Sustainable harvest: managing plasticity for resilient crops

Justin A. Bloomfield, Terry J. Rose and Graham J. King*

Southern Cross Plant Science, Southern Cross University, Lismore, NSW, Australia

**Summary**

Maintaining crop production to feed a growing world population is a major challenge for this period of rapid global climate change. No consistent conceptual or experimental framework for crop plants integrates information at the levels of genome regulation, metabolism, physiology and response to growing environment. An important role for plasticity in plants is assisting in homeostasis in response to variable environmental conditions. Here, we outline how plant plasticity is facilitated by epigenetic processes that modulate chromatin through dynamic changes in DNA methylation, histone variants, small RNAs and transposable elements. We present examples of plant plasticity in the context of epigenetic regulation of developmental phases and transitions and map these onto the key stages of crop establishment, growth, floral initiation, pollination, seed set and maturation of harvestable product. In particular, we consider how feedback loops of environmental signals and plant nutrition affect plant ontogeny. Recent advances in understanding epigenetic processes enable us to take a fresh look at the crosstalk between regulatory systems that confer plasticity in the context of crop development. We propose that these insights into genotype × environment (G × E) interaction should underpin development of new crop management strategies, both in terms of information-led agronomy and in recognizing the role of epigenetic variation in crop breeding.

**Crop plasticity, G × E and epigenetics**

Maintaining crop production to feed a growing world population is a major challenge for this period of rapid global climate change. The high crop yields following the Green Revolution arose from development of new varieties, irrigation and extensive application of fertilizers and pesticides during a period of atypical climate stability. Increases in crop yields have now slowed and are likely to decline further as productive regions experience greater temperature fluctuations and increased demand for finite phosphate and water resources.

Generating climate-resilient crops will require a comprehensive understanding of the relationship between the composition of crop genomes and the underlying gene regulatory mechanisms that confer environmental plasticity and climatic adaptation. Polyploidy has underpinned the evolution of plants, providing a level of gene redundancy that has facilitated adaptation in non-domesticated plants to previous periods of climate change. Our ability to harness the plasticity of complex crop genomes demands greater insights into epigenetic processes and how these mediate signals between the environment, regulatory networks and gene function.

No consistent conceptual or experimental framework for crop plants integrates information at the levels of genome regulation, metabolism, physiology and response to growing environment. The approach outlined here is to evaluate plant plasticity in the context of epigenetic regulation of developmental phases and transitions, and map these onto the key stages of crop establishment, growth, floral initiation, pollination, seed set and maturation of harvestable product. In particular, we consider how feedback loops of environmental signals and plant nutrition affect plant ontogeny. Recent advances in understanding epigenetic processes enable us to take a fresh look at the crosstalk between regulatory systems that confer plasticity in the context of crop development. We propose that these insights into genotype × environment (G × E) interaction should underpin development of new crop management strategies, both in terms of information-led agronomy and in recognizing the role of epigenetic variation in crop breeding.

**Keywords:** crop plants, plasticity, epigenetics, development, climate change, adaptation.
result of paralogous genes (Osborn et al., 2003; Zhao et al., 2011).

Plasticity in plants assists in maintaining homeostasis in response to variable environmental conditions. Of particular relevance to crops, this may occur in response to permanent (soil type, altitude, niche), regular (seasonal, day length and light quality) or intermittent (rain, ambient temperature, wind) abiotic factors. Biotic influences eliciting plastic responses include herbivory, disease and plant–plant competition (Latzel et al., 2012). Each of these factors may to some extent influence development and timing of reproductive organs and sexual reproduction. Crop cultivars are also likely to suffer the fate of plant species that lack a plastic response to environmental cues, when a change in environment may drive less plastic plant species more rapidly into decline (Böhnke and Brulheide, 2013).

Epigenetic processes confer plasticity

Definitions of epigenetics have varied over the past 60 years, from ‘how genotypes give rise to phenotypes during development’ (Waddington and Kacser, 1957) to ‘the study of mitotically and/or meiotically heritable changes in gene function that cannot be explained by changes in DNA sequence’ (Russo et al., 1996). More recently, Bird (2007) defined epigenetics as ‘the structural adaptation of chromosomal regions so as to register, signal or perpetuate altered activity states’, which encompasses current understanding of molecular epigenetics involving components of DNA methylation, histone variants, small RNAs, transposable elements (TEs) and associated chromatin modulation. These components may be categorized as either (i) genome plasticity: structural or organizational genome changes associated with environmental signals leading to novel phenotypes (Nicotra et al., 2010) or (ii) epigenetic plasticity: the ability to modulate a genome for discrete cellular functions (Zhu and Reinberg, 2011).

Dynamic chromatin structure contributes to regulation of cell stage and identity and is influenced by environmental and endogenous factors through variation in the genomic distribution of DNA and histone epigenetic marks (Jarillo et al., 2009). These marks affect chromatin condensation and packaging, with specific molecular modifiers on histone proteins able to influence DNA transcription. Transient chromatin modifications have been suggested as the primary epigenetic system regulating epigenetic marks and machinery (Meagher, 2010).

Nucleosomes are highly conserved among eukaryotes and form the building blocks of chromatin, comprised of 147 bp DNA wound around dimers of four core histones: H2A, H2B, H3 and H4 (Sarma and Reinberg, 2005), and a further 20 bp associated with H1 linker histones forming the chromatosome (Kowalski and Polyga, 2012; Simpson, 1978). Within these five histone families, there are 13 subfamilies comprising of at least 76 variants, each of which can be chemically modified (e.g. methylation, acetylation, phosphorylation, etc.), providing an additional epigenetic code superimposed on the genome (Punta et al., 2012). Histone remodelling in situ, dimer exchange or variant replacement can confer structural and functional modifications to the chromatin resulting in altered levels of transcription (Ahmad et al., 2010; Bernstein and Hake, 2006; Kamakaka and Biggins, 2005; Sarma and Reinberg, 2005), particularly by modifying the ability of the transcription machinery to bind up- or downstream promoter regions. This rich variation underlies many aspects of orchestrated ontogeny as well as providing scope for plasticity by affecting the ability of genes to be expressed at an appropriate level both spatially, temporally (Cohen et al., 2009) and in response to environment.

Cytosine methylation (5mC), replicated by methyltransferases during mitosis, provides a stable but plastic epigenetic mark superimposed on genomic DNA (Goettel and Messing, 2013; Zhang et al., 2013b), with a key role in silencing TEs and gene expression levels (He et al., 2011; Tsuchiya and Eulgem, 2013). The methyleme represents the full set of DNA methylation marks, with potential for further in vivo chemical modifications resulting in conversion to 5-hydroxymethyl, 5-formyl and 5-carboxyl cytosines, for which structural, regulatory and functional roles are currently being established (Kriukiene et al., 2012).

Transposable elements are often hypermethylated and comprise a large portion of many crop genomes, such as barley (84%) and wheat (80%), sorghum (55%) and soybean (59%; Cantu et al., 2010; Mayer et al., 2012; Paterson et al., 2009; Schmutz et al., 2010). TEs are also able to act as a source of novel genes, such as Daysleeper in Arabidopsis from the hoboActTam superfamily of TEs (Alzohairy et al., 2013), Gary in a number of cereal genomes (Muelhbauer et al., 2006) and SchAT in sugarcane (de Jesus et al., 2012). Silencing of TEs may involve a variety of epigenetic marks including DNA methylation, histone 3 lysine dimethylation and small interfering RNAs (Bucher et al., 2012; Sasaki et al., 2012), with perturbation of DNA methylation in TE regions able to reactivate their expression (Kantama et al., 2013). DNA methylation is generally recognized as providing a natural defence system for plants against the expansion of TEs (Kantama et al., 2013). Recent evidence in maize indicates that genes <500 bp from TEs are expressed less than genes further up- or downstream (Goettel and Messing, 2013), with repression of the gene able to be influenced by the epigenetic marks employed in silencing the TE.

In plants, cytosine methylation occurs in three sequence contexts, with decreasing abundance of CG, CHG and CHH (where H is any nucleotide except G). This contrasts with mammalian systems, where it occurs predominantly in a CG context (Jaenisch and Bird, 2003). Each methylation context in plants is thought to be regulated primarily by three different families of DNA methyltransferases MET1 for CG, CMT for CHG and DRM for CHH (Law and Jacobsen, 2010), although a more recent study has indicated the possibility of additional methyltransferases (Stroud et al., 2013). Variation in DNA methylation can have significant effects on chromatin structure, with increases in 5mC marks associated with the alignment of nucleosomes in plant genomes (Chodavarapu et al., 2010).

The distribution of epialleles superimposed on genetic maps can be revealed by methylation-sensitive AFLP and retrotransposon epimarkers. In Brassica napus biparental populations, this distribution appears nonrandom, with some clustering of parent-specific methylated alleles (Long et al., 2011). This study demonstrated a high level of stability, with 90% of mapped markers retaining their allelic pattern in contrasting environments and developmental stage, and stable transmission through multiple meioses.

