are common to eukaryotes (Pandey *et al.*, 2002): the RPD3 (Reduced Potassium Dependency Protein 3) - HDA1 (Histone Deacetylase 1) superfamily, and SIR2 (Silent Information Regulator 2) family. The third family, termed HD2 (type-2 Histone Deacetylase), is specific to plant cells (Fu *et al.*, 2007).



The first member of the RPD3-HDA1 superfamily was identified in yeast in a complementation screen of a mutant for a high affinity potassium transporter (Vidal *et al.*, 1990). It was latter shown that RPD3 encodes the catalytic subunit of the HDB (Histone Deacetylase B) complex activity (Rundlett *et al.*, 1996). The first plant RPD3-HDAC member, ZmRpd3, was identified in maize thanks to its ability to functionally complement a yeast *rpm3* null mutant (Rossi *et al.*, 1998). Among the eleven *RPD3* genes identified in the maize genome, three of them (*ZmHDA101*, *ZmHDA102* and *ZmHDA108*) exhibit the same expression pattern, suggesting a possible functional redundancy among this gene family (Varotto *et al.*, 2003). In term of specificity, ZmRPD3s, like its counterpart in yeast, seem to specifically remove the acetyl tail of lysines of histone H4 (H4K5, H4K12) prior to its incorporation in chromatin (Lechner *et al.*, 2000). Homologs of ZmRPD3 were also identified in *A. thaliana* and classified in three different clades : Class I for the RPD3 group, Class II for the HDA1-like group, and Class IV for the AtHDA2 group (Alinsug *et al.*, 2009). Whereas 18 RPD3-like genes were identified from the genome analysis data, only *AtHD1* (also called *AtHDA19* or *RPD3A*) and *AtHDA6* were largely characterized. *AtHD1*, that is constitutively expressed, encodes a protein that localises both in the cytoplasm and in the nucleus, but is predominantly accumulated in the euchromatic region and excluded from the nucleolus (Varotto *et al.*, 2003; Fong *et al.*, 2006). *AtHD1* exhibits a histone deacetylase activity that removes the acetyl group of histone H3 (H3K9) and H4 (H4K5, H4K8, H4K12, H4K16; Tian *et al.*, 2003). *AtHDA6*, although it is the close homolog of *AtHD1*, exhibits major differences in term of expression and specificity. *AtHDA6* is largely accumulated in the nucleoli (Probst *et al.*, 2004) and is a broad-specificity HDAC that removes the acetyl group of various lysines of histone H3 and H4 (H3K14, H4K5, H4K12; Earley *et al.*, 2006). In agreement with these differences in their expression profiles, *AtHD1* and *AtHDA6* are involved in different signalling pathways: *AtHD1* regulates several developmental processes such as early senescence, floral organ identity or late flowering (Wu *et al.*, 2000; Tian and Chen, 2001; Tian *et al.*, 2005), by controlling the expression of a set of genes involved in protein synthesis, ionic homeostasis or plant hormonal regulation (Tian *et al.*, 2005). *AtHDA6*, due to its localisation in the nucleolus, is involved in the inhibition of the NORs (nucleolus organisation region; Probst *et al.*, 2004; Earley *et al.*, 2006), and evidences supporting roles in silencing transgenes and transposons were also reported (Murfett *et al.*, 2001; Aufsatz *et al.*, 2002; Lippman *et al.*, 2003; May *et al.*, 2005). In a structural point of view, a huge study was conducted with the RPD3-like HDACs of *A. thaliana* (Alinsug *et al.*, 2009). All members are characterized by a variable catalytical domain characterized by a pocket that can either bind a Zn<sup>2+</sup> cation necessary to ensure the deacetylation reaction, or different inhibitors like sodium butyrate or trichostatine A (Finnin *et al.*, 1999). Different members of this family like HDA6, HDA7 or HDA19 contain a NLS and / or NES, confirming the nuclear localisation of these enzymes, but also that a cytosolic / nuclear shuttling could be of importance for their mode of action.

Several studies, mainly based on the use of mutants in *RPD3-HDA1 A. thaliana* genes, have reported that they play major roles in various biotic and abiotic stress responses (Figure 2; Alinsug *et al.*, 2009). Amongst the 18 HDAC *A. thaliana* genes belonging to the RPD3-HDA1 family, most of them appear to be partly or largely involved in response to various environmental stresses. For example, in the Class I RP3-HDAC, *AtHDA19* that is the best characterized member of this family, is highly expressed in germinating and imbibed seeds and also strongly accumulated in response to cold stress (Alinsug *et al.*,

2009), wounding (Zhou *et al.*, 2005) or light response (Tian *et al.*, 2003; Tian *et al.*, 2005). In fact, Tian *et al.* (2005) showed that approximately 7 % of the Arabidopsis genome is up- or down-regulated in *athda19* mutants. For example, Tian *et al.* (2003) showed that *hda19* mutant lines were affected in their flowering process under long day conditions, exhibiting the opposite phenotype of mutants altered in the expression of the histone acetyltransferase GCN5. Interestingly, the double mutant *gcn5:hda19* is characterized by a normal phenotype in response to light, suggesting that both HDA19 and GCN5 could target the same genes. This was shown by Benhamed *et al.* (2006): a reduced histone acetylation was monitored in the promoter of *CAB2*, *RBCS-1A* and *IAA3* genes in the *gcn5* mutants, whereas an increase histone acetylation was observed in the promoter of the same genes in the *hda19* mutants. Furthermore AtHDA19 expression is strongly induced in response to wounding and the stress related hormones JA and ethylene, suggesting that it could be involved in many abiotic stresses leading to the production of both compounds (Zhou *et al.*, 2005). AtHDA19 was also reported to be involved in response to abiotic through its interaction with the transcription corepressor LEUNIG by repressing gene transcription (Gonzalez *et al.*, 2007). In the same way, overexpression of AtHDA19 in *Brassica napus* demonstrated that it was involved in response to cold stress by interacting with bnKCP1, a novel protein containing a putative kinase-inducible domain (Gao *et al.*, 2003).

AtHDA6, another RPD3-type histone deacetylase in *A. thaliana*, is involved in response to ABA and salt stress. Chen *et al.* (2010) showed that an AtHDA6 mutant, *axe1-5*, as well as HDA6 RNA-interfering plants are hypersensitive to salt and ABA treatment, due to the down-regulation of various abiotic stress responsive genes like *ABI1*, *ABI2*, *RD29A* or *RD29B*. This hypersensitivity to salt stress is correlated with changes in H3 acetylation pattern. Without ABA treatment, an increase of H3 acetylation was shown both in the promoter and in exons of these genes in the *axe1-5* mutant compared to Col0. In response to ABA, an increase of H3 acetylation was only monitored in Col0 but not in the *axe1-5* mutant, indicating that HDA6 is required for the induction of acetylation by ABA and salt treatment. A similar phenotype was obtained with the *A. thaliana* HDA19 T-DNA insertion mutant, *hda19-1* (Chen and Wu, 2010). On the contrary, other RPD3 HDAC like AtHDA7 are not differentially expressed in regard to developmental stages but are induced in response to both biotic (*Pseudomonas syringae*) and abiotic stimuli such light intensity or heat stress, according to microarray data analyses (Alinsug *et al.*, 2009).

