

FLOWERING NEWSLETTER REVIEW

The role of epigenetic processes in controlling flowering time in plants exposed to stress

Mahmoud W. Yaish^{1,*}, Joseph Colasanti² and Steven J. Rothstein²

¹ Department of Biology, College of Science, Sultan Qaboos University, Muscat, Oman

² Department of Molecular and Cellular Biology, University of Guelph, Guelph, ON, Canada N1G 2W1

* To whom correspondence should be addressed: E-mail: myaish@squ.edu.om

Received 5 April 2011; Revised 5 May 2011; Accepted 9 May 2011

Abstract

Plants interact with their environment by modifying gene expression patterns. One mechanism for this interaction involves epigenetic modifications that affect a number of aspects of plant growth and development. Thus, the epigenome is highly dynamic in response to environmental cues and developmental changes. Flowering is controlled by a set of genes that are affected by environmental conditions through an alteration in their expression pattern. This ensures the production of flowers even when plants are growing under adverse conditions, and thereby enhances transgenerational seed production. In this review recent findings on the epigenetic changes associated with flowering in *Arabidopsis thaliana* grown under abiotic stress conditions such as cold, drought, and high salinity are discussed. These epigenetic modifications include DNA methylation, histone modifications, and the production of micro RNAs (miRNAs) that mediate epigenetic modifications. The roles played by the phytohormones abscisic acid (ABA) and auxin in chromatin remodelling are also discussed. It is shown that there is a crucial relationship between the epigenetic modifications associated with floral initiation and development and modifications associated with stress tolerance. This relationship is demonstrated by the common epigenetic pathways through which plants control both flowering and stress tolerance, and can be used to identify new epigenomic players.

Key words: Epigenetics, flowering, stress, vernalization.

Introduction

Plants can adapt their growth and developmental processes in response to environmental conditions. Under stress conditions such as drought, high salt, high temperature, and high light intensity, physiological processes are induced to reduce the cellular damage caused by stress and, at the same time, alter developmental timing to complete their life cycle in a timely manner. Plants that experience stress transition to reproductive development earlier than non-stress-treated plants, typically at the expense of decreased seed number that allows for some seed production to occur during periods of environmental stress. Stress environmental factors that induce flowering have been discussed thoroughly in a previous review (Wada and Takeno, 2010). Most notably, salicylic acid, which usually induces defence genes, also induces early flowering under UV-C light stress, presumably by interacting with key floral transcription repressors such as FLOWERING

LOCUS T (FT) and other components of the autonomous flowering pathway (Martinez *et al.*, 2004; Wada *et al.*, 2010). However, evidence of physical interaction is not yet available. Similarly, high temperature stress induces flowering, a process mediated by *FLOWERING LOCUS M* (*FLM*) and *FT*, which integrates input from *CONSTANS* and other floral inductive pathways (Blazquez *et al.*, 2003; Balasubramanian *et al.*, 2006), while stress associated with low nitrate availability induces early flowering through a novel pathway (Castro Marín *et al.*, 2010).

The effect of stress on flowering time can be ascribed, in part, to induced changes in the epigenome. Epigenetics refers to heritable, self-perpetuating changes in gene activities that are not caused by changes in nucleotide sequence and are associated with chemical modifications of chromatin (Bonasio *et al.*, 2010). These modifications take place in

the nucleosome at different levels through reversible biochemical reactions that include DNA methylation and histone tail modifications. DNA methylation occurs by covalently adding a methyl group to cytosine of the DNA backbone, while histone modifications occur when specific lysine or arginine residues within the amino acid terminal tail of histones are post-translationally modified either by acetylation (Grunstein, 1997), ADP-ribosylation (Tanigawa *et al.*, 1984), glycosylation (Cervantes-Laurean *et al.*, 1996), methylation (Zhang and Reinberg, 2001), phosphorylation (Lo *et al.*, 2001), ubiquitination (Sridhar *et al.*, 2007), or SUMOylation (David *et al.*, 2002; Miller *et al.*, 2010). Typically, DNA methylation leads to reduced gene expression, whereas histone modifications are more complicated and can lead to various gene expression alterations depending on the modification (Richards and Elgin, 2002). More recently, it was discovered that small non-coding RNA plays an important role in regulating gene expression by specifying DNA methylation patterns (Matzke and Birchler, 2005). Each of these types of modifications have been involved in modulating flowering, and many of these are associated with response to abiotic and biotic stress.

Plants that are adapted to extreme environments have the capacity to cope with adverse environmental cues with minimum cellular damage. Eukaryotic cells respond to the environment by modifying their gene expression profiles, a process which usually involves specific chromatin modifications. The correlation between epigenetic changes in plants and stress tolerance has been previously discussed (Boyko and Kovalchuk, 2008; Chinnusamy and Zhu, 2009; Alvarez *et al.*, 2010; M Chen *et al.*, 2010). Chromatin modifications both influence and are influenced by other responses to abiotic and biotic stresses.

DNA methylation, environmental stress, and the flowering process

DNA methylation (5-methylcytosine) can account for >30% of the cytosine (CpG) residues in plants (Gruenbaum *et al.*, 1981a, 1981b) and >60% in mammals (Gruenbaum *et al.*, 1981b; Razin *et al.*, 1984). In *Arabidopsis*, DNA methylation is often associated with gene repression (Zilberman *et al.*, 2007), although some reports show a weak relationship between the hypermethylation status of the genes and their expression level. For example, Vaillant *et al.* (2006) showed that expression levels of the *Arabidopsis* 5S rRNA gene repeats can be increased in the *MORPHEUS' MOLECULE 1* (*MOM1*) mutant lines despite the presence of the same amount of DNA methylation (Vaillant *et al.*, 2006). In addition, recent evidence showed that short-term heat stress induced the expression of genes in heterochromatin that contain transcriptionally inert non-coding repeated DNA. This occurs despite the presence of epigenetic modifications that are typically associated with repression of gene expression such as a high level of DNA methylation and histone deacetylation, suggesting that the effect can vary depending on circumstance (Pecinka *et al.*, 2010;

Tittel-Elmer *et al.*, 2010). DNA methylation is often a prerequisite for gene silencing via methylation directed by small RNAs. In particular, flowering time in *Arabidopsis* can be controlled by silencing of the homeodomain floral transcription factor *FWA* by *de novo* methylation of a specific region within the 5' end of the transcribed region. Once *FWA* is methylated, small interfering RNA (siRNA) is more efficient at directing further methylation to the locus, which subsequently enhances stable gene silencing (Chan *et al.*, 2006).