Methylome maps at base pair resolution have been generated for Arabidopsis (Zhang et al., 2006), rice (Oryza; Li et al., 2012b) and tomato (Solanum lycopersicum; Zhong et al., 2013) based on bisulphite sequencing, where unmodified cytosines are converted to uracil (sequenced as T) and 5mC remains sequenced as C. Methylation states are far from static, with reproductive tissues of
endosperm and embryo, from torpedo-stage seeds in particular, undergoing large-scale re-patterning in Arabidopsis (Gehring et al., 2009). Methylome mapping of tomato fruit has shown that while distinct methylation patterns are associated with specific tissues and reproductive organs, mean methylation levels remain similar (Zhong et al., 2013). However, demethylation of TE regions is observed, with otherwise variable patterns of DNA methylation throughout the developmental pathway. microRNAs (miRNAs), a class of small noncoding RNA, may also regulate initiation of fruit development in tomato, with miR393 and miR167 appearing to target a putative auxin receptor (SITIR1) and auxin response factors that consequently modulate auxin, a key regulator of fruit development (Karlova et al., 2013).

Comparison of tissue-specific methylomes can provide an indication of changing patterns of gene regulation associated with epigenetic plasticity. Actively transcribed regions of euchromatin are often associated with hypomethylated DNA, whereas condensed heterochromatin regions are frequently hypermethylated (May, 2010). The reversibility of DNA methylation states may confer plasticity to an organism by facilitating regulation of RNA transcription from genomic regions or specific genes. Hypermethylated DNA regions can lead to transcriptional silencing and result in a quiescent state, which can later be derepressed through demethylation triggered by signalling factors. For example, during rice endosperm biogenesis, DNA demethylation is crucial for correct gene transcription (Zemach et al., 2010).

Two broad classes of post-transcriptionally processed small noncoding RNAs (snRNAs), miRNA and small interfering RNA (siRNA), are associated with gene silencing as antisense complements to untranslated genome regions, which include DNA transcription factor (TF)-binding sites (Bartel, 2004; Pattanayak et al., 2013). snRNAs are generally short lived within cells, but can play key regulatory roles in plant development and $G \times E$ interactions via pre- and post-transcriptional regulation of gene expression (Ahmad et al., 2010). Crucially, their mobility enables signal transduction beyond the immediate site of initiation via plasmodesmata or over longer distances through the phloem (Uddin and Kim, 2011). This confers considerable plasticity, particularly in relation to mediating homeostasis of mineral nutrients from root source to vegetative and reproductive sinks. Several regulatory elements are responsible for the differential expression of miRNAs among cell types (Zeng, 2006), with variations in the stepwise nature of the process. RNA-directed DNA methylation (RdDM) is an important epigenetic process that in plants involves snRNA-mediated targeting of de novo DNA methylation by DNA methyltransferase DOMAINS REARRANGED METHYLTRANSFERASE2 (DRM2; Chan et al., 2004; Henderson, 2012; Matzke et al., 2007).

**A developmental framework for crop yield and quality**

Prior to harvest, most crops undergo phase transitions through one or more developmental stages. These include germination, seedling establishment and root and/or tuber development, juvenility, vegetative branching, floral induction, inflorescence development, gamete production, pollination, development and maturity of fruit and seed (Figure 1). For food crops including staple cereals and oilseed grains, the latter stages of seed development and maturity represent the final stages of yield potential, whereas fruit crops depend on the timely development of carpel or associated tissues. Vegetables represent a wide range of organs that are harvested at specific stages, with some such as cauliflower or broccoli arrested at defined stages during reproductive development. For vegetatively propagated crops, the regeneration of rooting systems is a key determinant of establishment (Shepherd et al. 2013).

**Crop establishment, vegetative growth and canopy architecture**

The rapid and synchronized establishment of crops is dependent upon successful germination and subsequent seedling vigour that enables rapid search and acquisition of water and nutrient resources while competing with weeds. Plasticity during vegetative growth provides flexibility in decisions relating to timing and patterning of stem and root branching, meristem identity variations and individual cell responses.

---

**Figure 1** Typical stages within the crop cycle, with corresponding stages of plant development.
It has become apparent that epigenetic mechanisms play important roles during these early growth phases. Of the more than 40 genes involved with chromatin remodelling in Arabidopsis, at least 17 are implicated in maintenance of vegetative growth (Jarillo et al., 2009). These include genes expressed in shoot apical meristems (SAMs) such as AtBRACH1MA (ABRM), BRUSHY1 (BRUT)/MGON3 (MGO3)/TONSOKU (TSK), FASCIATA 1/2 (FAS1/2), MULTICOPY SUPPRESSOR OF IRA 1 (MSI1) and SPLAYED (SYD); Table 1; Jarillo et al., 2009). Both vegetative and reproductive meristem identities are influenced by epigenetic regulation, such as the DNA methylation within the rice OsMADS1 promoter region, and OsLEC1 stimulation of histone H3 post-translational modifications including methylation and acetylation (Table 1; Zhang and Xue, 2013). Expression of specific histone modifiers can occur either in an organ specific manner or throughout the plant during growth phases. In tomato, 124 post-translational histone modifiers have been described that cover a broad functional range and include both novel and homologous motifs shared with Arabidopsis, maize and rice (Cigliano et al., 2013).

In Arabidopsis, the overall 5mC genome content increases from cotyledon emergence through to reproductive organogenesis (Ruiz-Garcia et al., 2005). This suggests a broad range of genes are involved early in plant life cycles, while in reproductive tissues, a more specialized set of genes are required. Although increased methylation has generally been associated with a decrease in gene expression, Arabidopsis RNA expression profiles lack a corresponding decrease in overall transcription throughout vegetative growth (Richards et al., 2012).

Adverse abiotic environments can induce plant miRNA expression profiles that may be unique to a given stressor, although many miRNAs are expressed in response to more than one stressor (López et al., 2012). In sugarcane (Saccharum spp.), miRNAs are expressed additively with increasing water deficit, suggesting a progressive up-regulation of genes contributing to drought resistance (Ferreira et al., 2012; Gentile et al., 2013). Accumulation of miR159 triggered by abscisic acid (ABA) appears to contribute to inactivation of sugarcane axillary bud outgrowth (Ortíz-More et al., 2013).

Involvement of plant hormones in signalling networks can also elicit plastic responses to environmental conditions (Xu et al., 2013), with crosstalk to the epigenome system including histone modifications. For example, ABA has been shown to induce H3K4 trimethylation, which acts with H3K9 acetylation as a gene activation marker (Kim et al., 2013a). Multiple ABA receptors may affect different subsets of pathways, affecting vegetative processes such as germination, stomatal movement and osmotic regulation, depending from which tissue or subcellular compartment signals arise (Golldack et al., 2013; Nakashima and Yamaguchi-Shinozaki, 2013; Xu et al., 2013).

Shoot branching can be regulated by auxin and strigolactones (Stirnberg et al., 2010; Yaish et al., 2010), with auxillary meristems undergoing an initial period of rapid cell division to form an axillary bud, often followed by temporary or permanent arrest (Leyser, 2009). In Arabidopsis, BRANCH1 (BRC1) is a key local factor contributing to bud arrest that is up-regulated in response to shading from neighbours, which is perceived as a decrease in red : far red (R : FR) light ratio, and is negatively regulated by phytochrome B (Gonzalez-Grandio et al., 2013; Hofmann, 2013; Niwa et al., 2013). Repression of BRC1 in axillary buds allows shoot development to restart. However, simultaneous up-regulation of FLOWERING LOCUS T (FT) and repression of BRC1 can result in a transition from axillary bud to an inflorescence meristem (Hofmann, 2013; Martin-Trillo et al., 2011; Stirnberg et al., 2010). Thus, the ability of plants to exhibit plasticity in response to external stimuli may not always be a consequence of epigenetic regulation.

Nutrient acquisition and root development

Crop productivity relies on adequate and balanced supplies of nutrients to ensure timely growth and progression through developmental stages. Plants require 16 elements to complete their life cycle, and the available quantities of these elements vary widely across soils and can fluctuate with seasonal changes. Plants have thus evolved a number of mechanisms that regulate the uptake and homeostasis of these elements throughout their life cycle. Nutrient homeostasis relies on several large families of transporters to facilitate root uptake and subsequent distribution of micronutrient anions and cations (Gierth and Maser, 2007; Rausch and Bucher, 2002; White and Broadley, 2009). The regulation of these transporters typically involves a series of gene networks and signalling systems that respond to external (i.e. at the root surface) or internal stimuli. For example, root plasticity in response to variation in soil temperature (soybean) and water availability (tomato) appears to be facilitated by modulation of 5mC and histone modifications (Gonzalez et al., 2013; Stepinski, 2012). These gene networks, their molecular regulation and post-transcriptional regulation have been widely studied (see reviews by Fox and Guerinot, 1998; Glass et al., 2002; White and Broadley, 2009).