Little information is available regarding the properties of HDA1-like HDACs in plants. The study of one member of this family in maize, ZmHDA1, reported that it is expressed in an inactive form of high molecular weight (84-kDa) that needs to be processed in an active form of 48-kDa by a proteolytic cleavage of the C-terminal end to regulate gene transcription (Pipal *et al.*, 2003). According to the data of the sequenced genomes, *A. thaliana* contains five members of the HDA1 group also termed class II. Members of this Class II are also involved in response to various environmental stresses: while heat stress seems to upregulate most of the Class II HDAs, NaCl treatment only stimulates AtHDA14 and AtHDA2 expression (Alinsug *et al.*, 2009). Furthermore, AtHDA18 expression is induced in response to cold treatment. Demetriou *et al.* (2009) reported that members of this HDAC family in Barley are also regulated by JA in response to abiotic stresses: whereas *HvHDAC1-I-1* is slightly reduced after 6 hr of treatment, other genes like *HvHDAC1-II-1* or *HvHDAC1-IV-1* are strongly accumulated after 6 hr.

The SIR2-like HDACs are characterised by their NAD-dependent histone deacetylase activity. They are homolog to the yeast SIR2 HDAC that is involved in longevity (Imai *et al.*, 2000). Although the genome of all sequenced plants contains several Sir2-like genes, their functions are yet to be determined. A recent study in *A. thaliana* showed that AtSIR2 regulates several defence related genes involved in the synthesis of SA, implying potentially SIR2 members in plant defence reactions (Wang *et al.*, 2010). To our knowledge, only one study recently reported the involvement of SIR2 in response to low temperature in the context of vernalization (Bond *et al.*, 2009). SIR2 class of HDAC would repress the expression of the MADS box transcription factor *FLC* (for Flowering Locus C, a central gene in the vernalization process) by altering the acetylation pattern of histones H3 and H4.

The last HDAC family, termed HD2-like, is specific to plants and do not share any sequence similarities with other HDAC proteins (Pandey *et al.*, 2002). Three genes HD2 HDAC genes /or homologues are coded in maize genome, four in *A. thaliana*, two in rice and in barley. All HD2 display similarities with the FKBP family peptidyl-propyl cis-trans isomerase (Aravind and Koonin, 1998; Dangl *et al.*, 2001) and display the same architecture: a conserved EFWG motif in the N-terminal region that comprises the catalytical domain, a central acidic domain involved both in enzymatic activity and its regulation, and in the C-terminal part a NLS and a Zn<sup>2+</sup> finger that may be involved in protein/protein or protein/DNA interactions. Several members of this family like ZmHD2 in maize and AtHD2A in *A. thaliana* were shown to be localized in the nucleolus and to deacetylate the lysine 9 of histone H3, suggesting that they should be involved in the regulation of ribosomal RNA expression (Lusser *et al.*, 1997; Earley *et al.*, 2006). However their mode of action is still largely unknown; they seem to be mainly involved in plant defence reactions (Bourque *et al.*, 2011) and in seed development (Wu *et al.*, 2000). In *A. thaliana*, Sridha and Wu (2006) showed that overexpression of *AtHD2C* enhances tolerance to salt stress and drought compare to wild-type plants by affecting the expression of several abscisic acid-responsive genes. However, we do not know whether or not it affects the acetylation of these genes.

### 3.2 Histone acetyltransferases (HATs)

The action of the HDAC proteins is reversed by the one of the HATs that catalyse the transfer of an acetyl group from acetyl~SCoA to the amine function of a lysine residue, particularly in histone proteins (Servet *et al.*, 2010). Like HDACs, HATs are divided into several groups based on primary homology with yeast and mammalian HATs: GNAT (for GCN5-related N-acetyltransferase), MYST (for MOZ, Ybf2/Sas2 and Tip60), p300/CBP (for CREB-binding protein) and TAF1 (for TATA-binding protein (TBP)-associated factor 1) groups. The GNAT group is usually subdivided into three subfamilies termed GCN5 (for General Control Nonderepressive protein 5), ELP3 (for transcriptional ELongator complex Protein 3) and HAT1. In a structural point of view, HATs are usually constituted by two fundamental domains: the catalytical acetyltransferase domain, and the bromodomain. The bromodomain is composed of 110 aminoacids that can bind to acetylated lysine residues (Owen *et al.*, 2000). Bromodomains are generally found in proteins that regulate chromatin structure and gene expression, such as HATs and the ATPase component of certain nucleosomes-remodeling complexes. The mode of recognition of acetyl-lysine by the bromodomain is similar to the one of acetyl~SCoA by HATs, since the bromodomain is the only domain known to interact with acetylated lysine containing peptides. Among the

different HATs expressed in *A. thaliana*, AtGCN5/HAG1, which belongs to the GNAT HAT family, is one of the best characterized in terms of function and is involved both in abiotic and developmental responses (see Servet *et al.*, 2010 for a recent review). Regarding its specificity, the major targets of this HAT are histone H3 (H3K9, H3K14, H3K18 and H3K27) and histone H4 (H4K5, H4K8, H4K12 and H4K16; Zhang *et al.*, 2007). The bromodomain of AtGCN5, that was shown to bind to acetylated histone lysine motifs, is probably not required for its binding to most of its targets (Benhamed *et al.*, 2008). Among its targets, in addition to histones H3 and H4, AtGCN5 also interacts and acetylates other proteins such as AtADA2 that could regulate HAT activity (Servet *et al.*, 2010). Furthermore, AtGCN5 activity could be regulated by phosphorylation/dephosphorylation, since it interacts with protein phosphatase 2C *in vitro* and mutation in PP2C gene increases H3K14 acetylation, one of the targets of AtGCN5. The other HAT proteins are less characterized in terms of target and mode of action.

Works in the group of D.X Zhou have shown that AtGN5 is required for light-regulated gene expression by promoting the acetylation of the promoter of target genes (Benhamed *et al.*, 2006; Benhamed *et al.*, 2008; Servet *et al.*, 2010). Several studies reported that abiotic stresses involve the association/regulation of HAT activities with various proteinaceous partners in the regulation of specific genes leading to the establishment of the biological response. For example, the GCN5 HAT is known to physically interact with the transcriptional coactivator Ada2 (Stockinger *et al.*, 2001), this one enhancing the ability of GCN5 to acetylate histones *in vitro* and enabling GCN5 to acetylate nucleosomal histones (Mao *et al.*, 2006). Hark *et al.* (2009) showed that mutants of one of both ADA2 genes, ADA2b, display hypersensitive phenotype to salt stress and altered responses to low temperature stress, a phenotype close to the one of AtGCN5 mutants. A recent study showed that ADA2b and GCN5 interact with a third partner, the coactivator SGF29a, to enhance the acetylation in the promoter region of target genes like COR6.6, RAB18, and RD29b (Kaldis *et al.*, 2011). In the same vein, Gao *et al.* (2007) showed that AtGCN5 HAT activity is required in response to cold and stress treatment by its physical interaction with the transcription factor AtEML. The authors suggest that AtEML would co-ordinates the expression of target stress regulated genes through involvement in recruiting AtGCN5 to their promoters.