The *Arabidopsis* genome encodes 12 methyl-CpG-binding domain (MBD) proteins, which function with chromatin remodelling proteins to inactivate gene expression (Berg *et al.*, 2003; Springer and Kaeppler, 2005). These proteins interact with other proteins to form chromatin modifier complexes. For example, *AtMBD7* interacts with arginine methyltransferase (*PRMT11*) (Scebba *et al.*, 2007), and the *AtMBD5–AtMBD7* proteins co-localize *in vivo* and bind *in vitro* to the *DECREASE IN DNA METHYLATION 1* (*DDM1*) protein (Zemach *et al.*, 2008). Loss-of-function studies showed that plants with mutations in *AtMBD9* display a pleiotropic phenotype that leads to a decrease in histone acetylation and an increase in DNA methylation at the *FLC* locus (Peng *et al.*, 2006; Yaish *et al.*, 2009). As a result, transcript levels for *FLC* decline, resulting in an early flowering phenotype. Prolonged exposure of some plant species to cold conditions or vernalization induces flowering, a process which is widely considered as a non-stress condition. *AtMBD8* has been shown to control flowering in the *Arabidopsis* vernalization-responsive C24 ecotype. Mutation of *AtMBD8* leads to a delay in flowering under both long- and short-day photoperiods. While *FLC* expression is not affected in *atmbd8-1*, the expression of *FT* and *SOC1*, which are major flowering promoters, is down-regulated in the mutant (Stangeland *et al.*, 2009). The mechanism by which the expression of these genes is decreased in the *atmbd8-1* mutant has not yet been determined. Global gene expression analysis revealed that the C24 ecotype differentially expresses a set of biotic and abiotic stress-related genes during the vegetative stage compared with the Columbia ecotype. This finding may highlight a relationship between the flowering process and stress response, although the direct role of MBD proteins in the stress tolerance phenotype has not been determined.

The level of CpG methylation in *Arabidopsis* is controlled by the *METHYTRANSFERASE1* (*MET1*), *MET2*, and *MET3* genes (Henderson and Jacobsen, 2007), which are homologous to the (*Dnmt1*) mammalian DNA methyltransferase. In addition, the methylation level is also affected by the *CHROMOMETHYLASE3* (*CMT3*) *DNA METHYLTRANSFERASE* (Lindroth *et al.*, 2001), which helps maintain DNA methylation at CpNpG and CpNpN sites. The *met1-6* mutation leads to late flowering, and *met1* and *cmt3* mutants exhibit improper embryo development, cell division, seed viability, and abnormal auxin gradient (Xiao *et al.*, 2006). Moreover, loss of DNA methylation reduces the ability of *Arabidopsis* plants to tolerate salt stress conditions. Loss-of-function *met1-3* mutants are hypersensitive to salt stress due to a major loss in cytosine

methylation in a putative small RNA target region that lowers the expression of the sodium transporter gene (*AtHKT1*), which is essential for salt tolerance (Baek *et al.*, 2011). In rice, drought stress increases DNA methylation in a genotypic-specific fashion and only 70% of the total changes in DNA methylation are reset even after recovery in non-drought conditions (Wang *et al.*, 2010). In addition, temperature stress modulates the flowering pattern by reducing the number of spikelets and overall fertility at anthesis in some rice genotypes (Jagadish *et al.*, 2007).

Treating plants with the cytosine methyltransferase inhibitor 5-azacytidine (5-azaC) (Jones, 1985; Haaf, 1995) promotes flowering in the vernalization-requiring *Arabidopsis* ecotype C24 (Burn *et al.*, 1993a; Dennis *et al.*, 1998; Finnegan *et al.*, 1998a) and in wheat (Brock and Davidson, 1994). This treatment was sufficient to substitute for the vernalization process. Reducing the amount of DNA methylation can also be achieved by genetically manipulating the enzymes that catalyse DNA methylation and demethylation in the cell. Alterations in DNA methylation levels show inconsistent effects on observed phenotypes. Reverse genetic studies have shown that mutations within the genes *DECREASE IN DNA METHYLATION1* (*DDM1*) and *DDM2*, the *DNA METHYLTRANSFERASE1* gene (*MET1*) (Vongs *et al.*, 1993; Kakutani *et al.*, 1996; Jackson *et al.*, 2004), and the DNA demethylase gene, *REPRESSOR OF SILENCING GENES1* (*ROS1*) (Agius *et al.*, 2006), affect the global level of cytosine methylation and lead to some developmental abnormalities in *Arabidopsis* including changes in flowering time. The effect of DNA methylation level on *Arabidopsis* phenotype depends on the *Arabidopsis* ecotype studied. For example, reduction of DNA methylation in *ddm1* and *met1-1* mutant lines causes late flowering in Columbia and Landsberg erecta ecotypes (Kakutani *et al.*, 1996; Kakutani, 1997; Kankel *et al.*, 2003). However, low DNA methylation induced by vernalization or 5-azaC treatment promoted flowering in the vernalization-responsive *Arabidopsis* ecotype C24 (Burn *et al.*, 1993b; Finnegan *et al.*, 1998b). In other plant species such as the long-day plant *Silene armeria*, whose flowering state is photoperiodically stable, and the short-day plant *Pharbitis nil*, whose flowering state is photoperiodically unstable, DNA demethylation using 5azaC induced flowering under non-inductive photoperiod. However, floral induction of other species such as *Xanthium strumarium* and *Lemna paucicostata* could not be achieved using similar agents under the same conditions (Kondo *et al.*, 2007).

Histone modifications associated with environmental stress and flowering

The role of histone acetylation and methylation in controlling eukaryotic gene expression was first described in 1964 (Allfrey *et al.*, 1964). Trichostatin A (TSA) has been used to reduce histone deacetylation globally and, consequently, leads to an increase in acetylated histones. However, TSA has negative pleiotropic effects since increased acetylation has been shown

to lead to impaired sister chromatid separation in human fibroblasts (Cimini *et al.*, 2003) and also induces chromosomal abnormalities during tobacco cell division (Li *et al.*, 2005). In addition, increasing histone acetylation activity in *Arabidopsis* by expressing antisense of the histone deacetylase gene *AtHD1* results in pleiotropic phenotypes with various developmental defects including ectopic expression of silenced genes, suppression of apical dominance, heterochronic shift toward juvenility, floral structure abnormalities, and male and female sterility (Tian and Chen, 2001).

Similar to DNA methylation, histone modification is regulated by environmental conditions (Boyko and Kovalchuk, 2008; Kim *et al.*, 2010). Recently, global gene expression analysis coupled with chromatin immunoprecipitation (ChIP) assays showed that histone H3 Lys4 methylation (H3K4) patterns respond dynamically to dehydration stress in *Arabidopsis* (van Dijk *et al.*, 2010). One example of the interplay between environmental stressors and flowering is demonstrated in studies of the floral initiator SHK1 KINASE BINDING PROTEIN1 (*SKB1*) mutant line *skb1*. *SKB1* binds to chromatin and increases the histone 4 Arg3 (H4R3) symmetric dimethylation (H4R3me2) level, which in turn leads to the down-regulation of *FLC* expression as well as a number of stress-responsive genes. As a result, the phenotypes present in this mutant exhibit salt hypersensitivity, late flowering, and growth retardation (Zhang *et al.*, 2011). In the same study, H4R3me2 expression is reduced in wild-type *Arabidopsis* plants that are exposed to high salinity conditions, allowing for the release of *SKB1* from chromatin and therefore enhancing the expression of *FLC* and other stress-induced genes.