To respond to changing mineral availability and requirements during crop development, and in impoverished soils, it is important for crop cultivars to incorporate plasticity in management of source/sink relationships. It has been demonstrated in Arabidopsis that miRNAs are part of a programmed response to fluctuating nutrient availability, with several plant miRNAs found to regulate TF expression, such as miR169 targeting HAP2, and target genes involved in phosphate, sulphate and copper metabolism (Kehr, 2013; López et al., 2012; Zeng et al., 2014). For example, inorganic phosphorus deprivation leads to induced expression of miR156, miR399, miR778, miR827 and miR2111 and repression of the expression of miR169, miR395 and miR398 (Hsieh et al., 2009). To date, the role of miR399 has been elucidated (reviewed by Rouached et al., 2010), and miR395 has been shown to be induced by sulphate limitation (Kawashima et al., 2009), while miR398 is induced by copper deficiency (Beauciel et al., 2010). An overlapping web of miRNAs associated with nutrient stress response has been inferred from the response of a number of these miRNAs to nitrogen starvation in maize, rice and common bean (Fischer et al., 2013). Understanding the dynamics of epigenetic regulation affecting nutrient homeostasis will open up new approaches for crop agronomic management.

Epigenetic processes have also been strongly implicated in root development. A combination of auxin and histone modulation regulate 5-PHASE KINASE-ASSOCIATED PROTEIN2B (SKP2B) expression (Table 1), a repressor of meristem cell division in Arabidopsis that can regulate root branching (Manzano et al., 2012; Saini et al., 2013). Roots tend to proliferate and physiologically enhance their nutrient uptake capacity when encountering a nutrient-rich zone (Hodge, 2004). However, the actual benefit to the plant from root plasticity, while seemingly obvious, has been challenging to quantify due to the technical difficulties in assessing traits such as quantifiable root responses to nitrogen-rich soil
| Species          | Crop trait                          | Gene | Gene class       | Gene function                                                                 | Epigenetic mode                                                                 | References                                                   |
|------------------|-------------------------------------|------|------------------|--------------------------------------------------------------------------------|--------------------------------------------------------------------------------|--------------------------------------------------------------|
| Arabidopsis      | Vernalization                       | AG   | MADS domain type | Reduces H3K27 trimethylation of KNU                                             | –                                                                              | Ito (2012), Lamesch et al. (2011)                            |
| Arabidopsis      | Vernalization                       | AGL19 | MADS-box         | H3K27 trimethylation, possibly regulated by PRC2                              | –                                                                              | Lamesch et al. (2011), Schonrock et al. (2006)               |
| Arabidopsis      | Flowering                           | AP1  | MADS domain protein | –                                                                          | –                                                                              | Lamesch et al. (2011), Saleh et al. (2000Bb)                 |
| Arabidopsis      | Vegetative development and flowering| AtBRCM| SWI/SNF chromatin-remodelling ATPase | Involved in chromatin remodelling                                              | –                                                                              | Jarillo and Pineiro (2011), Lamesch et al. (2011)           |
| Brassica         | Flowering and fertilization         | BcIM30| jmjC domain-containing histone demethylase | Putative histone demethylase regulating cell fate                             | –                                                                              | Lamesch et al. (2011), Li et al. (2012c)                    |
| Arabidopsis      | Plant architecture                  | BNS  | Anaphase-promoting complex | Methylated                                                                     | Hypermethylation induces by ddm1 dominance and abnormal floral morphology     | Saaze and Kakutani (2007)                                   |
| Arabidopsis      | Vegetative development              | BRU1/ MGO3/T5K | Tetratricopeptide repeat | Putative part of a protein complex involved in chromatin organization         | –                                                                              | Jarillo and Pineiro (2011), Lamesch et al. (2011)           |
| Arabidopsis      | –                                   | CMT3 | Chromomethylase   | DNA methylation maintenance in CHG contexts                                    | –                                                                              | Lamesch et al. (2011), Law and Jacobsen (2010)             |
| Solanum lycopersicon | Fruit (pericarp) ripening       | CNR  | MADS TF          | Hypomethylated                                                                 | Hypermethylation                                                               | Manning et al. (2006)                                       |
| Linaria vulgaris | –                                   | CYCLOIDEA Class II TCP transcription activator | Hypomethylated. Normal floral symmetry                                         | Hypermethylated allele confers irregular floral symmetry                       | Cubas et al. (1999)                                        |
| Oryza            | Stature                            | D1   | –                | –                                                                              | Transcriptional initiation site differentially hypermethylated in metastable Epi-d1 | Miura et al. (2009b)                                       |
| Arabidopsis      | Flowering/fertilization             | DDM1 | SWI2/SNF2-like chromatin-remodelling protein | DNA methylation and heterochromatin maintenance                                | –                                                                              | Lamesch et al. (2011), Melamed-Besudo and Levy (2012)       |
| Arabidopsis      | –                                   | DME  | DNA glycosylase DEMETER | Maternal-allele-specific hypomethylation at the MEDEA (MEA) gene               | –                                                                              | Lamesch et al. (2011)                                       |
| Arabidopsis      | –                                   | DRM2 | Dormancyauxin-associated family protein | DNA methylation maintenance in CHH contexts                                    | –                                                                              | Law and Jacobsen (2010)                                    |
| Arabidopsis      | –                                   | FAS1/2| Chromatin Assembly Factor-1 | De novo nucleosome assembly during DNA replication                            | Reduced heterochromatin content                                                | Jarillo and Pineiro (2011), Lamesch et al. (2011)          |
| Arabidopsis      | Seed development                    | PIE  | Polycomb protein | –                                                                              | Mediated by DEMETER                                                           | Ghad et al. (1996), Luo et al. (1999)                      |
| Arabidopsis      | Seed development                    | FIS2 | TF                | Methylated                                                                     | Modified histone derepresses                                                   | Bastow et al. (2004), Saleh et al. (2000Bb)                 |
| Arabidopsis      | Vernalization                       | FLC  | Nuclear localized | –                                                                              | –                                                                              | Lamesch et al. (2011)                                       |
| Arabidopsis, Brassica | Flowering, vernalization          | FT   | Phosphatidylethanolamine-binding protein | Paralogues independently silenced by 5mC                                       | –                                                                              | Kinoshita et al. (2004), Soppe et al. (2000)                |
| Arabidopsis      | Seed development                    | FWA  | Homeodomain-containing TF | Hypermethylated and positively regulates flowering                               | Hypomethylated allele confers late flowering, mediated by DEMETER             | Kinoshita et al. (2004), Soppe et al. (2000)                |

Managing plasticity for resilient crops 521
| Species     | Crop trait                      | Gene (Gene class) | Gene function                                      | Epigenetic mode                                      | References                                      |
|-------------|---------------------------------|-------------------|----------------------------------------------------|------------------------------------------------------|------------------------------------------------|
| *Helianthus*| Embryogenesis                   | Hal1L CCAAT box-binding factor | Differential methylation of CG rich regions        | –                                                    | Salvini et al. (2012)                           |
| *Arabidopsis* | Floral number                   | KNU C2H2-type zinc finger protein | Reduction in H3K27 trimethylation resulting in its derepression | Precocious flowering                               | Ito and Sun (2009), Lamesch et al. (2011), Sun et al. (2009) |
| *Arabidopsis* | Seed development                | MEA Polycomb protein | Methylated                                          | Mediated by DEMETER                                | Grossniklaus et al. (1998), Gutierrez-Marcos et al. (2004) |
| *Zea mays*  | Seed development                | MEG1 Cys-rich protein | Biallelic at later stages                          | Maternal parent-of-origin expression during early stages of endosperm; development |                                                           |
| *Arabidopsis* | Vegetative development, seed set, ripening | MET1 Bromo adjacent homology (BAH) domain, C-5 cytosine methyltransferase | Maternal hypomethylation patterning and transgenerational epigenetic inheritance | Perturbation of auxin gradients in embryos          | Lamesch et al. (2011), Law and Jacobsen (2010), Paszkowski and Grossniklaus (2011) |
| *Arabidopsis* | Seed development                | MPC Poly(A)-binding protein | –                                                   | –                                                    | Tiwari et al. (2008), Jarillo and Pineiro (2011), Lamesch et al. (2011) |
| *Arabidopsis* | –                               | MS1 WD-40 repeat-containing protein | Involved in de novo nucleosome assembly            | –                                                   |                                                           |
| *Oryza*     | Vegetative and reproductive development | OsLECT1 CCAAT box-binding factor | Stimulates histone post-translational modification | –                                                    | Kawahara et al. (2013), Sakai et al. (2013)            |
| *Oryza*     | Sexual reproduction             | OsMADS1 MADS-box TF | Methylated promoter region                         | –                                                   | Kawahara et al. (2013), Sakai et al. (2013), Zhang and Xue (2013) |
| *Arabidopsis* | –                               | PAI2 Phosphoribosylanthranilate isomerase | Unmethylated. Does not fluoresce under UV light | Methylated allele leads to fluorescent shoots under UV light | Kohler and Makarevich (2006)                        |
| *Arabidopsis* | Seed development                | PHOREST MADS TF | –                                                   | –                                                    | Das and Messing (1994)                            |
| *Zea mays*  | Grain colour                    | PI DNA binding, similar to MYB oncogenes | Unmethylated allele P-pr confers uniform pigmentation of pericarp | Methylated alleles of P-pr-1 and P-pr-2 give variegated pigmentation of pericarp |                                                           |
| *Arabidopsis*, *Brassica* | Nucleolar dominance, Establishment | rDNA Ribosomal RNA | –                                                   | Nucleolar dominance                                 | Preuss and Pikaard (2007), Lamesch et al. (2011), Manzano et al. (2012), Shiba et al. (2006) |
| *Arabidopsis* | Establishment                   | SKP2B F-box       | Represses lateral root formation                   | –                                                    | Jacobsen and Meyerowitz (1997)                     |
| *Brassica*  | Self-incompatibility            | SP11 Cys-rich protein | Promoter methylated                                | Demethylation leads to transcription                | Jarillo and Pineiro (2011), Lamesch et al. (2011) |
| *Arabidopsis* | Male appendages                 | SUPERMAN Zinc finger protein | Unmethylated. Normal flower development            | Hypermethylated allele results in excessive staminoid organs | Bastow et al. (2004), Lamesch et al. (2011), Sung and Amasino (2004) |
| *Arabidopsis* | –                               | SYD SW12/SNF2-like protein | –                                                   | –                                                    |                                                           |
| *Arabidopsis* | Vernalization                   | VRN1/VRN3 TF      | Reduces H3K9 acetylation and dimethylation of FLC  | –                                                    |                                                           |