#### 4. Protein methylation

Protein methylation involves transfer of a methyl group from S-adenosylmethionine (the universal methyl donor in cells) to acceptor groups on substrate proteins (Aletta *et al.*, 1998). It commonly occurs on carboxyl groups of glutamate, leucine, and isoprenylated cysteine, or on the side-chain nitrogen atoms of lysine, arginine, and histidine residues (Clarke, 1993). In eukaryotes nuclei, one of the best known examples of protein methylation is probably histone methylation. Like acetylation, histone methylation is considered as an important process regulating the chromatin dynamics and function (Strahl and Allis, 2000; Jenuwein and Allis, 2001; Zhang and Reinberg, 2001; Kouzarides, 2002). Histone methylation can occur at different residues and on distinct sites. For one residue, different numbers of methyl groups can be added. Even if some methylation has been characterized in the globular domain of H3 in animals (Feng *et al.*, 2002), methylation seems to concern most of the time the N-terminal part of histones (named histone tail) (Bannister and Kouzarides, 2005). Histones methylation has been described mainly on histones H3 and H4 and occurs on both arginine and lysine residues.



#### 4.1 Histone lysine methylations

Lysine methylation consists on addition of one or more methylgroups to the  $\epsilon$ -amino group of lysine residues, resulting in mono-, di-, or trimethylated lysine. Unlike acetylation, methylation of these residues does not change the charge but progressively increases the bulk and hydrophobicity. This may impact intra- or intermolecular hydrogen-bond interactions of the amino group or create new sites recognized by reader proteins that bind preferentially to the methylated domain (Lee *et al.*, 2005). In eukaryotes, histone lysine methylation occurs on histone H3 at lysines 4, 9, 14, 27, 36, and 79 and on histone H4 at lysines 20 and 59 (Strahl and Allis, 2000; Berger, 2002; Zhang *et al.*, 2002; Zhang *et al.*, 2003). A recent study provide evidences that methylation can also occurs on Lysine 37 of histone H2B *in vivo* (Gardner *et al.*, 2011).

In *A. thaliana*, the best known histone lysine methylation occurs at Lys4 (K4), Lys9 (K9), Lys27 (K27), and Lys36 (K36) of histone H3 while methylation on lysine 20 of H4 has only been observed with immunostaining. Presence of methylation on H3 K79 which is highly conserved in non-plant systems has not been reported in plant. Methylations of lysine are catalyzed by HKMTs (histone lysine methyltransferases) that almost all share a SET [Su(var), Enhancer of zeste, trithorax] domain, a conserved motif containing approximately 130 amino acids which was originally identified in *Drosophila*. This domain is responsible for catalysis and binding of cofactor S-adenosyl-lmethionine (Lee *et al.*, 2005). Plant genome encodes number of protein with set domain; for example, *A. thaliana* genome encodes 41 while grapes encode 32 and maize 37 (<http://www.chromdb.org>). Function of their homology with their *Drosophila* homologues E(Z), TRX, ASH1 and SU(VAR)3-9, they are assigned to four groups (Jenuwein *et al.*, 1998). In *A. thaliana*, certain families of HKMTs seem to catalyse methylation on one particular site. It is the case for HKMTs homologues of SU(VAR)3-9 that are acting on H3K9 and for HKMTs relative to E(Z) that methylate H3K27. E(z) proteins are associated with other members in PRC2 (polycomb-group repressive complex 2) to performed H3K27 methylation. Members of other families seem to be able to act at different sites. It is the case of TRX homologue where different members can contribute to methylation of H3K4 or H3K27. Also ASH1 (for Absent, Small, or Homeotic discs 1) family seems to act on both H3K36 and H3K4. Nevertheless the link between this protein and histone methylation can be direct or indirect since methyl transferase activity has been not tested for all members of these different families (for review Liu *et al.*, 2010). Methylated lysine can be then recognized by protein reader leading in a direct or indirect way to a particular function like gene silencing (Schotta *et al.*, 2002; Jackson *et al.*, 2004). These proteins comported domain that can recognized methylated lysine such as chromolike domains of the royal superfamily (including chromodomain, tudor domain, malignant brain tumor (MBT), PWWP, and plant Agenet module), or a plant homeodomain finger (PHD) or the WD40 repeat (Taverna *et al.*, 2007). At this time only fews readers are known in plants and the way by which they translate the histone marks to direct downstream functions it is not fully understood.

#### 4.2 Stoechiometrie and localization of histone lysine methylation in plant

In plants like in animals the three degrees of methylation (mono, di et trimethylation) on histone H3 at lysines 4, 9, 14, 27, 36 are found but proportions between the different degrees change. For example in *A. thaliana*, higher levels of H3K4 di-methylation (H3K4me<sub>2</sub>) and lower H3K9me<sub>2</sub> and H3K9me<sub>3</sub> levels have been detected compare to animals (Jackson *et al.*,



2004; Guo *et al.*, 2006). Histones methylation profile has mainly be determined in *A. thaliana* thanks to Immunostaining of nuclei, chromatin immunoprecipitation (ChIP) , ChIP coupled with high-resolution microarray analysis (ChIP-chip) and mass spectrometry in combination with high-performance liquid chromatography (HPLC) separation methods (Liu *et al.*, 2010). H3K4me1/2/3 are highly enriched in euchromatin in *A. thaliana* and about 90 % of annotated genes carry one or more of the H3K4 methylation marks, suggesting an important role of this histone modification in the control of gene expression (van Dijk *et al.*, 2010). H3K9 methylation is critical for maintenance of transcriptional gene silencing and genome stability (Vaillant and Paszkowski, 2007). H3K9me1 and H3K9me2 are predominant and enriched in heterochromatin (Johnson *et al.*, 2004) while H3K9me3 is enriched in euchromatin (Mathieu *et al.*, 2005; Turck *et al.*, 2007). H3K9me2 is particularly present in transposons and repeated sequences according to the repressing transposon activities that have been attribute to this histone mark (Lippman *et al.*, 2004; Bernatavichute *et al.*, 2008). H3K27me1 and H3K27me2 are enriched in heterochromatin (Mathieu *et al.*, 2005; Fuchs *et al.*, 2006) while H3K27me3 is localized in euchromatin (Turck *et al.*, 2007). H3K27me3 is found in about 4400 genes and is often localized upstream of promoters and of 5'UTR suggesting like for H3K4, an important role of this methylation in controle of gene expression in plant (Turck *et al.*, 2007; Zhang *et al.*, 2007). H3K36me1/3 are enriched in euchromatin while H3K36me2 is present in both euchromatin and heterochromatin (Lin *et al.*, 2008).