The histone deacetylase *HDA6* of *Arabidopsis* is involved in modulating seed germination and salt stress as well as the abscisic acid (ABA) response. *HDA6* RNA interfering lines are hypersensitive to salt and ABA (Chen and Wu, 2010; LT Chen *et al.*, 2010). Along with phytochrome B, *HDA6* regulates the global chromatin organization in some *Arabidopsis* genotypes that are typically grown in different geographical latitudes (Tessadori *et al.*, 2009). Quantitative trait locus (QTL) mapping based on relative heterochromatin fraction (RHF) analysis and microscopic examination showed that *HDA6* controls chromatin remodelling capacity, which also depends on light intensity, a factor that usually regulates flowering time, thereby providing evidence of direct involvement of *HDA6* in environmental adaptation. Similarly, *hda19-1* mutants are hypersensitive to salt and ABA, and the expression of ABA-responsive genes, *ABI1*, *ABI2*, *KAT1*, *KAT2*, and *RD29B*, is reduced in this mutant (Chen and Wu, 2010).

The *Arabidopsis* histone deacetylase 2 gene (*AtHD2C*) is highly expressed in ovules, embryos, shoot apical meristems, and primary leaf tissues (Sridha and Wu, 2006). The same study showed that *AtHD2C* is repressed by ABA, and transgenic lines overexpressing *AtHD2C* showed an ABA insensitivity phenotype where the expression of several ABA-related genes is affected. In addition, transgenic lines exhibited a reduction in the transpiration rate and enhanced tolerance to salt and drought stresses.

In *Brassica napus*, the putative transcription factor harbouring a kinase-inducible domain bnKCP1 interacts with HDA19, through which it controls expression of the gene. The *bnKCP1* gene, which is induced by cold and highly expressed in flowers, may have a transcriptional regulatory role in cold stress (Gao *et al.*, 2003). Interestingly, overexpression of *HDA19* resulted in increased expression of jasmonic acid (JA)- and ethylene-regulated pathogenesis-related genes such as the *ETHYLENE RESPONSE FACTOR1*, basic chitinase, and β -1,3-glucanase. Moreover, these overexpression lines are more resistant to the pathogen *Alternaria brassicicola* but also displayed late flowering and a reduction in seed fertility (Zhou *et al.*, 2005). Therefore, HDA19 interconnects the hormone response to pathogen pathways and floral induction through a common epigenetic mechanism.

The *Arabidopsis* acetyltransferase GENERAL CONTROL NON-REPPRESSED PROTEIN5 (AtGCN5) (Stockinger *et al.*, 2001) is a major histone acetyltransferase in *Arabidopsis*. Mutation within the coding region of this gene causes pleiotropic effects on plant development and also leads to impaired floral production where petals are transformed into stamens and sepals into filamentous like-structures (Bertrand *et al.*, 2003). It was also found that *gcn5* mutants have altered expression of a large number of genes, including those involved in floral initiation and development as well as those associated with stress tolerance. The transcriptional co-activators ADA2a and ADA2b are components of AtGCN5-containing complexes in *Arabidopsis* (Stockinger *et al.*, 2001). Mutation of *ADA2a* leads to delayed flowering and fruit setting and to the production of shorter inflorescences. Recently it was shown that ADA2b positively regulates salt-induced genes by maintaining the required acetylation level of histones H4 and H3, with the *ada2b-1* mutant being hypersensitive to salt and ABA (Hark *et al.*, 2009; Kaldis *et al.*, 2010). Interestingly, the *gcn5-1* mutant line also displays an ABA hypersensitivity phenotype (Hark *et al.*, 2009), indicating that AtGCN5 and ADA2b integration are important for proper ABA response in *Arabidopsis*. SGF29A-1 is another component of the AtGCN5 complex that helps control floral initiation. Compared with wild-type plants, the *sgf29a-1* mutant displays late flowering, and smaller and fewer rosette leaves. Unlike the *ada2b-1* mutant, *sgf29a-1* displays enhanced salt tolerance compared with the wild type (Kaldis *et al.*, 2010).

In addition to its conventional role in controlling gene expression by acetylating and deacetylating specific histones, a recent study showed that AtGCN5 is also involved in the production of microRNAs (miRNAs), including those induced by environmental stress (W Kim *et al.*, 2009). These results demonstrate a diverse role for the AtGCN5 complex in controlling the expression of stress- and flowering-related genes by tightly controlling the histone acetylation levels of their loci. Hence AtGCN5 represents a central point in the relationship between histone modification and miRNA production, which is discussed below.

Cold treatment affects flowering via epigenetic modifications

As was noted earlier, exposure to cold conditions for a sufficient time induces flowering in some plant species through the vernalization process and is a comparatively well studied example of how cold induces epigenetic changes that in turn affect flowering. In addition to vernalization, which is crucial to induce flowering in some plant species by modulating the expression of certain genes, cold stress also modulates the expression of some genes, including those involving chromatin modulation. For example, global gene expression analysis of cold-stressed *Arabidopsis* showed up-regulation of some epigenetic modifiers such as NRPD1, which is a DNA-binding bromodomain-containing protein, AtGCN5-related GNAT family 5 (acetyltransferase 5), and histone deacetylase (Lee *et al.*, 2005). In general, low temperature often has been shown to be associated with DNA demethylation in *Arabidopsis* and other plant species such as maize (Steward *et al.*, 2002), *Antirrhinum majus* (Hashida *et al.*, 2003), and wheat (Sherman and Talbert, 2002). Vernalization down-regulates the expression of *FLC*, a MADS box transcriptional repressor that maintains the vegetative stage in *Arabidopsis* apices. Thus, epigenetic changes at the *FLC* locus accelerate flowering (DH Kim *et al.*, 2009). Trimethylation of Lys27 of H3 histones (H3K27me3) is crucial for the regulation of some genes that are involved in plant development, including those that control flowering time in *Arabidopsis*. Interestingly, the same genes are also affected by vernalization (Shindo *et al.*, 2006; Finnegan and Dennis, 2007; Greb *et al.*, 2007). Likewise, H3K27me3 decreases the expression of the floral regulators *AGL19*, *FT*, and *AGAMOUS* (Schonrock *et al.*, 2006; Schubert *et al.*, 2006; Saleh *et al.*, 2007; Jiang *et al.*, 2008).

Exposure to cold induces expression of the *Arabidopsis* *VERNALIZATION INSENSITIVE 3* gene (*VIN3*), a chromatin remodelling plant homeodomain (PHD) finger protein that increases acetylation levels. This protein is required to repress *FLC* and enhance flowering. Mutant lines for *VIN3* do not respond to vernalization and therefore remain in a vegetative state longer because *FLC* expression is not reduced by cold treatment (Sung and Amasino, 2004). Increased H3K27me3 levels at *FLC* after vernalization are due to a reaction mediated by the Polycomb-group Repressive Complex 2 (PRC2) (De Lucia *et al.*, 2008). This complex binds to chromatin of the *VIN3* locus during vernalization (Schonrock *et al.*, 2006). In contrast, a decrease in H3K27me3 modifications within histones of the cold-responsive gene *COR15A* and the *GALACTINOL SYNTHASE* gene *ATGOLS3* (Taji *et al.*, 2002) leads to increased gene expression in *Arabidopsis* (Kwon *et al.*, 2009). Likewise, the plant trithorax factor (ATX1) (Alvarez-Venegas *et al.*, 2003) tri-methylates Lys4 residues of histone H3 (H3K4me3), thereby regulating floral organ development and modulating expression of transcription factor *WRKY70* during dehydration stress (Alvarez-Venegas *et al.*, 2007; Ndamukong *et al.*,

2010). Mutation of *ATXI* causes major defects in the floral architecture (Alvarez-Venegas *et al.*, 2003).