TF, transcription factor.
patches (Hodge, 2004) and their effects on root epigenetic marks and mechanisms (Manzano et al., 2012). Recent work has demonstrated that miR390 is involved in lateral root initiation and is possibly mobile within the root primordia (reviewed in Marin-Gonzalez and Suarez-Lopez, 2012). Loss of SDC2-mediated chromatin modulation resulting in reduced H3K4 methylation in root stem cells also impairs later root establishment and causes a loss of auxin gradient maximum (Yao et al., 2013).

Climate control of floral initiation

Development of resilient crop cultivars requires adaptation to increased variability in the seasonal patterns of temperature and precipitation, where significant changes in phenotype have been observed over the past two decades. This leads to the prospect of optimal growing regions for particular crops migrating to different latitudes, with consequent changes in photoperiod affecting key stages of floral induction and reproductive development.

Plasticity enables over-wintering annuals and perennial crops to respond to the length and severity of winter, while retaining tightly regulated mechanisms that ensures individuals are coordinated in reaching reproductive maturity. The passing of winter perceived as the vernalization signal enables promotion of the flowering program (Auszin et al., 2005; Guzy-Wrobelska et al., 2013; Song et al., 2012; Srikanth and Schmid, 2011; Yamaguchi and Abe, 2012), with considerable variation in the cardinal temperatures (from 4 to 19 °C), reflecting regional adaptation to latitude and altitude (Wollenberg and Amasino, 2012; Wurr et al., 2004). In vernalization-sensitive species, the length of winter is perceived as an integral of daytime degrees below a threshold temperature by an additive effect of histone modifications that regulate silencing of FLOWERING LOCUS C (FLC; Table 1; Sheldon et al., 2009).

The vernalization signal can occur at different developmental stages depending on species and is recorded by epigenetic switches that can be maintained through in vitro vegetative propagation, but is reset during sexual reproduction (Song et al., 2012). The mechanism typically involves active repression of FLC or FLC-like genes until a target threshold has been perceived (Sheldon et al., 2009; Xiao et al., 2013). In Arabidopsis, FLC is repressed by reducing H3 acetylation and dimethylation of H3K9 through the action of REDUCED VERNALIZATION 1/VERNALIZATION INSENSITIVE 3 (VRN1/VRN3; Table 1; Bastow et al., 2004; Sung and Amasino, 2004). After winter, derepression of FLC occurs gradually by histone remodification (Song et al., 2012). In both winter and spring rape (B. napus) 5mC is significantly decreased in response to cold treatment, with subsequent gradual re-methylation to pretreatment levels in spring rape, but only up to 70% in winter rape (Guzy-Wrobelska et al., 2013). Similar cold-induced changes in 5mC patterning has been reported in other crop species, including cotton, maize, rice and wheat, suggesting some overall mechanistic conservation of epigenetic regulation across plant taxa (Fan et al., 2013; Pan et al., 2011; Sherman and Talbert, 2002; Steward et al., 2002).

A network of TFs associated with vernalization mediates signal transduction to floral initiation. Although this control pathway is not fully understood, the AGAMOUS-like MADS-box gene AGL19 is expressed in response to vernalization (Kim et al., 2013b; Schonrock et al., 2006) and activates LEAFY (LFY) and APETALA1 (AP1), both involved in floral meristem induction and transition (Lamesch et al., 2011). Elevated H3K27 trimethylation in the AGL19 chromatin region suggests epigenetic regulation (Table 1), which may itself be regulated by POLYCOMB REPRES-

SIVE COMPLEX 2 (PRC2), also acting in response to vernalization (Schonrock et al., 2006). Small RNAs are involved in the transcription and regulation of flowering time signals in response to vernalization (Oh et al., 2007) and include miR399, first reported as associated with inorganic phosphorus homeostasis (Fuji et al., 2005). miR399 appears to respond to temperature and induce floral development via its target gene AT2G33770.1 (PHO2; Kim et al., 2011). This suggests that nutrient uptake may also promote flowering after a nutrient concentration switch in vegetative tissue is triggered (Matsoukas et al., 2012).

The light programme

Plants have innate pathways that lead to phenotypic variation under different conditions of day length, light quality and quantity (Song et al., 2012). The photoperiod pathway is an ancient adaptation (Valverde, 2011), with photoreceptors, including phytochromes (PHYA—PHYE) and cryptochromes (CRY1 and CRY2; Ausin et al., 2005) detecting photoperiodicity, with signalling integrated into the regulatory network of the internal circadian clock (Auszin et al., 2005; Boss et al., 2004). A variety of epigenetic mechanisms have been shown to underlie the photoperiod pathway, with modulation of DNA methylation in several plant species (Kondo et al., 2010; Thanananta et al., 2006) including B. napus (Guzy-Wrobelska et al., 2013), histone modification in rice (Wang et al., 2013) as well as transcriptional, post-transcriptional and post-translational regulation in Arabidopsis (Auszin et al., 2005).

Circadian rhythm and ageing contribute as components of the autonomous pathway and are able to provide a more resilient route to floral initiation (Arana et al., 2011). The circadian pathway allows pre-empting of expected daily and seasonal fluctuations via multiple feedback loops and light inputs (Mouradov et al., 2002; Troein et al., 2009). Genes involved fall into two broad categories of RNA-processing proteins and chromatin modulation and maintenance (Srikanth and Schmid, 2011). Circadian rhythms are ability to influence strong control of flowering time; in Arabidopsis, MADS AFFECTING FLOWERING 5 and FLC transcription is affected by the circadian clock mutation late elongated hypocotyl 1 (Fujiwara et al., 2010). For perennial crops, plant age can be a significant factor in floral initiation (Srikanth and Schmid, 2011). This can have significant economic impact in terms of the number of years taken for crop establishment prior to productive yields. In Arabidopsis and maize, miR156 and miR172 play key roles in enabling floral development in an age-dependent manner (Jarillo and Pineiro, 2011; Yamaguchi and Abe, 2012).

Managing juvenility

Many plants undergo vegetative phase change (VPC), where pronounced changes in leaf morphology, orientation, anatomy and chemistry accompany puberty (Figure 1). The duration of the juvenile growth period has considerable consequences for economic production and scheduling of many crops including sustainable forest and tree fruit production, where long periods of juvenility are often required prior to reproductive or harvestable maturity (Thomas, 2013).