### 4.3 Histones arginine methylation

Arginine methylation can impact histone and more generally protein properties. In fact, arginine is a positively charged amino acid that has five potential hydrogen bond donors positioned for favorable interactions with biological hydrogen bond acceptors (Bedford and Clarke, 2009). These biochemical properties give to this amino acid a crucial role for protein structure and interaction with other molecules. In proteins interacting with DNA, arginine residues are the most frequent hydrogen bond donors to backbone phosphate groups and to thymine, adenine, and guanine bases (Luscombe *et al.*, 2001). Protein arginine methylation results in the addition of one or two methyl groups to the guanidino nitrogen atoms of arginine (Gary and Clarke, 1998). Each addition of a methyl group to an arginine residue changes its form and removes a potential hydrogen bond donor (Bedford and Clarke, 2009). Since no protein able to interact with histone arginine methylation are known, it is possible that the only fact of methylate arginine is to impact interaction between histones and DNA, leading to an impact of chromatin structure and finally of gene expression.

In Eukaryotes, the best known arginine methylation concerned Arg2 (R2), Arg8 (R8), Arg17 (R17), Arg26 (R26) of histone H3, and Arg3 (R3) of histone H4. In *A. thaliana*, at this time only methylation on H4R3 and H3R17 have been detect *in vivo*. Protein arginine methylation is catalyzed by a family of protein named arginine methyltransferases (PRMTs). PRMTs are classified into four classes depending of the final methylated product of reaction that they can catalyze. Type I and type II enzymes are among others, involved in histone methylation and are one of the best characterized (Bedford and Richard, 2005). Both of them catalyze first addition of single methyl group on the terminal nitrogen atom of Arginine to form Mono methylated Arginine (MMA). Then, Type I PRMTs form asymmetric di-methylated Arg meaning that two methyl groups are added on the same nitrogen atom of the guanidine leading to an  $\omega$ -NG,NG-di-methyl arginine, while type II PRMTs performed symmetric

dimethylation of Arg meaning that the two methyl groups are on two different nitrogen atoms leading to an  $\omega$ -NG,N\_G-d i-methyl arginine (Mitchell *et al.*, 1992). *A. thaliana* genome codes for nine PRMTs (Niu *et al.*, 2007). AtPRMT4a and AtPRMT4b, are homologs of human CARM1 and can be performed asymmetrically H3R17me2a *in vivo*. H4R3 can be di-methylated symmetrically by AtPRMT5/SKB1 (Pei *et al.*, 2007; Wang *et al.*, 2007; Schmitz *et al.*, 2008) and asymmetrically by AtPRMT1a, AtPRMT1b (Yan *et al.*, 2007) and AtPRMT10 (Niu *et al.*, 2007).

#### 4.4 Histones demethylation

Histone methylation has been considered as irreversible until the discovery in 2004 of LSD1 (lysine-specific demethylase 1) in animals (Shi *et al.*, 2004). This discovery proved that histone methylation is a dynamic process regulated by HMTs (the writers) but also histones demethylases (the erasers). Two types of demethylases exist with distinct mechanisms to remove lysine methylation: Flavin adenine dinucleotide (FAD)-dependent KDM1/LSD act by amine oxidation and need the cofactor Flavin adenine dinucleotide. JmjC domain-containing proteins act by hydroxylation and most of them use Fe(II) and  $\alpha$ -ketoglutarate (Shi *et al.*, 2004; Tsukada *et al.*, 2006). These two classes of enzymes act on different substrates: Flavin adenine dinucleotide (FAD)-dependent KDM1/LSD1 are able to demethylate mono and dimethylation while JmjC domain-containing proteins demethylase act one mono-di and tri methylated lysines (Klose and Yi, 2007). In *A. thaliana*, potential histone demethylases have been predicted based on conservation of cofactor-binding amino acids (Lu *et al.*, 2008). There are four KDM1/LSD1 homologs in *A. thaliana* and one of them, LDL1, has been shown to demethylate di- and mono-methylated H3K4 (Spedaletti *et al.*, 2008). *A. thaliana* genome also contains 21 JmjC domain-containing proteins (JMJs). These JMJs are grouped into five subfamilies according to sequence similarities. The biochemical properties and biological functions of histone demethylases are emerging and how these enzymes work, are recruited to their target loci, and play roles are still largely unknown (Liu *et al.*, 2010).

In animals, H3 and H4 arginines can be desiminate by PADI4 (peptidyl arginine deiminase 4). Deimination could be antagonist of arginine methylation since citrulline prevents arginine from being methylated (Cuthbert *et al.*, 2004). Moreover it could be a way to remove methylation of arginine. In fact, monomethylated arginine could be converted to citrullin by PADI4 (Wang *et al.*, 2004). In addition a family of amine oxidases may be able to demethylate arginine residues using a similar mechanism as they demethylate lysine residues (Bedford and Richard, 2005). In plant, arginine demethylation process is still unknown.

#### 4.5 Histone methylation in responses to abiotic stresses

Abiotic stresses modulate expression of different genes. As it has been explained before, gene regulation can be due to chromatin remodeling involving histone modification. In plants, modification of histone methylation occurs during stress responses even if the mode of action and consequence of these changes are still not well understand. These modifications could control stress relative genes. For example, hundreds of stress-responsive genes are targets for H3K27me3 in *A. thaliana* (Zhang *et al.*, 2007).

During a cold stress, methylation of H3K27me3 gradually decreases at the loci of two cold-responsive genes, COR15A and AtGolS3 while expressions of genes increase. Even if Tri-methylation of histone H3 Lys27 (H3K27me3) is generally considered as a negative marker of transcription (Zhang *et al.*, 2007), the link between reduction of H3K27me3 and increase of transcription seems to be not obvious in this case : first COR15A and ATGOLS3 are not

targets for LHP1 (Zhang *et al.*, 2007), an *A. thaliana* protein that binds H3K27me3 *in vitro* (Zhang *et al.*, 2007; Exner *et al.*, 2009) and that has been shown to be required for silencing of genes with H3K27me3 (Mylne *et al.*, 2006; Sung *et al.*, 2006; Zhang *et al.*, 2007; Exner *et al.*, 2009). Also, when cold-exposed plants are returned to normal growth conditions, transcription of COR15A and ATGOLS3 was repressed to the initial level before cold exposure while decrease in H3K27me3 is still maintained. Also, this decrease does not enhance the induction of transcription when plants are returned to cold temperatures (Kwon *et al.*, 2009). According to these results, it has been proposed that H3K27me3 could act as a memory marker for recent transcriptional activity in *A. thaliana*. In this case, previous exposure of plants to certain environmental stresses may negatively affect the level of H3K27me3 and lower the chance of stress-responsive genes being silenced.