Small RNA production is associated with environmental stress tolerance and flowering

Flowering in *Arabidopsis* is induced through several pathways including autonomous, gibberellic acid, photoperiod, and vernalization. Global gene expression analysis of *Arabidopsis* harbouring defective genes in the photoperiod signal pathway and the pathway integrator genes suggests a critical involvement of miRNAs in mediating the effects of floral induction (Schmid *et al.*, 2003).

miRNAs that control gene expression at a post-transcriptional level are encoded by 20–24 nucleotides that are not translated. These small RNA molecules are also able to direct DNA methylation to a particular locus by an RNA-directed DNA methylation (RdDM) process (Matzke *et al.*, 2001, 2007; Pikaard, 2006). miRNAs have been shown to control the expression of some genes when plants are exposed to biotic (Madlung and Comai, 2004; Ruiz-Ferrer and Voinnet, 2009; Covarrubias and Reyes, 2010) and abiotic stress (Madlung and Comai, 2004; Hirayama and Shinozaki, 2010; Urano *et al.*, 2010). This is often accompanied by a reprogramming of genes associated with floral initiation and development.

Environmental cues regulate the expression of miRNAs in plants. For example, stress-inducible miRNAs and their predicted targets were identified in *Arabidopsis* and found to be conserved among other plant species (Sunkar and Zhu, 2004). In rice, global expression analysis revealed a crucial role for miRNAs in controlling gene expression when plants are exposed to stress conditions such as cold, drought, high salt, and ABA treatment (Shen *et al.*, 2010). A study of loss-of-function mutations in the miRNA biogenesis machinery *DICER-LIKE 1–4* genes (*DCL1*, *DCL2*, *DCL3*, and *DCL4*) revealed a predominant epigenetic role for miRNAs in controlling gene expression in *Arabidopsis* (Laubinger *et al.*, 2010). In addition to conventional mechanisms of gene repression via binding of miRNA to the target genes, the same study showed that *DCL1* is involved in a process that leads to the repression of a subset of transposons by enhancing DNA methylation. Because they control the production of miRNA, *DCL2* and *DCL3* proteins are believed to direct the transgenerational memory of stress in plants (Boyko and Kovalchuk, 2010).

The relationship between miRNA biogenesis machinery proteins, stress response, and flowering is clear in some *Arabidopsis* mutant lines. For example, *ABH1* and *CBP20* (Papp *et al.*, 2004) encode cap-binding factors that are necessary for RNA maturation. The *abh1* mutant displays ABA hypersensitivity and the *cbp20* mutant line shows enhanced drought tolerance as well as ABA hypersensitivity (Hugouvieux *et al.*, 2001; Kwak *et al.*, 2005). The *abh1* mutant also displays an early flowering phenotype due to the production of an alternative form of mRNAs for the key

flowering time genes *CONSTANS*, *FLC*, and *FLM* compared with the wild type (Kuhn *et al.*, 2007). The *STRESS RESPONSE SUPPRESSOR 1* and 2 (*STRS1* and 2) genes code for DEAD-box RNA helicases that are suppressed when plants are exposed to salt and osmotic stress conditions. Mutant lines for these genes display higher tolerance than the wild type (Kant *et al.*, 2007). Once again, the relationship between stress conditions and flowering is clear in this example as the *strs* mutants showed slightly early flowering, perhaps suggesting a common epigenetic pathway in controlling both mechanisms.

In addition to their role in environmental stress responses (Sunkar and Zhu, 2004), miRNAs are also involved in controlling flowering in *Arabidopsis* (Aukerman and Sakai, 2003; Chen, 2004). Interestingly, recent evidence showed that H3K27me3 at *FLC* is mediated by a long intronic non-coding RNA (*COLD AIR*). The association of *COLD AIR* triggers PRC2 targeting to *FLC*, a situation which leads to *FLC* repression during vernalization (Heo and Sung, 2010). Expression of *FLC* is partially controlled by miRNAs since mutations within miRNA biogenesis genes *DCL1* and *DCL3* lead to delayed flowering due to excessively high expression of *FLC* in these mutant backgrounds (Schmitz *et al.*, 2007). Late flowering phenotypes were also observed in *HYPONASTIC LEAVES 1* (*HYL1*) mutant lines (Lu and Fedoroff, 2000). This gene encodes a double-stranded RNA (dsRNA)-binding protein that also plays a role in miRNA-mediated gene regulation (Han *et al.*, 2004). Recent studies also show that, in addition to *hyl1*, mutants within the miRNA biogenesis factors *SERRATE* (*SE*), *DCL1*, *HUA-ENHANCER 1* (*HEN1*), and *HASTY* of *Arabidopsis* display a salt and ABA hypersensitivity phenotype (Lu and Fedoroff, 2000; Han *et al.*, 2004; Zhang *et al.*, 2008; Rasia *et al.*, 2010).

miRNAs are important regulators of ABA and salt tolerance genes; sets of these molecules were identified recently and found to have roles in stress tolerance in different plant species such as *Arabidopsis* (Liu *et al.*, 2008), rice (Zhao *et al.*, 2007), and maize (Ding *et al.*, 2009). For example, miR159, which controls the expression of *MYB101* and *MYB33* transcription factors by mediating their cleavage and is also involved in floral development (Reyes and Chua, 2007), and miR160, which controls floral morphology by modulating the expression of an *AUXIN RESPONSE FACTOR 10* (*ARF10*) (Liu *et al.*, 2007), are also potential ABA regulatory miRNA molecules and are induced by ABA.

Plants interact with their environment and accordingly modify their flowering programmes. Recent research shows that plants use common and parallel epigenetic modification pathways in order to modify the expression of genes that are involved in stress tolerance and flowering processes. These modifications are associated with changes in DNA methylation, histone modifications such as acetylation and methylation, and also the production of specific miRNA molecules. Together these changes underlie intricate mechanisms that ensure plant survival and optimize reproductive success under a variety of stress conditions. Information derived

from epigenomic profiles of plants exposed to abiotic stresses is highly important for the production of genetically fertile crop species that can tolerate a warmer globe.