Vegetative phase change is most evident in trees, where it often occurs earlier than the transition to reproductive competiveness and is thought to be largely regulated independent of the floral transition (Poethig, 2003), although some tree species may have the ability to initiate floral transitions on branches exhibiting juvenile foliage (Jaya et al., 2010a, b; 2011; Wiltshire et al., 2013; Thomas, 2013).
It has long been recognized that epigenetics plays a major role in regulation of the plasticity associated with relative stability and immortality to environmental influences, yet reversibility of VPC at gametogenesis (Greenwood and Hutchison, 1993). In Arabidopsis, VPC is regulated by a set of TFs (SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE [SBP/SPL proteins]) which are repressed during the juvenile phase by miR156 and miR157. Reduction in these miRNAs leads to expression of SBP/SPL proteins (Poethig, 2003), with miR172 having an inverse expression pattern. Suppression of flowering by miR156 can be overcome, demonstrating the independence of flowering and VPC (Poethig, 2010). More recently, HYPONASTIC LEAVES1 has been shown to regulate levels of miR156-targeted SPL genes, enabling plants to maintain the juvenile phase, ensuring maximum growth and productivity (Li et al., 2012a). This miRNA-mediated regulation appears conserved across a range of annual and woody perennial plants (Wang et al., 2011), despite the diverse and taxa-specific phenotypic manifestation of VPC.

As many pathways can be influenced by epigenetic marks (Brown et al., 2012; Cazzonelli and Pogson, 2010; Chinnusamy and Zhu, 2009; McGarry and Kragler, 2013; Pauli et al., 2011; Popova et al., 2013), it may be possible to use targeted epigenetic manipulation to decouple vegetative maturation and reproductive organogenesis in crop species (McGarry and Kragler, 2013). Rapid germination of a mature tree in response to extensive damage (e.g. fire) can occur from primed dormant meristematic nodes and may involve phenotypic reversion to a juvenile appearance for a short period. The ability to revert to a juvenile expression programme suggests significant epigenetic similarities between adult and juvenile meristems.

Inflorescence induction

Induction of flowering represents the key transition affecting harvestable potential of many crops. The inflorescence induction pathway is highly regulated and complex (Tan and Swain, 2006) and can also exhibit extremely large plastic responses (Bernier, 1986). This has led to multiple routes to flowering, with extensive involvement of epigenetic regulation in the autonomous, vernalization, gibberellin and photoperiod induction pathways (Yaish et al., 2011). Among plant species, the location of floral induction varies. In crops such as wheat (Danielevskaya et al., 2008) or common bean (Repinski et al., 2012), the SAM develops into an inflorescence meristem (IM), resulting in terminal determinate inflorescence (Figure 1). In contrast, Brassica species develop indeterminate raceme inflorescences, while in some eucalypt trees, axillary inflorescences are induced along lateral branches (Jaya et al., 2010a).

For crops such as canola, plasticity of flowering is apparent in the very large number of environment-specific quantitative trait loci (QTLs) identified (Shi et al., 2009). Plasticity regulated by epigenetic mechanisms is likely to have been under selection in landraces and modern cultivars adapted to different latitudes. Brassica napus FT paralogues may be independently silenced by 5mC (e.g. FT-C2) to repress expression (Table 1), with FT-A7 and FT-C6 paralogues having distinct expression profiles under vernalization-free conditions in cultivar types selected specifically for winter or spring planting (Wang et al., 2012).

The autonomous floral promoting pathway can be influenced by signals from the vernalization, photoperiod, hormonal and circadian pathways. In Arabidopsis, the autonomous pathway can itself intervene in these floral enabling pathways via FLC suppression (Adams et al., 2009). Expression of GA INSENSITIVE DWARF 1 (GID1) genes in Arabidopsis oscillates diurnally and may be a result of circadian clock activity (Arahal et al., 2011). There is evidence for diurnal oscillation of gibberellic acid (GA) in both Arabidopsis (Hisamatsu et al., 2005; Zhao et al., 2007) and sorghum (Lee et al., 1998), indicating a link between autonomous and hormone pathways.

Modulation of epigenetic marks to modify and fix novel phenological profiles that accelerate onset of floral initiation and anthesis would enhance productivity in crops such as canola (Kondo et al., 2010). Conversely, bioenergy crops and potato tuber (Solanum) production would benefit from an increase in length of the juvenile growth stage. Accelerated flowering has been achieved in Solanum sp. treated with 5-Azac (Marfil et al., 2012). In rice, hypomethylation by 5-Azac and zebularine has induced stable transgenerational dwarfsim (Akimoto et al., 2007; Sano et al., 1990), although the specific genomic networks involved have not been characterized.

Synchronization of flowering in crops

Precocious flowering can reduce crop yield; in Arabidopsis, this may occur where the TF WUSCHEL (WUS) is not repressed by KNUCKLES (KNU), resulting in floral stem cell over-proliferation (Ito and Sun, 2009). KNU is derepressed by reduction in the H3K27me3 chromatin mark just prior to induction of its transcription at initiation of flower development (Table 1; Ito and Sun, 2009; Sun et al., 2009). The AGAMOUS (AG) MADS domain type TF is induced by WUS in floral meristem primordia, and 2 days later, AG reaches a tipping point where its own action represses WUS (Table 1; Ikeda et al., 2009). This period of activity by AG is also responsible for the reduction in H3K27me3 in the KNU locus, although how AG itself is involved in histone demethylation is unclear (Ito and Sun, 2009). The overarching result of these interactions acts to specify reproductive organ identity, and a number of floral stem cells to ensure flowers of different individuals are all similar in size (Ito and Sun, 2009).

Phloem mobile signals such as siRNAs, miRNAs and messenger RNAs can play pivotal roles in Arabidopsis inflorescence induction (McGarry and Kragler, 2013). Of approximately 200 miRNA families in Arabidopsis, only three (miR156, miR159 and miR172) have been shown to influence flowering time control (Yamaguchi and Abe, 2012). It is possible that the negative feedback from high fruit loading influencing inflorescence induction in crop species (Samach and Smith, 2013) is regulated by phloem mobile signals as these. This feedback system may have evolved to ensure that fitness of developing fruits is not encumbered by overcommitting to excessive fruit quantity.

The photoperiod pathway promoting flowering regulates CONSTANS (CO), which activates several gene networks. One of these gene networks involves the key TF integrators: SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1) and FLOWERING LOCUS T (FT) that together initiate IM induction (Valverde, 2011; Wigge et al., 2005). FT and FT-like genes have homologs in many angiosperms and a number of gymnosperms (Klitenka et al., 2012). However, FTERMINAL FLOWER1-like (FTL1 & FTL2) genes in Picea (spruces) and Pinus (pines) are thought to act conversely to FT in angiosperms as their ectopic expression in Arabidopsis represses flowering (Klitenka et al., 2012). The FT gene encodes the transmissible ‘florigen’, a phosphatidylethanolamine-binding protein (PEBP; Klitenka et al., 2012), which is small, globular and phloem mobile. PEBP can travel from...
leaves to SAMs where it induces the flowering programme (McGarry and Kragler, 2013; Wigge et al., 2005). FT requires the basic-leucine zipper TF AT4G35900 (FD) for floral promotion. FD RNA is highly expressed in both leaf and floral anlagen (the cluster of meristematic tissue which develops into an organ), although after floral primordia begin to express AP1 FD transcript levels decrease (Wigge et al., 2005). The interaction between FT and FD is thought to be reciprocal. In Arabidopsis, FT integrates promotional environmental cues enabling inflorescence induction while FD expressed in SAMs provides a target for FT (Wigge et al., 2005). In Arabidopsis, the FT/FTL1 family is comprised of six genes (Kim et al., 2013b). Additional complexity is conferred in B. napus by the six primary FT paralogues, each of which may be epigenetically regulated (Wang et al., 2012), leading to scope for exquisite differences in expression profiles for cultivars adapted to different environments.

Inflorescence development

In most crops, establishment of meristem identity and reproductive organ development following floral initiation is a key determinant of harvest potential. Regulation of these phase changes by chromatin modification allows for plastic responses to the environment (Jarillo et al., 2009). Epigenetic marks influence development and relative timing of reproductive organs, with snRNA-mediated chromatin remodelling having the potential to maintain developmental patterns without positional signalling (Kidner and Martienssen, 2005).

Although the floral transition may be somewhat plastic, many of the subsequent regulatory circuits appear highly conserved within species, with around 20 chromatin-remodelling genes implicated in regulatory networks associated with floral identity and reproductive organogenesis (Jarillo et al., 2009).

Epigenetic modulation is apparent in the regulation of TFs such as AP1 and LFY, which are key to both floral meristem and floral organ identity determination during transitional development (Kidner and Martienssen, 2005; Saleh et al., 2008a). Crosstalk between hormone and epigenetic systems may also contribute to floral meristem initiation. Auxin expression can elicit floral meristem initiation, while cytokinins and other pre-existing signals from inflorescence induction may regulate positional reproductive compartment initiation in floral primordia (Chandler, 2012).

In rice, trans-acting snRNAs and their associated machinery contribute to meristem maintenance (Pautler et al., 2013), with mir166 accumulation in some rice mutants partially implicated in SAM defects (Nagasaki et al., 2007). Although LEAFY COTYLEDON 1 (LEC1) is fundamental to late embryo development in Arabidopsis, in rice, it is thought to regulate fine control of meristem identity, indicating different functions in monocotyledon and dicotyledon systems (Zhang and Xue, 2013), with OsLEC1 regulating meristem identity by hypermethylating specific regions of OsMADS1 (Zhang and Xue, 2013).