Dehydration stress also induces variations on histone methylation. In fact, histone H3 modifications at the coding regions of four dehydration stress responsive genes, RD29A, RD29B, RD20, and an AP2 transcription factor have been reported during a drought stress in *A. thaliana* (Kim *et al.*, 2008), characterized by an enrichment of H3K4me3 and H3K9ac (a positive marker of gene activation) at these four loci. Another study presents the whole-genome distribution patterns of histone H3 H3K4me1, H3K4me2, and H3K4me3 and its modification after a drought stress in *A. thaliana*. While H3K4me1 and H3K4me2 levels changed modestly during dehydration stress, drastic changes in the H3K4me3 levels are observed. These changes are correlated with modification in level of transcription of responding genes: a large increase of H3K4me3 level was found on nucleosomes of the genes which had a high expression and a large decrease in H3K4me3 levels has been reported in highly down-regulated genes (van Dijk *et al.*, 2010). By analyzing the H3K4me3 distribution profiles on nucleosomes of stress-induced genes, this study provided specific chromatin pattern associated with many genes involved in dehydration stress response and confirm the putative role of H3K4me3 in transcription activation.

The *A. thaliana* SKB1 protein is a type II Arg methyltransferase homologue to PRMT5 in mammals that catalyzes Arg symmetric dimethylation H4R3me2. SKB1 is associated to chromatin region of FLC promoting flowering by suppressing its expression through H4R3me2 (Wang *et al.*, 2007; Schmitz *et al.*, 2008). SKB1 is also associated in chromatin of other genes involving among others in stress responses like HAB1, who is really important in ABA and salt stress (Saez *et al.*, 2004; Saez *et al.*, 2006) where it represses transcription through H4R3me2. Salt stress and ABA treatment (that is accumulated under a salt stress) lead to dissociation of SKB1 from chromatin leading to a reduced level of H4R3me2 and to an higher expression of genes in ABA and salt response like HAB1, suggesting a direct mechanism by which salt and ABA impact gene transcription (Figure 3). This theory is supporting by the fact that SKB1 invalidation leads to a decrease of H4R3me2 levels, an increase of HAB1 and some other stress-responsive gene expression and a bigger susceptibility to salt stress (Zhang *et al.*, 2011). During a salt stress, SKB1 not only leaves chromatin of some loci but also methylates U6 small nuclear ribonucleoprotein (snRNP)-specific Sm-like protein LSM4. SKB1 invalidation leads to splicing defects in hundreds of genes that are involved in many biological processes, including the abiotic stress responses. Furthermore, *lsm4* mutant, similarly to *Skb1*, is hypersensitive to salt and shows similar splicing defects in some genes (Zhang *et al.*, 2011). In conclusion, SKB1 plays a dual role in salt response by altering the methylation status of H4R3me2 and LSM4.

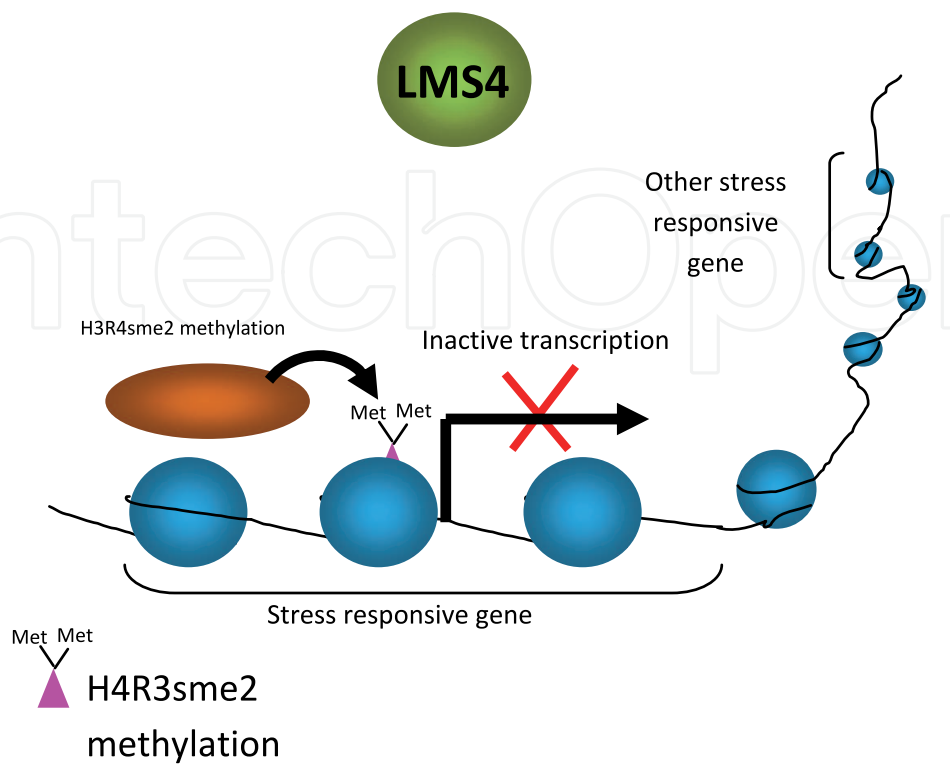
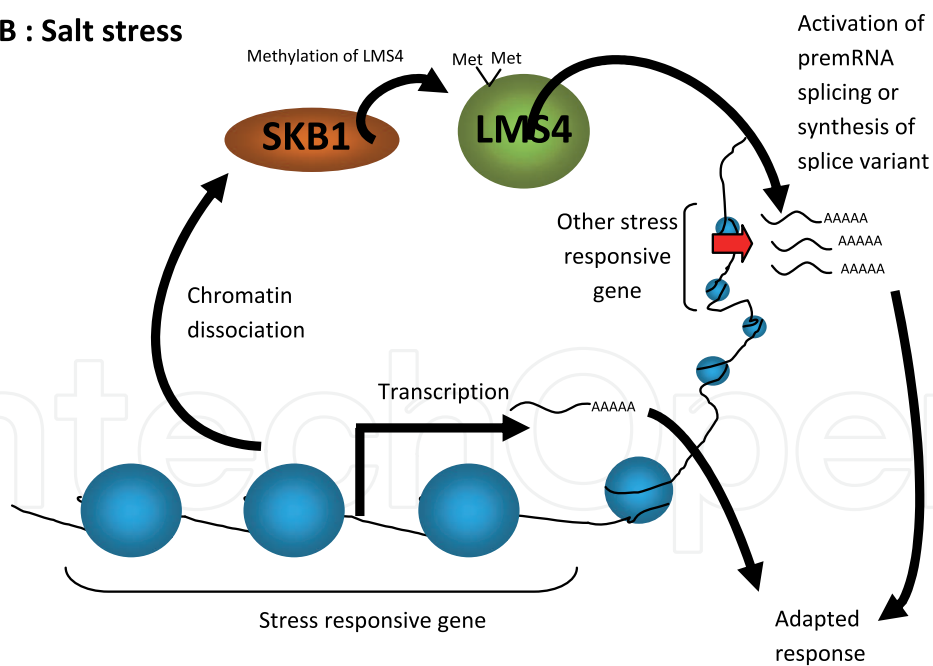
**A : No stress****B : Salt stress**