References

- Agius F, Kapoor A, Zhu JK.** 2006. Role of the Arabidopsis DNA glycosylase/lyase ROS1 in active DNA demethylation. *Proceedings of the National Academy of Sciences, USA* **103**, 11796–11801.
- Allfrey VG, Faulkner R, Mirsky AE.** 1964. Acetylation and methylation of histones and their possible role in the regulation of RNA synthesis. *Proceedings of the National Academy of Sciences, USA* **51**, 786–794.
- Alvarez ME, Nota F, Cambiagno DA.** 2010. Epigenetic control of plant immunity. *Molecular Plant Pathology* **11**, 563–576.
- Alvarez-Venegas R, Abdallat AA, Guo M, Alfano JR, Avramova Z.** 2007. Epigenetic control of a transcription factor at the cross section of two antagonistic pathways. *Epigenetics* **2**, 106–113.
- Alvarez-Venegas R, Pien S, Saddler M, Witmer X, Grossniklaus U, Avramova Z.** 2003. ATX-1, an Arabidopsis homolog of trithorax, activates flower homeotic genes. *Current Biology* **13**, 627–637.
- Aukerman MJ, Sakai H.** 2003. Regulation of flowering time and floral organ identity by a MicroRNA and its APETALA2-like target genes. *The Plant Cell* **15**, 2730–2741.
- Baek D, Jiang J, Chung JS, Wang B, Chen J, Xin Z, Shi H.** 2011. Regulated AtHKT1 gene expression by a distal enhancer element and DNA methylation in the promoter plays an important role in salt tolerance. *Plant and Cell Physiology* **52**, 149–161.
- Balasubramanian S, Sureshkumar S, Lempe J, Weigel D.** 2006. Potent induction of Arabidopsis thaliana flowering by elevated growth temperature. *PLoS Genetics* **2**, e106.
- Berg A, Meza TJ, Mahic M, Thorstensen T, Kristiansen K, Aalen RB.** 2003. Ten members of the Arabidopsis gene family encoding methyl-CpG-binding domain proteins are transcriptionally active and at least one, ATMBD11, is crucial for normal development. *Nucleic Acids Research* **31**, 5291–5304.
- Bertrand C, Bergounioux C, Domenichini S, Delarue M, Zhou DX.** 2003. Arabidopsis histone acetyltransferase AtGCN5 regulates the floral meristem activity through the WUSCHEL/AGAMOUS pathway. *Journal of Biological Chemistry* **278**, 28246–28251.
- Blazquez MA, Ahn JH, Weigel D.** 2003. A thermosensory pathway controlling flowering time in Arabidopsis thaliana. *Nature Genetics* **33**, 168–171.
- Bonasio R, Tu S, Reinberg D.** 2010. Molecular signals of epigenetic states. *Science* **330**, 612–616.
- Boyko A, Kovalchuk I.** 2008. Epigenetic control of plant stress response. *Environmental Molecular Mutagenesis* **49**, 61–72.
- Boyko A, Kovalchuk I.** 2010. Transgenerational response to stress in Arabidopsis thaliana. *Plant Signaling and Behavior* **5**, 995–998.
- Brock RD, Davidson JL.** 1994. 5-Azacytidine and gamma rays partially substitute for cold treatment in vernalising winter wheat. *Environmental and Experimental Botany* **31**, 195–199.
- Burn JE, Bagnall DJ, Metzger JD, Dennis ES, Peacock WJ.** 1993a. DNA methylation, vernalization, and the initiation of flowering. *Proceedings of the National Academy of Sciences, USA* **90**, 287–291.
- Burn JE, Bagnall DJ, Metzger JD, Dennis ES, Peacock WJ.** 1993b. DNA methylation, vernalization, and the initiation of flowering. *Proceedings of the National Academy of Sciences, USA* **90**, 287–291.
- Castro Marín I, Loeffler I, Bartetzko L, Searle I, Coupland G, Stitt M, Osuna D.** 2010. Nitrate regulates floral induction in Arabidopsis, acting independently of light, gibberellin and autonomous pathways. *Planta* **233**, 539–552.
- Cervantes-Laurean D, Jacobson EL, Jacobson MK.** 1996. Glycation and glycooxidation of histones by ADP-ribose. *Journal of Biological Chemistry* **271**, 10461–10469.
- Chan SW, Zhang X, Bernatavichute YV, Jacobsen SE.** 2006. Two-step recruitment of RNA-directed DNA methylation to tandem repeats. *PLoS Biology* **4**, e363.
- Chen LT, Luo M, Wang YY, Wu K.** 2010. Involvement of Arabidopsis histone deacetylase HDA6 in ABA and salt stress response. *Journal of Experimental Botany* **61**, 3345–3353.
- Chen LT, Wu K.** 2010. Role of histone deacetylases HDA6 and HDA19 in ABA and abiotic stress response. *Plant Signaling and Behavior* **5**, 1318–1320.
- Chen M, Lv S, Meng Y.** 2010. Epigenetic performers in plants. *Developmental Growth and Differentiation* **52**, 555–566.
- Chen X.** 2004. A microRNA as a translational repressor of APETALA2 in Arabidopsis flower development. *Science* **303**, 2022–2025.
- Chinnusamy V, Zhu JK.** 2009. Epigenetic regulation of stress responses in plants. *Current Opinion in Plant Biology* **12**, 133–139.
- Cimini D, Mattiuzzo M, Torosantucci L, Degrassi F.** 2003. Histone hyperacetylation in mitosis prevents sister chromatid separation and produces chromosome segregation defects. *Molecular Biology of the Cell* **14**, 3821–3833.
- Covarrubias AA, Reyes JL.** 2010. Post-transcriptional gene regulation of salinity and drought responses by plant microRNAs. *Plant, Cell and Environment* **33**, 481–489.
- David G, Neptune MA, DePinho RA.** 2002. SUMO-1 modification of histone deacetylase 1 (HDAC1) modulates its biological activities. *Journal of Biological Chemistry* **277**, 23658–23663.
- De Lucia F, Crevillen P, Jones AM, Greb T, Dean C.** 2008. A PHD-polycomb repressive complex 2 triggers the epigenetic silencing of FLC during vernalization. *Proceedings of the National Academy of Sciences, USA* **105**, 16831–16836.
- Dennis ES, Bilodeau P, Burn J, Finnegan EJ, Genger R, Helliwell C, Kang BJ, Sheldon CC, Peacock WJ.** 1998. Methylation controls the low temperature induction of flowering in Arabidopsis. *Symposia of the Society for Experimental Biology* **51**, 97–103.
- Ding D, Zhang L, Wang H, Liu Z, Zhang Z, Zheng Y.** 2009. Differential expression of miRNAs in response to salt stress in maize roots. *Annals of Botany* **103**, 29–38.
- Finnegan EJ, Dennis ES.** 2007. Vernalization-induced trimethylation of histone H3 lysine 27 at FLC is not maintained in mitotically quiescent cells. *Current Biology* **17**, 1978–1983.