Photoperiod- and thermo-sensitive genic male sterility (PGMS/TGMS) is important for hybrid rice breeding. A novel spontaneous PGMS mutant was characterized in 1973, which is sterile under long-day conditions and has been incorporated into rice breeding germplasm (Zhang et al., 1994). A single base mutation has been identified, which may lead to loss of function of a unique snRNA that regulates key genetic networks involved in male reproductive organ development (Zhou et al., 2012).

Fertilization, orchestration of the reproductive programme and seed set

Timing of flower opening can exhibit substantial plasticity in response to external stimuli, with light and temperature able to independently regulate opening and closing of petals (van Doorn and van Meeteren, 2003). This may be important to reduce pollen loss when pollinators are not operating or to limit rain damage. The number of hours a flower remains open and receptive can vary in response to pollinators (Arathi et al., 2002; Frund et al., 2011). Flower longevity can exhibit considerable plasticity, such as in Mimulus guttatus (monkey flower), where plasticity facilitates unpollinated flowers to remain open longer (Arathi et al., 2002).

Epigenetic marks accumulated in the SAM during growth are to a large extent removed, reset or reprogrammed during meiosis (Paszkowsk and Grossniklaus, 2011). In Arabidopsis, MET1 expression is down-regulated during gametogenesis in pollen sperm and egg cells, resulting in hypomethylation compared with the parental genomes (Table 1; Saze et al., 2003; Schmidt et al., 2013). However, not all 5mC marks are removed during reproduction as a number of important genomic regions can remain imprinted (Borges and Martienssen, 2013; Calarco et al., 2012). Although epigenetic regulation is critical in this stage of reproductive development, little plasticity has been directly observed.

Maintaining pollen viability until fertilization is a complex process. In maize pollen, over 20 000 genes appear to be expressed in the short period prior to fertilization (Walbot and Evans, 2003). DECREASED DNA METHYLATION 1 (DDM1) appears to be part of the pollen maintenance system as it is expressed in the sperm cell nuclei but not the vegetative nuclei (Law and Jacobsen, 2010). In Arabidopsis sperm cells, DNA methylation levels at most TE loci are hypermethylated, with those repressed solely by DNA methylation becoming expressed and mobile (Wollmann and Berger, 2012). This suggests that a more permanent repression of TFs requires additional epigenetic controls.

Diploid Brassica crops are able to limit self-fertilization via the sporophytic self-incompatibility system, with the SP11 locus in another tapetal tissue regulated by de novo 5mC (Table 1; Henderson and Jacobsen, 2007). Here, plasticity provides variation in strength of incompatibility dominance under different conditions (Shiba et al., 2003).

Pollen recognition on the stigma involves protein–protein interactions followed by pollen hydration, recognition, pollination, germination and penetration into the style (Edlund et al., 2004). Self-pollination in self-incompatible species inhibits pollen germination. The CENTRAL CELL GUIDANCE (CCG) domain is associated with long-distance guidance of germinated pollen tubes (Chen et al., 2007). Within the central cell, specific reproductive genes are derepressed (i.e. hypomethylated) by suppression of MET1 and activation of DME (DEMETER; Wollmann and Berger, 2012), although chromatin modulation may precede genome-wide DNA hypomethylation (Gutierrez-Marcos and Dickinson, 2012).

DEMETER regulates at least five parent-of-origin genes, and another 40 candidates remain to be experimentally verified (Law and Jacobsen, 2010). The central cell is a participant in double fertilization and initiates the development of endosperm tissue after fertilization, both distinguishing features of angiosperms (Wollmann and Berger, 2012). In the Arabidopsis central cell prior to fertilization, expression of DME results in hypomethylation of
the endosperm genome (Lamesch et al., 2011), although to what extent is still unclear (Wollmann and Berger, 2012; Zemach et al., 2010). Moreover, whole-genome demethylation by DME appears primarily to affect CG sites (Wollmann and Berger, 2012). Although DME is rapidly down-regulated after fertilization, it is present during endosperm development, perhaps imprinting at the MEDEA (MEA) locus (Garnier et al., 2008). MEA in Arabidopsis is thought to encode a TF that represses fruit development in the absence of fertilization (Lamesch et al., 2011). In plants, 5mC in CHG contexts can be maintained by CHROMOMETHYLASE3 (CMT3) and CHH by DRM2 (Table 1; Law and Jacobsen, 2010). Both CMT3 and DRM2 are expressed in the embryo and seed, but only DRM2 is expressed in the pollen sperm cell (Lamesch et al., 2011). The Arabidopsis INCREASE IN BONSAI METHYLATION 1 (IBM1) has been associated with 5mC in both CHG and CHH contexts (Miura et al., 2009a).

Yields and seed viability of grain crops are dependent on the outcome of a battle between maternal and paternal genomes over expression of respective alleles, which is mediated by differential maintenance of epigenetic marks. Maternal DME activity can mediate the activation of maternal specific alleles, while paternal alleles are silenced by MET1 and may be regulated by RdDM via FLOWERING WAGENINGEN (FWA) and FERTILIZATION INDEPENDENT SEED 2 (FIS2) or histone modulation by MEA on H3Lys27 (Table 1; Kohler and Makarevich, 2006; Vu et al., 2013). The challenge for plant sexual reproduction is to reprogramme DNA methylation in each set of chromosomes while ensuring maintenance of TE silencing (Wollmann and Berger, 2012), with the latter in rice achieved by mechanisms such as demethylation of H3K4 by JUMONJI703 (JMJ703; Cui et al., 2013).

Gamete fusion and seed development

Both histone (H3K27me3) and DNA methylation regulate repression of TEs and genes in Arabidopsis endosperm (Schmidt et al., 2013), with significant variation in methylation patterning between embryo and endosperm tissues (Gehring et al., 2009) including overall hypomethylation in both tissues, although some CHH hypermethylation occurs, which may result from RdDM (Law and Jacobsen, 2010). In rice, endosperm hypomethylation occurs in all sequence contexts, although CHG and CHH contexts are hypomethylated similarly across the genome in comparison with targeted CG methylation (Zemach et al., 2010). Arabidopsis embryogenesis requires activity of both MET1 and CMT3 for seed viability (Xiao et al., 2006). This leads to preferential maternal hypomethylation in the endosperm while paternal methylated alleles are maintained. However, the function of the remaining methylated genes is largely unknown (Zhang et al., 2013a).

At the earliest stages of embryo development, epigenetic regulation can play a crucial role in directing the partitioning of tissues into distinct anlagen cell lineages and driving inheritance of each transcriptional programme through mitosis (Bantignies and Cavalli, 2006). MET1 is not only expressed following gametogenesis in the egg cell, but may also be expressed in the developing embryo, endosperm and seed coat (Schmidt et al., 2013). In Brassica rapa, BcIM30 (Table 1) encodes the jmjC domain-containing histone demethylase, which is associated with pollen development and fertilization (Li et al., 2012c), while the Helianthus LEAFY COTYLEDON1-LIKE (Halu1) is involved in early stages of zygotic and somatic embryogenesis, with multiplexed transcriptional regulation by DNA methylation, TEs, auxin and ABA (Table 1; Salvini et al., 2012). The MATERNALLY EXPRESSED GENE 1 (MEG1) in maize is expressed only in the basal nutrient transfer region of the endosperm (Table 1; Gutierrez-Marcos et al., 2004), with genomic imprinting of MEG1 assisting nutrient transfer from endosperm to the developing embryo (Costa et al., 2012).

Genomic imprinting

Transgenerational inheritance of epigenetic marks involved in genomic imprinting can result in a greater than expected expression of alleles from either maternal or paternal origin (Mosher and Melnyk, 2010). Imprinting ensures TEs remain epigenetically silenced throughout plant gametogenic reprogramming (Wollmann and Berger, 2012) and can also facilitate seed germination. Pathogen exposure can initiate differential 5mC patterning, with transgenerational priming of a genome appearing to elicit pre-emptive pathogen-associated molecular patterns, such as the activation of the defence regulatory gene NON EXPRESSION OF PR GENES (NPR1; Downen et al., 2012; Luna and Ton, 2012). It has been suggested that post-translational histone modifications and expression of RNA Polymerase V act alongside siRNA to recruit methylation machinery, leading to transgenerational genomic imprinting of NPR1 (Luna and Ton, 2012; You et al., 2013). This defence system is similar to priming the human immune system by immunization, with a significant difference being its heritability.