Fig. 3. Involvement of methylation in salt stress responses. A : Without stress, SKB1 a PRMT is associated to the chromatin of some stress related genes where it methylates histone on H4R3sme2. These methylations are repressive mark leading to transcription inactivation of these genes. B: During a salt stress, there is a chromatin dissociation of SKB1. This dissociation has a dual role in stress related gene control to insure an adapted response: Firstly SKB1 do not maintains H3R4sme2 in the loci where it was associated leading to an



higher expression of many stress relative genes. Secondly, SKB1 will methylated another protein LMS4 connected to splicing. This last methylation leads to an activation of premRNA splicing and /or synthesis of splice variant of some other genes connected to stress responses.

## 5. Redox modification of nuclear proteins

### 5.1 ROS and RNS in the nucleus

Reactive oxygen species (ROS) are chemically reactive species of oxygen formed by successive one-electron reduction of molecular oxygen. It includes superoxide anion ( $O_2^{\cdot-}$ ), hydrogen peroxide ( $H_2O_2$ ), perhydroxyl radical ( $HO_2^{\cdot}$ ) and the highly reactive hydroxyl radical ( $OH^{\cdot}$ ) (Apel and Hirt, 2004). ROS is produced in different organelles such as mitochondria, chloroplast, peroxisome, endoplasmic reticulum and in the cytosol (Gill and Tuteja, 2010) but to our knowledge, only one study has described ROS accumulation in the nucleus, in response to an elicitor of plant defense (Ashtamker *et al.*, 2007). However, recent data indicate that plant cell nucleus possesses antioxidant redox system to control ROS homeostasis (Pulido *et al.*, 2009a; Pulido *et al.*, 2009b). Furthermore, ROS production in other cellular compartments results in changes in gene expression, indicating that ROS production can influence gene transcription in the nucleus. Another reactive radical, Nitric Oxide (NO), has been known for years as a signaling molecule in animal and plant cells (Besson-Bard *et al.*, 2008). Reactive Nitrogen Species (RNS) contains all the NO derived molecules and their chemistry have been documented elsewhere (Stamler *et al.*, 1992). For instance, NO can be oxidized or reduced to  $NO^+$  or  $NO^-$  or can react with  $O_2^{\cdot-}$  to form the strong oxidant peroxynitrite ( $ONOO^-$ ). Through its different chemical forms, NO can react with a great variety of molecules including proteins, lipids, metals, molecular oxygen or nucleic acids. Evidences for NO production in the nucleus of various plant cell types (stomata guard cells, stomata subsidiary cells, epidermal cells) have been documented in some studies in response to different stimuli such as heat stress, green light, osmotic stress, plant defense elicitors (Foissner *et al.*, 2000; Gould *et al.*, 2003; Vitecek *et al.*, 2008). As observed for ROS, NO can have an impact on gene expression (Palmieri *et al.*, 2008).

### 5.2 Redox-based post-translational modification in plant cell nuclei

ROS and RNS could affect gene expression through different mechanisms. These reactive compounds can activate components of signaling pathways controlling gene expression or can directly affect the DNA binding activity of several kinds of transcription factors. Heat shock transcription factors (HSF) bind to a consensus sequence found in the promoter of many stress-responsive genes. HSF transcription factors have been thought to be ROS sensors as reviewed by (Miller and Mittler, 2006). Other transcription factors are regulated in a redox dependent manner through a dithiol/disulfide exchange and some examples are detailed below.

The activity of transcription factors from the R2R3 MYB family have been shown to be involved in abiotic stress responses including salt stress, drought stress (Jung *et al.*, 2008). Using the typical R2R3 MYB protein P1 from *Zea mays*, Heine *et al.* (2004) have shown that DNA binding of this transcription factor is redox-dependent. More precisely, the two cysteines residues 49 and 53 are necessary for DNA binding and under non-reducing conditions, they formed a disulfide bridge that prevents DNA binding. Another R2R3 MYB



plant transcription factor of *A. thaliana*, AtMYB2, has been shown to be redox-modulated (Serpa *et al.*, 2007). AtMYB2 has been suggested to play a role in response to stresses that induce NO production such as ABA or salt treatment. Contrary to P1, cysteine 49 is absent in AtMYB2 (Heine *et al.*, 2004) and the S-nitrosylation of Cys 53 by NO donors blocks its binding to a specific DNA sequence (Serpa *et al.*, 2007). In this case, it indicates that the S-nitrosylation of AtMYB2 could be a mechanism to turn off the activity of this protein. However, the role of the redox regulation of R2R3 MYB transcription family protein needs to be addressed *in vivo* in response to abiotic stresses.

The DNA binding of RAP2.4a (At1g36060), a AP2/DREB-type transcription factors, to the promoter of 2-Cys peroxiredoxin-A gene (2CPA) is redox-regulated by dithiol/disulfide transition of regularoty cysteinyl residues (Wormuth *et al.*, 2007; Shaikhali *et al.*, 2008). Reducing conditions lead to the monomerisation of RAP2.4a whereas oxidizing conditions dimerize or oligomerize RAP2.4a proteins through the formation of disulfide bridges which increased binding affinity of the protein to DNA. Loss-of-function of *RAP2.4a* affects the adaptation of plants to changes in environmental conditions such as naturally fluctuating light conditions. Furthermore, RAP2.4a transcription factor regulates the expression of genes known to be induced by ROS and involved in abiotic stress tolerance such as ZAT 10 (Mittler *et al.*, 2006). A closed homologue, RAP2.4b (At1g78080) has also been involved in stress response. Mutations in *RAP2.4b* cause altered expression of light and drought-responsive genes and defects in developmental processes or drought tolerance. However, its redox control as observed with RAP2.4a has not been investigated.