- Finnegan EJ, Genger RK, Kovac K, Peacock WJ, Dennis ES.** 1998a. DNA methylation and the promotion of flowering by vernalization. *Proceedings of the National Academy of Sciences, USA* **95**, 5824–5829.
- Finnegan EJ, Genger RK, Kovac K, Peacock WJ, Dennis ES.** 1998b. DNA methylation and the promotion of flowering by vernalization. *Proceedings of the National Academy of Sciences, USA* **95**, 5824–5829.
- Gao MJ, Schafer UA, Parkin IA, Hegedus DD, Lydiate DJ, Hannoufa A.** 2003. A novel protein from *Brassica napus* has a putative KID domain and responds to low temperature. *The Plant Journal* **33**, 1073–1086.
- Greb T, Mylne JS, Crevillen P, Geraldo N, An H, Gendall AR, Dean C.** 2007. The PHD finger protein VRN5 functions in the epigenetic silencing of Arabidopsis FLC. *Current Biology* **17**, 73–78.
- Gruenbaum Y, Naveh-Many T, Cedar H, Razin A.** 1981b. Sequence specificity of methylation in higher plant DNA. *Nature* **292**, 860–862.
- Gruenbaum Y, Stein R, Cedar H, Razin A.** 1981a. Methylation of CpG sequences in eukaryotic DNA. *FEBS Letters* **124**, 67–71.
- Grunstein M.** 1997. Histone acetylation in chromatin structure and transcription. *Nature* **389**, 349–352.
- Haaf T.** 1995. The effects of 5-azacytidine and 5-azadeoxycytidine on chromosome structure and function: implications for methylation-associated cellular processes. *Pharmacology and Therapeutics* **65**, 19–46.
- Han MH, Goud S, Song L, Fedoroff N.** 2004. The Arabidopsis double-stranded RNA-binding protein HYL1 plays a role in microRNA-mediated gene regulation. *Proceedings of the National Academy of Sciences, USA* **101**, 1093–1098.
- Hark AT, Vlachonasios KE, Pavangadkar KA, Rao S, Gordon H, Adamakis ID, Kaldis A, Thomashow MF, Triezenberg SJ.** 2009. Two Arabidopsis orthologs of the transcriptional coactivator ADA2 have distinct biological functions. *Biochimica et Biophysica Acta* **1789**, 117–124.
- Hashida SN, Kitamura K, Mikami T, Kishima Y.** 2003. Temperature shift coordinately changes the activity and the methylation state of transposon Tam3 in *Antirrhinum majus*. *Plant Physiology* **132**, 1207–1216.
- Henderson IR, Jacobsen SE.** 2007. Epigenetic inheritance in plants. *Nature* **447**, 418–424.
- Heo JB, Sung S.** 2010. Vernalization-mediated epigenetic silencing by a long intronic noncoding RNA. *Science* **331**, 76–79.
- Hirayama T, Shinozaki K.** 2010. Research on plant abiotic stress responses in the post-genome era: past, present and future. *The Plant Journal* **61**, 1041–1052.
- Hugouvieux V, Kwak JM, Schroeder JI.** 2001. An mRNA cap binding protein, ABH1, modulates early abscisic acid signal transduction in Arabidopsis. *Cell* **106**, 477–487.
- Jackson JP, Johnson L, Jasencakova Z, Zhang X, PerezBurgos L, Singh PB, Cheng X, Schubert I, Jenuwein T, Jacobsen SE.** 2004. Dimethylation of histone H3 lysine 9 is a critical mark for DNA methylation and gene silencing in Arabidopsis thaliana. *Chromosoma* **112**, 308–315.
- Jagadish SV, Craufurd PQ, Wheeler TR.** 2007. High temperature stress and spikelet fertility in rice (*Oryza sativa* L.). *Journal of Experimental Botany* **58**, 1627–1635.
- Jiang D, Wang Y, Wang Y, He Y.** 2008. Repression of FLOWERING LOCUS C and FLOWERING LOCUS T by the Arabidopsis Polycomb repressive complex 2 components. *PLoS One* **3**, e3404.
- Jones P.** 1985. Altering gene expression with 5-azacytidine. *Cell* **40**, 485–486.
- Kakutani T.** 1997. Genetic characterization of late-flowering traits induced by DNA hypomethylation mutation in Arabidopsis thaliana. *The Plant Journal* **12**, 1447–1451.
- Kakutani T, Jeddelloh JA, Flowers SK, Munakata K, Richards EJ.** 1996. Developmental abnormalities and epimutations associated with DNA hypomethylation mutations. *Proceedings of the National Academy of Sciences, USA* **93**, 12406–12411.
- Kaldis A, Tsementzi D, Tarriverdi O, Vlachonasios KE.** 2010. Arabidopsis thaliana transcriptional co-activators ADA2b and SGF29a are implicated in salt stress responses. *Planta* **233**, 749–762.
- Kankel MW, Ramsey DE, Stokes TL, Flowers SK, Haag JR, Jeddelloh JA, Riddle NC, Verbsky ML, Richards EJ.** 2003. Arabidopsis MET1 cytosine methyltransferase mutants. *Genetics* **163**, 1109–1122.
- Kant P, Kant S, Gordon M, Shaked R, Barak S.** 2007. STRESS RESPONSE SUPPRESSOR1 and STRESS RESPONSE SUPPRESSOR2, two DEAD-box RNA helicases that attenuate Arabidopsis responses to multiple abiotic stresses. *Plant Physiology* **145**, 814–830.
- Kim DH, Doyle MR, Sung S, Amasino RM.** 2009. Vernalization: winter and the timing of flowering in plants. *Annual Review of Cell and Developmental Biology* **25**, 277–299.
- Kim JM, To TK, Nishioka T, Seki M.** 2010. Chromatin regulation functions in plant abiotic stress responses. *Plant, Cell and Environment* **33**, 604–611.
- Kim W, Benhamed M, Servet C, Latrasse D, Zhang W, Delarue M, Zhou DX.** 2009. Histone acetyltransferase GCN5 interferes with the miRNA pathway in Arabidopsis. *Cell Research* **19**, 899–909.
- Kondo H, Miura T, Wada KC, Takeno K.** 2007. Induction of flowering by 5-azacytidine in some plant species: relationship between the stability of photoperiodically induced flowering and flower-inducing effect of DNA demethylation. *Physiologia Plantarum* **131**, 462–469.
- Kuhn JM, Breton G, Schroeder JI.** 2007. mRNA metabolism of flowering-time regulators in wild-type Arabidopsis revealed by a nuclear cap binding protein mutant, abh1. *The Plant Journal* **50**, 1049–1062.
- Kwak KJ, Kim YO, Kang H.** 2005. Characterization of transgenic Arabidopsis plants overexpressing GR-RBP4 under high salinity, dehydration, or cold stress. *Journal of Experimental Botany* **56**, 3007–3016.
- Kwon CS, Lee D, Choi G, Chung WI.** 2009. Histone occupancy-dependent and -independent removal of H3K27 trimethylation at cold-responsive genes in Arabidopsis. *The Plant Journal* **60**, 112–121.
- Laubinger S, Zeller G, Henz SR, Buechel S, Sachsenberg T, Wang JW, Ratsch G, Weigel D.** 2010. Global effects of the small