Maternally produced RNAs in plant reproductive tissue can be mobile and may target specific loci in developing embryos for genomic imprinting (Gutierrez-Marcos et al., 2012; Mosher et al., 2009). Environmentally induced RNA in maternal somatic cells may also contribute to embryo genomic imprinting. In fact, a range of miRNAs, including at least four involved in nutrient homeostasis (miR169, miR395, miR398 and miR399), are mobile, present in the phloem and graft-transmissible (Marin-Gonzalez and Suarez-Lopez, 2012), adding to growing evidence that maternally produced RNAs may be present in the next generation. RNA present at fertilization can persist during seed maturation (Mosher et al., 2009) and possibly during seed dormancy. Maternal RNA may therefore influence gene regulation during germination to assist seedling establishment (Figure 1). This is an aspect of maternally influenced genomic imprinting, which may have evolved to impart a fitness advantage to offspring that germinate within the maternal niche (Gorecki et al., 2012).

METHYLTRANSFERASE 1 has been suggested as a key integrator maintaining transgenerational inheritance of epigenetic marks throughout vegetative growth (Paszkowski and Grossniklaus, 2011). Hypomethylation is less noticeable during plant embryogenesis compared with mammalian systems, with a higher proportion of parental DNA methylation states transmitted to the next generation (Reinders et al., 2009). In Arabidopsis, the methylation state of the PHE1 (PERES1) paternal allele is methylated in contrast to the hypomethylated maternal allele (Table 1; Kohler and Makarevich, 2006; Makarevich et al., 2008). Where salt tolerance in rice has been induced and transgenerationally inherited in selfed progenies, methylation profiles suggested that salt-tolerant genotypes were hypermethylated while salt-sensitive genotypes were hypomethylated (Feng et al., 2012).

Imprinting in plants was thought only to occur in the triploid endosperm and therefore expected that gymnosperms would lack imprinting mechanisms (Garnier et al., 2008). However, more recently, it has been shown that genomic imprinting can occur in angiosperm embryos (Scholten, 2010). The gymnosperm
Norway spruce also has capacity to store environmental conditions in an epigenetic memory during embryogenesis, with exposure to different temperatures during embryo development fixing epigenetic marks prior to seed maturation, leading to modified germination time and seedling development (Yakovlev et al., 2010). The epigenetic memory in long-lived plant species may confer adaptive plasticity to environmental drift in a single generation, with important consequences for perennial and clonally propagated crops.

**Fruit development and ripening**

Fruit development from the ovule normally commences following fertilization of the egg cell (Figure 1), with suppression of endosperm growth following fertilization signalling the start of fruit development. *MEA* and *MET1* are thought to be involved in the repression of both endosperm development and central cell proliferation (Schmidt et al., 2013). Parthenocarpic fruit also demonstrates the independence of fruit ripening from signalling arising from oocyte fertilization (Mesejo et al., 2013; Wang et al., 2009).

The development of the complex structures of fruit is regulated by a network of TFs. In the dry dehiscent fruit of Brassicaceae, a network of genes, TFs and hormones are involved in regulating the development of the carpel tissue compartments into valve, lignified layer, separation layer and replum (Alonso-Cantabrana et al., 2007; Girin et al., 2010; Lewis et al., 2006; Muhlhausen et al., 2013; Ripoll et al., 2011; Romera-Branchat et al., 2013; Seymour et al., 2008). In crops with indehiscent fruit, such as canola and soybean, development is general tightly regulated and programmed, with the primary plastic trait being the decision to abort individual embryos or even the entire silique. The decision to abort embryos in the Brassicaceae can come from at least two abiotic stimuli, water and nutrient availability (Guo et al., 2013).

In fleshy fruits such as tomato and peach, development and ripening of carpel tissues is regulated by a subset of conserved TF networks (Chapman et al., 2012; Fujisawa et al., 2013; Karlova et al., 2013; Luo et al., 2013; Manning et al., 2006; Seymour et al., 2013a; Zhong et al., 2013), with additional taxon-specific regulators. In tomato, the MADS-box gene RIPENING INHIBITOR (RIN) induces the expression of COLOURLESS NONRIPENING (CNR), FRUITFULL homolog TDR4/FUL1, Solyoc70502960 and a network of at least another 22 genes with TF activity thought to influence aroma and flavour, pathogen defence, stress response, fruit softening and pigmentation during ripening (Fujisawa et al., 2012). The SBP-box (SQUAMOSA promoter-binding protein-like) gene CNR (Manning et al., 2006; Seymour et al., 2008) was first identified in a commercial crop and characterized as a dominant mutant allele (*Cnr*) that had undergone spontaneous hypermethylation in the promoter region. Comparative deep methylome sequencing at four stages of tomato fruit development has identified several candidate genes underlying phenotypic traits (Zuo et al., 2012; King et al., 2010).

We have shown that a significant proportion of phenotypic variation and plasticity observed in crop plants appears to be influenced by modulation of epigenetic marks. Although in many cases the architecture of regulatory networks is sufficiently complex to provide developmental plasticity, the additional complexity and behaviour of epigenetic processes allows a more dynamic response to environmental signals. It has recently been suggested that phenotypes influenced by epigenotypes are primarily facilitated by gene expression (Springer, 2013). However, our broader examination of epigenetic processes suggests a complex web of negative and positive feedback, which can act independently of specific gene expression. Epigenetic regulation is now understood to be a key factor in homeostasis of developmental and response networks in plants, with considerable crosstalk affecting hormonal, TF and other genomic regulatory networks. This inherent complexity provides plants with additional plasticity and enabled evolution of diverse vegetative and reproductive structures that contribute to crop productivity.

The extent to which epialleles may affect *trans*-regulation of gene expression remains poorly characterized, particularly in complex crop genomes. The few studies to date that have taken a genetical genomics approach indicate that a large proportion of expression QTL (eQTL) have *trans*-regulatory effects (Cubillos et al., 2012; Hammond et al., 2011). The complexity of these pleiotropic effects is likely to be confounded by the tissue- or environment-specific epiallelic status of *trans*-regulated loci. Simultaneous characterization of eQTL and methylome mapping in crop plant systems will provide greater insights into the molecular basis of *G* × *E* interactions.

As a more detailed understanding of the specific molecular mechanisms underlying crop plasticity emerges, increasingly more sophisticated strategies are likely to be developed to intervene in
the epigenetic status of cultivars and contribute to developing climate-resilient crops. These approaches may involve epiallelic selection including retrospective characterization of DNA methylation (Hauben et al., 2009), chemical hypomethylation and selection (Amoah et al., 2012), tissue-culture-induced epiallelic variation (Rhee et al., 2010), targeted modulation of epigenetic status or mRNA engineering (Zhou and Luo, 2013).

Recognition of the potential impact and value of epigenetic selection is increasing, with new strategies for managing epialleles being developed alongside conventional and transgenic programmes. However, any approach to crop improvement based on modification of epiallelic status ideally requires knowledge of the specific molecular changes and potential epistatic consequences on gene regulation. Although we have referred to a number of studies that have shown genome-wide hypo- or hypermethylation in crop plants, to date, many of these failed to distinguish between direct modulation of SmC affecting gene transcription and trans-effects resulting from activation of TEs. The availability of new sequencing technologies that are able to rapidly generate comprehensive methylome profiles associated with different tissues and cultivation environments will contribute to the platforms required for predictive crop epi-breeding.

Acknowledgements

The authors were supported by Southern Cross Plant Science and Division of Research at Southern Cross University. GK is also supported by a Chutian scholarship from Hubei Province, China.

References

Adams, S., Allen, T. and Whitelam, G.C. (2009) Interaction between the light quality and flowering time pathways in Arabidopsis. Plant J. 60, 257–267.

Ahmad, A., Zhang, Y. and Cao, X.-F. (2010) Decoding the epigenetic language of plant development. Mol. Plant 3, 719–728.

Akimoto, K., Takakami, H., Kim, H.J., Ogawa, E., Sano, C.M., Wada, Y. and Sano, H. (2007) Epigenetic inheritance in rice plants. Ann. Biol. 100, 205–217.

Alonso-Canabaras, H., Ripoll, J.J., Ochando, I., Vera, A., Fernandez, C. and Martinez-Laborda, A. (2007) Common regulatory networks in leaf and fruit patterning revealed by mutations in the Arabidopsis ASYMMETRIC LEAVES1 gene. Development, 134, 2663–2671.

Abzhoinai, A.M., Guylai, G., Jansen, R.K. and Baehlend, A. (2013) Transposable elements domesticated and neo-functionalized by eukaryotic compositions. Plasmid, 69, 1–15.

Amoah, S., Kurup, S., Lopez, C.M.R., Welham, S.J., Powers, S.J., Hopkins, C.J., Wilkinson, M.J. and King, G.J. (2012) A hypomethylated population of Brassica rapa for forward and reverse epi-genetics. BMC Plant Biol. 12, 193.