In the last decades, studies in the animal field have indicated that the main mode of action of NO is based on the post-translational modification of proteins. Firstly, S-nitrosylation consists of the oxidation by NO of reduced sulfidryl groups of cysteins residues of proteins thus forming a nitrosothiol (SNO). Secondly, tyrosine nitration is based on the addition of a NO<sub>2</sub> group on a tyrosyl residue of a protein. And thirdly, NO can bind covalently transition metal of metalloproteins. This last process is called metal nitrosation. These NO-based post-translational modifications of proteins finally affect the activity of the modified proteins. While thousand proteins have been identified in animals to be modified by NO, only a few have been characterized in plants (Astier *et al.*, 2011; Seth and Stamler, 2011). Among them, some are linked with the nucleus function. The best example on the role of NO in the modification of proteins associated with nuclear functions is the transcription coactivator NPR1 (for Non-expressor of Pathogenesis Related-1) in *A. thaliana*. Although data indicate that NPR1 is important for plant resistance to abiotic stresses (Quilis *et al.*, 2008; Yasuda *et al.*, 2008; Rao *et al.*, 2002), its mode of action and its regulation have been discovered in plants infected by avirulent pathogens or treated by elicitors of plant defense reactions. In untreated cells, NPR1 forms a homo multimeric complex that is sequestered in the cytosol and stabilized by intermolecular disulphide bonds (Mou *et al.*, 2003). In this case, NPR1 monomers still exist. To prevent target gene activation in the absence of inducing stimulus, they are translocated to the nucleus at low rate and finally targeted to the proteasome (Spoel *et al.*, 2010). A role of NO in this process has been recently discovered. It was reported that S-nitrosylation of NPR1 by S-nitrosoglutathione (GSNO) at cysteine-156 facilitates its oligomerization and blocks its nuclear translocation (Tada *et al.*, 2008). After the perception of stimuli such as pathogen infection, redox changes dependent on the production of salicylic acid occur. Multimeric NPR1 is reduced to monomers by thioredoxins and NPR1 monomers are then translocated to the nucleus where their interaction with transcription

factors allowed the regulation of the expression of several genes (Despres *et al.*, 2003; Tada *et al.*, 2008; Fan and Dong, 2002; Boyle *et al.*, 2009). Particularly, NPR1 activates the binding of the b-ZIP transcription factor TGA1 to the activation sequence-1 (as-1) element of the promoter region of defense genes. Disulfide bridge formation involving cysteyle residues 260 and 266 precludes the interaction of TGA1 with NPR1 and then prevents binding of TGA1 to its target DNA element (Despres *et al.*, 2003). Recent mass spectrometry analysis indicated that these cysteyle residues of TGA1 are S-nitrosylated and S-glutathionylated after GSNO treatment (Lindermayr *et al.*, 2010). Furthermore, GSNO enhanced the DNA binding activity of TGA1 to its DNA element in the presence of NPR1. It can be the consequence of conformational changes of both proteins which allow a more effective TGA1-NPR1 interaction and finally a more effective DNA-binding of TGA1. Interestingly, a GSNO-induced nuclear translocation of NPR1 has also been observed by these authors. It could be due to SA-mediated redox-changes since NO induced SA production (Durner *et al.*, 1998; Huang *et al.*, 2004). All these results indicate that NO has a major regulatory role of NPR1 functions by controlling its translocation from the cytosol to the nucleus and by affecting the NPR1/TGA1 complex and downstream dependent responses. Other proteins might be involved in this process. The small oxidoreductases glutaredoxins that mediate redox regulation of proteins through the reduction of disulphide bridges or the glutathionylation of cysteyle residues (Dalle-Donne *et al.*, 2009; Rouhier *et al.*, 2010) has been recently shown to interact with transcription factors from the TGA family in the nucleus of plant cells (Ndamukong *et al.*, 2007; Li *et al.*, 2009). However, the role of GRX in TGA function has not been described yet.

Another protein is redox-modified by NO. In a recent paper, Wawer *et al.* (2010) have shown that *Nicotiana tabacum* GAPDH (glyceraldehyde-3-phosphate dehydrogenase) localized in the nucleus and in the cytosol of plant cells. GAPDH was transiently S-nitrosylated after the salt treatment of *N. tabacum* cell suspensions but the role of this NO-dependent modification is not known.

## 6. Ubiquitin and ubuquitin-like post-ranslational modifications

Protein post-translational modifications by ubiquitin and ubiquitin-like proteins are essential for a plethora of cell functions in eukaryotic cells and are involved in development processes but also in the responses to biotic and abiotic stresses (Fu *et al.*, 2010; Miura and Hasegawa, 2010; Trujillo and Shirasu, 2010). Ubiquitination is a post-translational modification of proteins corresponding to the reversible attachment of the 76-amino acid protein ubiquitin to target proteins through a well-characterized process (Fu *et al.*, 2010). This three-step enzymatic cascade is catalyzed by ubiquitin-activating enzyme (E1), ubiquitin-conjugating enzyme (E2) and ubiquitin ligase enzyme (E3). A major function of protein ubiquitination is to address proteins to the proteasome for their degradation. However, it can also control intracellular localization of proteins, transcription of DNA and cell cycle. Thus, ubiquitination regulates a great number of cellular processes. There are evidences that the ubiquitination system is involved in regulating signaling pathways controlling plant adaptation to stresses and especially abiotic stresses. Some proteins belonging to the ubiquitination enzymatic machinery and involved in abiotic stress tolerance have been shown to localized in the nucleus of plant cell. AtHOS1, a E3-ubiquitin ligase that control cold tolerance in *A. thaliana* have been shown to localized in the nucleus after cold stress (Lee *et al.*, 2001, see below). Furthermore, AtDRIP1 and AtDRIP2 (DREB2A-

interacting protein) are two E3-ubiquitin ligase (Qin *et al.*, 2008). AtDRIP1 is localized in the nucleus of *A. thaliana* cells where it interact with AtDREB2A (Dehydration-responsive element binding protein 2A), a transcription factor that is important for drought tolerance and controls the expression of water deficit-inducible gene expression. As proposed by (Qin *et al.*, 2008), the ubiquitination of AtDREB2A may occur in a no-stress condition leading to its degradation by the proteasome. However, during drought stress, AtDREB2A is activated by an unknown mechanism. It is possible that the ubiquitination and degradation of AtDREB2A is blocked leading to the accumulation of effective AtDREB2A protein that in turn activate the expression of drought-responsive genes. This result highlights the importance of ubiquitination process in controlling gene transcription in the nucleus.

In addition to ubiquitin, post-translational modification of proteins by ubiquitin-like proteins (Ubls) such as SUMO (small ubiquitin-like modifier), RUB (related to ubiquitin), NEDD8 (neural precursor cell expressed, developmentally down-regulated), ATG8 and ATG12 (autophagy 8 and 12) have been shown to be functional in plants and to control essential cellular processes as observed in other eukaryotes (reviewed by (Miura and Hasegawa, 2010). Among them, modification of proteins by SUMO (SUMOylation) has been one of the most described Ubl-post-translational modifications in plants. SUMO proteins are synthesized as precursors that need to be cleaved by specific proteases to expose a glycyl residue necessary for their ligation to target proteins. The addition of SUMO proteins to a lysyl residue of the target protein is catalyzed in a three-step enzymatic reaction similar to ubiquitinylation (Kurepa *et al.*, 2003).