- RNA biogenesis machinery on the Arabidopsis thaliana transcriptome. *Proceedings of the National Academy of Sciences, USA* **107**, 17466–17473.
- Lee BH, Henderson DA, Zhu JK.** 2005. The Arabidopsis cold-responsive transcriptome and its regulation by ICE1. *The Plant Cell* **17**, 3155–3175.
- Li Y, Butenko Y, Graf G.** 2005. Histone deacetylation is required for progression through mitosis in tobacco cells. *The Plant Journal* **41**, 346–352.
- Lindroth AM, Cao X, Jackson JP, Zilberman D, McCallum CM, Henikoff S, Jacobsen SE.** 2001. Requirement of CHROMOMETHYLASE3 for maintenance of CpXpG methylation. *Science* **292**, 2077–2080.
- Liu HH, Tian X, Li YJ, Wu CA, Zheng CC.** 2008. Microarray-based analysis of stress-regulated microRNAs in Arabidopsis thaliana. *RNA* **14**, 836–843.
- Liu PP, Montgomery TA, Fahlgren N, Kasschau KD, Nonogaki H, Carrington JC.** 2007. Repression of AUXIN RESPONSE FACTOR10 by microRNA160 is critical for seed germination and post-germination stages. *The Plant Journal* **52**, 133–146.
- Lo WS, Duggan L, Emre NCT, Belotserkovskaya R, Lane WS, Shiekhhattar R, Berger SL.** 2001. Snf1—a histone kinase that works in concert with the histone acetyltransferase Gcn5 to regulate transcription. *Science* **293**, 1142–1146.
- Lu C, Fedoroff N.** 2000. A mutation in the Arabidopsis HYL1 gene encoding a dsRNA binding protein affects responses to abscisic acid, auxin, and cytokinin. *The Plant Cell* **12**, 2351–2366.
- Madlung A, Comai L.** 2004. The effect of stress on genome regulation and structure. *Annals of Botany* **94**, 481–495.
- Martinez C, Pons E, Prats G, Leon J.** 2004. Salicylic acid regulates flowering time and links defence responses and reproductive development. *The Plant Journal* **37**, 209–217.
- Matzke MA, Birchler JA.** 2005. RNAi-mediated pathways in the nucleus. *Nature Reviews Genetics* **6**, 24–35.
- Matzke M, Kanno T, Huettel B, Daxinger L, Matzke AJ.** 2007. Targets of RNA-directed DNA methylation. *Current Opinion in Plant Biology* **10**, 512–519.
- Matzke MA, Matzke AJ, Pruss GJ, Vance VB.** 2001. RNA-based silencing strategies in plants. *Current Opinion in Genetics and Development* **11**, 221–227.
- Miller MJ, Barrett-Wilt GA, Hua Z, Vierstra RD.** 2010. Proteomic analyses identify a diverse array of nuclear processes affected by small ubiquitin-like modifier conjugation in Arabidopsis. *Proceedings of the National Academy of Sciences, USA* **107**, 16512–16517.
- Ndamukong I, Jones DR, Lapko H, Divecha N, Avramova Z.** 2010. Phosphatidylinositol 5-phosphate links dehydration stress to the activity of ARABIDOPSIS TRITHORAX-LIKE factor ATX1. *PLoS One* **5**, e13396.
- Papp I, Mur LA, Dalmadi A, Dulai S, Koncz C.** 2004. A mutation in the cap binding protein 20 gene confers drought tolerance to Arabidopsis. *Plant Molecular Biology* **55**, 679–686.
- Pecinka A, Dinh HQ, Baubec T, Rosa M, Lettner N, Mittelsten Scheid O.** 2010. Epigenetic regulation of repetitive elements is attenuated by prolonged heat stress in Arabidopsis. *The Plant Cell* **22**, 3118–3129.
- Peng M, Cui Y, Bi YM, Rothstein SJ.** 2006. AtMBD9: a protein with a methyl-CpG-binding domain regulates flowering time and shoot branching in Arabidopsis. *The Plant Journal* **46**, 282–296.
- Pikaard CS.** 2006. Cell biology of the Arabidopsis nuclear siRNA pathway for RNA-directed chromatin modification. *Cold Spring Harbor Symposia on Quantitative Biology* **71**, 473–480.
- Rasia RM, Mateos J, Bologna NG, Burdisso P, Imbert L, Palatnik JF, Boisbouvier J.** 2010. Structure and RNA interactions of the plant MicroRNA processing-associated protein HYL1. *Biochemistry* **49**, 8237–8239.
- Razin A, Webb C, Szyf M, Yisraeli J, Rosenthal A, Naveh-Many T, Sciaky-Gallili N, Cedar H.** 1984. Variations in DNA methylation during mouse cell differentiation *in vivo* and *in vitro*. *Proceedings of the National Academy of Sciences, USA* **81**, 2275–2279.
- Reyes JL, Chua NH.** 2007. ABA induction of miR159 controls transcript levels of two MYB factors during Arabidopsis seed germination. *The Plant Journal* **49**, 592–606.
- Richards EJ, Elgin SC.** 2002. Epigenetic codes for heterochromatin formation and silencing: rounding up the usual suspects. *Cell* **108**, 489–500.
- Ruiz-Ferrer V, Voinnet O.** 2009. Roles of plant small RNAs in biotic stress responses. *Annual Review of Plant Biology* **60**, 485–510.
- Saleh A, Al-Abdallat A, Ndamukong I, Alvarez-Venegas R, Avramova Z.** 2007. The Arabidopsis homologs of trithorax (ATX1) and enhancer of zeste (CLF) establish 'bivalent chromatin marks' at the silent AGAMOUS locus. *Nucleic Acids Research* **35**, 6290–6296.
- Scebba F, De Bastiani M, Bernacchia G, Andreucci A, Galli A, Pitto L.** 2007. PRMT11: a new Arabidopsis MBD7 protein partner with arginine methyltransferase activity. *The Plant Journal* **52**, 210–222.
- Schmid M, Uhlenhaut NH, Godard F, Demar M, Bressan R, Weigel D, Lohmann JU.** 2003. Dissection of floral induction pathways using global expression analysis. *Development* **130**, 6001–6012.
- Schmitz RJ, Hong L, Fitzpatrick KE, Amasino RM.** 2007. DICER-LIKE 1 and DICER-LIKE 3 redundantly act to promote flowering via repression of FLOWERING LOCUS C in Arabidopsis thaliana. *Genetics* **176**, 1359–1362.
- Schonrock N, Bouveret R, Leroy O, Borghi L, Kohler C, Grissem W, Hennig L.** 2006. Polycomb-group proteins repress the floral activator AGL19 in the FLC-independent vernalization pathway. *Genes and Development* **20**, 1667–1678.
- Schubert D, Primavesi L, Bishopp A, Roberts G, Doonan J, Jenuwein T, Goodrich J.** 2006. Silencing by plant Polycomb-group genes requires dispersed trimethylation of histone H3 at lysine 27. *EMBO Journal* **25**, 4638–4649.
- Shen J, Xie K, Xiong L.** 2010. Global expression profiling of rice microRNAs by one-tube stem-loop reverse transcription quantitative PCR revealed important roles of microRNAs in abiotic stress responses. *Molecular and General Genetics* **284**, 477–488.
- Sherman JD, Talbert LE.** 2002. Vernalization-induced changes of the DNA methylation pattern in winter wheat. *Genome* **45**, 253–260.