In *A. thaliana*, genetic analysis of SUMOylation process indicates that this post-translational modification of proteins is essential for plant development. Thus, mutation in the gene coding AtSCE1 (Arabidopsis Sumo-conjugating Enzyme1) or AtSAE2 (Arabidopsis Sumo-activating Enzyme 2) proteins results in embryo lethality (Saracco *et al.*, 2007). The same phenotype was observed in plants in which the genes coding both AtSUMO1 and AtSUMO2 proteins were mutated (Saracco *et al.*, 2007). Number of proteins modified by SUMO have been shown to increase *in planta* after abiotic stresses including heat, oxidative stress, ethanol, phosphate starvation, salt and cold stress (Kurepa *et al.*, 2003; Miura *et al.*, 2005; Yoo *et al.*, 2006; Miura *et al.*, 2007; Conti *et al.*, 2008; Miller *et al.*, 2010). Furthermore, mutants defective in proteins of the SUMO-conjugating pathway such as AtSIZ1 (arabidopsis SUMO E3 ligase) are impaired in stress responses such as thermotolerance and have been shown to exhibit exaggerated phosphate starvation responses (Miura *et al.*, 2005; Miura *et al.*, 2007) indicating that SUMOylation of proteins is an essential process mediating stress acclimation. As observed in other eukaryotic cells, SUMOylation enzymes (*e.g.* AtSCEA and SUMO1/2) localized in the nucleus in Arabidopsis (Lois *et al.*, 2003) indicating a role of SUMOylation in controlling many aspects of nuclear function. In rice (*Oryza sativa*), SUMO-conjugating enzyme (OsSCE1) has been shown to localize in the nucleus. Yeast-two hybrid experiments indicated that OsSCE1 interacts with the heat-inducible pyrophosphatase (PPIase) OsFKBP20, a class of proteins that assist molecular chaperones in reactions associated with protein folding and protein transport across membrane. It was proposed that OsSCE1 and OsFKBP20 proteins mediate in concert the stress response of rice plants (Nigam *et al.*, 2008). In Arabidopsis, heat stress dramatically increased the pool of SUMO conjugates which were mainly detected in the nucleus (Saracco *et al.*, 2007). In a recent proteomic analyses, Miller *et al.* (2010) have identified 357 SUMOylated proteins in Arabidopsis. Many of them are nuclear proteins that participate in a wide range of processes related to nuclear function,

such as chromatin modification, DNA maintenance/repair or gene transcription. Furthermore, nuclear SUMOylated proteins identified in non-stressed plants were enriched in oxidative and/or heat-stressed plants. Among the nuclear SUMO conjugates, some transcription factors have been identified (Miura and Hasegawa, 2010). For instance the SUMOylation of AtICE1, a MYC transcription factor involved in cold stress responses in *Arabidopsis* has been characterized (see below). Protein SUMOylation is a reversible process and de-SUMOylation is catalyzed by SUMO proteases a class of enzymes that is also involved in the generation of mature SUMO proteins. Recently, the *Arabidopsis* mutants *overly tolerant to salt 1 (ots1)* and *2 (ots2)* has been shown to be mutated in two SUMO proteases OTS1 and OTS2 that act redundantly to regulate salt stress response (Conti *et al.*, 2008). Both proteins are localized in the nucleus indicating that SUMOylation/deSUMOylation of nuclear proteins is likely to control essential processes required for salt stress responses.

It has been shown recently that both ubiquitination and SUMOylation can affect the same protein. During cold stress, *Arabidopsis* cold responsive genes are induced transiently indicating that their expression is finely regulated. Among the transcription factors that controls cold-gene expression and cold stress tolerance, AtICE1 is a MYC transcription factor that is constitutively expressed. It controls the cold induction of other transcription factors such as AtCBF3 which in turn drive the expression of cold responsive genes. On the contrary, AtMYB15 is a repressor of such genes (Agarwal *et al.*, 2006). ICE1 is post translationally modified by both ubiquitination and SUMOylation processes and these processes are thought to provide a fine-tuning for the expression of cold-responsive genes. More precisely, the nuclear-localized SUMO E3 ligase AtSIZ1 (Cheong *et al.*, 2009) mediate the SUMOylation of AtICE1. SUMOylation of AtICE1 is thought to stabilize or activate the protein, leading to the expression of genes required for low temperature tolerance, such as AtCBF3 (Miura *et al.*, 2007). Furthermore, the RING-E3-ubiquitin ligase HOS1 (for *high expression of osmotically responsive gene*) have been shown to relocalize to the nucleus after a cold treatment (Lee *et al.*, 2001) where it interacts with ICE1. HOS1 mediates the polyubiquitination of ICE1 targeting this transcription factor for degradation by the proteasome (Dong *et al.*, 2006). This leads to the repression of cold responsive genes such as CBF3 by the transcription factor AtMYB15. A model for the opposite role of ubiquitination and SUMOylation in the control of cold-responsive genes during cold episode has been proposed (Miura *et al.*, 2007; Miura and Hasegawa, 2010).

## 7. Conclusion

As we illustrate in this review using studies reporting the involvement of nuclear posttranslational modifications in response to numerous environmental changes, almost all known major abiotic stresses induce one or more nuclear protein modifications to regulate the expression of specific target genes.

After reading this chapter, three main conclusions emerge. Firstly, histone modifications and associated chromatin and gene expression changes appear to be a critical point necessary for establishment of an appropriate biological response. Understanding the regulation of histone modifications, competitions that can occur between different posttranslational modifications (the famous “histone code”) and interpretation of these



modifications by readers proteins is being initiated and should greatly highlight our comprehension of gene expression regulation in response to stresses in the coming years.

Secondly, we should keep in mind that protein modifications do not occur only on histones, but also concern many others proteins such as transcription regulators. However the number of non-histone proteins targeted by the nuclear posttranslational modification machinery remains sparse probably due to the technical difficulties for identification and purification of these very low abundant proteins in the nuclear compartment.

Thirdly, in almost all cases, the chemical and / or physical signals leading to nuclear machinery through the nuclear envelop are still unknown. Here too our knowledge about nuclear pore channels functioning in plant is emerging, but recent discoveries in this field should extend our understanding of how nuclear protein posttranslational modifications are controlled and lead the plant in an appropriate response to stress.

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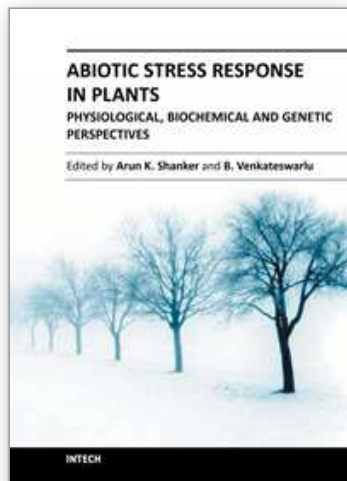
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## **Abiotic Stress Response in Plants - Physiological, Biochemical and Genetic Perspectives**

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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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