- Shindo C, Lister C, Crevillen P, Nordborg M, Dean C.** 2006. Variation in the epigenetic silencing of FLC contributes to natural variation in Arabidopsis vernalization response. *Genes and Development* **20**, 3079–3083.
- Springer NM, Kaeppeler SM.** 2005. Evolutionary divergence of monocot and dicot methyl-CpG-binding domain proteins. *Plant Physiology* **138**, 92–104.
- Sridha S, Wu K.** 2006. Identification of AtHD2C as a novel regulator of abscisic acid responses in Arabidopsis. *The Plant Journal* **46**, 124–133.
- Sridhar VV, Kapoor A, Zhang K, Zhu J, Zhou T, Hasegawa PM, Bressan RA, Zhu JK.** 2007. Control of DNA methylation and heterochromatic silencing by histone H2B deubiquitination. *Nature* **447**, 735–738.
- Stangeland B, Rosenhave EM, Winge P, Berg A, Amundsen SS, Karabeg M, Mandal A, Bones AM, Grini PE, Aalen RB.** 2009. AtMBD8 is involved in control of flowering time in the C24 ecotype of Arabidopsis thaliana. *Physiologia Plantarum* **136**, 110–126.
- Steward N, Ito M, Yamaguchi Y, Koizumi N, Sano H.** 2002. Periodic DNA methylation in maize nucleosomes and demethylation by environmental stress. *Journal of Biological Chemistry* **277**, 37741–37746.
- Stockinger EJ, Mao Y, Regier MK, Triezenberg SJ, Thomashow MF.** 2001. Transcriptional adaptor and histone acetyltransferase proteins in Arabidopsis and their interactions with CBF1, a transcriptional activator involved in cold-regulated gene expression. *Nucleic Acids Research* **29**, 1524–1533.
- Sung S, Amasino RM.** 2004. Vernalization in Arabidopsis thaliana is mediated by the PHD finger protein VIN3. *Nature* **427**, 159–164.
- Sunkar R, Zhu JK.** 2004. Novel and stress-regulated microRNAs and other small RNAs from Arabidopsis. *The Plant Cell* **16**, 2001–2019.
- Taji T, Ohsumi C, Iuchi S, Seki M, Kasuga M, Kobayashi M, Yamaguchi-Shinozaki K, Shinozaki K.** 2002. Important roles of drought- and cold-inducible genes for galactinol synthase in stress tolerance in Arabidopsis thaliana. *The Plant Journal* **29**, 417–426.
- Tanigawa Y, Tsuchiya M, Imai Y, Shimoyama M.** 1984. ADP-ribosyltransferase from hen liver nuclei. Purification and characterization. *Journal of Biological Chemistry* **259**, 2022–2029.
- Tessadori F, van Zanten M, Pavlova P, et al.** 2009. Phytochrome B and histone deacetylase 6 control light-induced chromatin compaction in Arabidopsis thaliana. *PLoS Genetics* **5**, e1000638.
- Tian L, Chen ZJ.** 2001. Blocking histone deacetylation in Arabidopsis induces pleiotropic effects on plant gene regulation and development. *Proceedings of the National Academy of Sciences, USA* **98**, 200–205.
- Tittel-Elmer M, Bucher E, Broger L, Mathieu O, Paszkowski J, Vaillant I.** 2010. Stress-induced activation of heterochromatic transcription. *PLoS Genetics* **6**, e1001175.
- Urano K, Kurihara Y, Seki M, Shinozaki K.** 2010. ‘Omics’ analyses of regulatory networks in plant abiotic stress responses. *Current Opinion in Plant Biology* **13**, 132–138.
- Vaillant I, Schubert I, Tourmente S, Mathieu O.** 2006. MOM1 mediates DNA-methylation-independent silencing of repetitive sequences in Arabidopsis. *EMBO Reports* **7**, 1273–1278.
- van Dijk K, Ding Y, Malkaram S, et al.** 2010. Dynamic changes in genome-wide histone H3 lysine 4 methylation patterns in response to dehydration stress in Arabidopsis thaliana. *BMC Plant Biology* **10**, 238.
- Vongs A, Kakutani T, Martienssen RA, Richards EJ.** 1993. Arabidopsis thaliana DNA methylation mutants. *Science* **260**, 1926–1928.
- Wada KC, Takeno K.** 2010. Stress-induced flowering. *Plant Signaling and Behavior* **5**, 944–917.
- Wada KC, Yamada M, Shiraya T, Takeno K.** 2010. Salicylic acid and the flowering gene FLOWERING LOCUS T homolog are involved in poor-nutrition stress-induced flowering of Pharbitis nil. *Journal of Plant Physiology* **167**, 447–452.
- Wang WS, Pan YJ, Zhao XQ, Dwivedi D, Zhu LH, Ali J, Fu BY, Li ZK.** 2010. Drought-induced site-specific DNA methylation and its association with drought tolerance in rice (*Oryza sativa* L.). *Journal of Experimental Botany* **62**, 1951–1960.
- Xiao W, Custard KD, Brown RC, Lemmon BE, Harada JJ, Goldberg RB, Fischer RL.** 2006. DNA methylation is critical for Arabidopsis embryogenesis and seed viability. *The Plant Cell* **18**, 805–814.
- Yaish MW, Peng M, Rothstein SJ.** 2009. AtMBD9 modulates Arabidopsis development through the dual epigenetic pathways of DNA methylation and histone acetylation. *The Plant Journal* **59**, 123–135.
- Zemach A, Gaspan O, Grafi G.** 2008. The three methyl-CpG-binding domains of AtMBD7 control its subnuclear localization and mobility. *Journal of Biological Chemistry* **283**, 8406–8411.
- Zhang JF, Yuan LJ, Shao Y, Du W, Yan DW, Lu YT.** 2008. The disturbance of small RNA pathways enhanced abscisic acid response and multiple stress responses in Arabidopsis. *Plant, Cell and Environment* **31**, 562–574.
- Zhang Y, Reinberg D.** 2001. Transcription regulation by histone methylation: interplay between different covalent modifications of the core histone tails. *Genes and Development* **15**, 2343–2360.
- Zhang Z, Zhang S, Zhang Y, et al.** 2011. Arabidopsis floral initiator SKB1 confers high salt tolerance by regulating transcription and pre-mRNA splicing through altering histone H4R3 and small nuclear ribonucleoprotein LSM4 methylation. *The Plant Cell* **23**, 396–411.
- Zhao B, Liang R, Ge L, Li W, Xiao H, Lin H, Ruan K, Jin Y.** 2007. Identification of drought-induced microRNAs in rice. *Biochemical and Biophysical Research Communications* **354**, 585–590.
- Zhou C, Zhang L, Duan J, Miki B, Wu K.** 2005. HISTONE DEACETYLASE19 is involved in jasmonic acid and ethylene signaling of pathogen response in Arabidopsis. *The Plant Cell* **17**, 1196–1204.
- Zilberman D, Gehring M, Tran RK, Ballinger T, Henikoff S.** 2007. Genome-wide analysis of Arabidopsis thaliana DNA methylation uncovers an interdependence between methylation and transcription. *Nature Genetics* **39**, 61–69.