Anana, M.V., Marin-de-la Rosa, N., Maloof, J.N., Blazquez, M.A. and Alabadi, D. (2011) Circadian oscillation of gibberellin signaling in Arabidopsis. Proc. Natl Acad. Sci. USA, 108, 9292–9297.

Arathi, H.S., Rasch, A., Cox, C. and Kelly, J.K. (2002) Autogamy and floral longevity in Mimulus guttatus. Int. J. Plant Sci. 163, 567–573.

Ausin, I., Alonso-Blanco, C. and Martinez-Zapater, J.M. (2005) Environmental regulation of flowering. Int. J. Dev. Biol. 49, 689–705.

Bastin, R. and Cavalli, G. (2006) Cellular memory and dynamic regulation of polycycomb group proteins. Curr. Opin. Cell. Biol. 18, 275–283.

Bartel, D.P. (2004) MicroRNAs: genomics, biogenesis, mechanism, and function. Cell, 116, 281–297.

Bastow, R., Mylene, J.S., Lister, C., Lippman, Z., Martienssen, R.A. and Dean, C. (2004) Vernalization requires epigenetic silencing of FLC by histone methylation. Nature, 427, 164–167.

Beaucarol, L., Yu, A. and Bouche, N. (2010) microRNA-directed cleavage and transitional repression of the copper chaperone for superoxide dismutase mRNA in Arabidopsis. Plant J. 62, 454–462.

Bender, J. and Fink, G.R. (1995) Epigenetic control of an endogenous gene family is revealed by a novel blue fluorescent mutant of Arabidopsis. Cell, 83, 725–734.

Bernier, G. (1986) The flowering process as an example of plastic development. Symp. Exp. Biol. 40, 257–286.

Bernstein, E. and Hake, S.B. (2006) The nucleosome: a little variation goes a long way. Biochem. Cell. Biol. 84, 505–507.

Bird, A. (2007) Perceptions of epigenetics. Nature, 447, 396–398.

Böhne, M. and Bruehlheide, H. (2013) How do evergreen and deciduous species respond to shade?—Tolerance and plasticity of subtropical tree and shrub species of South-East China. Environ. Exp. Biol. 87, 179–190.

Borges, F. and Martienssen, R.A. (2013) Establishing epigenetic variation during genome reprogramming. RNA Biol. 10, 490–494.

Boiss, P.K., Bastow, R.M., Mylne, J.S. and Dean, C. (2004) Multiple pathways ideally require knowledge of the decision to flower: enabling, promoting, and resetting. Plant Cell, 16, 518–531.

Brown, S.J., Stoilov, P. and Xing, Y. (2012) Chromatin and epigenetic regulation of pre-mRNA processing. Hum. Mol. Genet. 21, R90–R96.

Bucher, E., Reinders, J. and Mironou, M. (2012) Epigenetic control of transposon transcription and mobility in Arabidopsis. Curr. Opin. Plant Biol. 15, 503–510.

Calarco, J.P., Borges, F., Donoghue, M.T.A., Van Ex, F., Julien, P.E., Lopes, T., Gardner, R., Berger, F., Feijo, J.A., Becker, J.D. and Martienssen, R.A. (2012) Reprogramming of DNA methylation in pollen guides epigenetic inheritance via small RNA. Cell, 151, 194–205.

Cantu, D., Vanzetti, L.S., Sumner, A., Dubcovsky, M., Matvenko, M., Distelfeld, A., Michelmore, R.W. and Dubcovsky, J. (2010) Small RNAs, DNA methylation and transposable elements in wheat. BMC Genomics, 11, 408.

Cazzonelli, C.I. and Pogson, B.J. (2010) Source to sink: regulation of carotenoid biosynthesis in plants. Trends Plant Sci. 15, 266–274.

Chan, S.W.L., Zilberman, D., Xie, Z., Johansen, L.K., Carrington, J.C. and Jacobsen, S.E. (2004) RNA silencing genes control de novo DNA methylation. Science, 303, 1336.

Chandler, J.W. (2012) Floral meristem initiation and emergence in plants. Cell. Mol. Life Sci. 69, 3807–3818.

Chapman, N.H., Bonnet, J., Grivet, L., Lynn, J., Graham, N., Smith, R., Sun, G.P., Walley, P.G., Poole, M., Causse, M., King, G.J., Baxter, C. and Seymour, G.B. (2012) High-resolution mapping of a fruit firmness-related quantitative trait locus in tomato reveals epistatic interactions associated with a complex combinatorial locus. Plant Physiol. 159, 1644–1657.

Chen, Y.-H., Li, H.-J., Shi, Q.-O., Yuan, L., Liu, J., Sreenivasan, R., Baikar, R., Grossniklaus, U. and Yang, W.-C. (2007) The central cell plays a critical role in pollen tube guidance in Arabidopsis. Plant Cell, 19, 3563–3577.

Chinnusamy, V. and Zhu, J.-K. (2009) Epigenetic regulation of stress responses in plants. Curr. Opin. Plant Biol. 12, 133–139.

Choudhuraparva, R.K., Feng, S.H., Bernatavichute, Y.V., Chen, P.Y., Stroud, H., Hetzel, J.A., Kuo, F., Kim, J., Cokus, S.J., Casero, D., Bernal, M., Huijser, P., Zhang, X.Y., Hetzel, J.A., Kuo, F., Kim, J., Cokus, S.J., Caseo, D., Bernal, M., Huijser, P., Clark, A.T., Kramer, U., Merchant, S.S., Zhang, X.Y., Jacobsen, S.E. and Pellegrini, M. (2010) Relationship between nucleosome positioning and DNA methylation. Nature, 466, 388–392.

Cigliano, R.A., Sanseverino, W., Cremona, G., Ercolano, M.R., Conicella, C. and Consiglio, F.M. (2013) Genome-wide analysis of histone modifiers in tomato: gaining an insight into their developmental roles. BMC Genomics, 14, 562.

Cohen, R., Schocken, J., Kaldis, A., Vlachonasios, K.E., Hark, A.T. and McCain, E.R. (2009) The histone acetyltransferase GCN5 affects the inflorescence meristem and stem development in Arabidopsis. Planta, 230, 1207–1221.

Costa, L.M., Yuan, J., Rouster, J., Paul, W., Dickinson, H. and Gutierrez-Marcos, J.F. (2012) Maternal control of nutrient allocation in plant seeds by genomic imprinting. Curr. Biol. 22, 160–165.

Cubillos, F.A., Coutham, V. and Loudet, O. (2012) Lessons from eQTL mapping studies: non-coding regions and their role behind natural phenotypic variation in plants. Curr. Opin. Plant Biol. 15, 192–198.

Cui, X.K., Jin, P., Cui, X., Liu, L.F., Lu, Z.K., Yue, Y.M., Wei, L.Y., Qi, J.F., Song, X.W., Luo, M., An, G. and Cao, X.F. (2013) Control of transposon activity by a histone H3K4 demethylase in rice. Proc. Natl Acad. Sci. USA, 110, 1953–1958.
Gonzalez, R.M., Ricardi, M.M. and Iseue, N.D. (2013) Epigenetic marks in an adaptive water-stress-responsive gene in tomato roots under normal and drought conditions. *Epigenetics, 8*, 864–872.

Gonzalez-Grandio, E., Poza-Carrion, C., Sorzano, C.O.S. and Cubas, P. (2013) BRANCHED1 promotes axillary bud dormancy in response to shade in *Arabidopsis*. *Plant Cell, 25*, 834–840.

Gorecki, M.J., Long, R.L., Flematti, G.R. and Stevens, J.C. (2012) Parental environment changes the dormancy state and karikinolide response of *Brassica tournesolii* seeds. *Ann. Bot. 109*, 1369–1378.

Greenwood, M.S. and Hutchison, K.W. (1993) Maturation as a developmental process. In *Clonal Forestry I—Genetics and Biotechnology* (Ahuja, M.R. and Libby, W.J., eds), pp. 14–33 Berlin: Springer-Verlag.

Grossniklaus, U., Vielle-Calzada, J.P., Hoeppner, M.A. and Gaglio, W.B. (1998) Maternal control of embryogenesis by medea, a Polyclome group gene in *Arabidopsis*. *Science, 280*, 446–450.

Guo, Y.M., Chen, S., Nelson, M.N., Cowling, W. and Turner, N.C. (2013) Delayed water loss and temperature rise in floral buds compared with leaves of *Brassica rapa* subjected to a transient water stress during reproductive development. *Plant Physiol. 160*, 690–699.

Gutierrez-Marcos, J.F. and Dickinson, H.G. (2012) Epigenetic reprogramming in plant reproductive lineages. *Plant Cell Physiol. 53*, 817–823.

Gutierrez-Marcos, J.F., Costa, L.M., Biderre-Petit, C., Khbaya, B., O’Sullivan, D.M., Wormald, M., Perez, P. and Dickinson, H.G. (2004) Maternally expressed gene 1 is a novel maize endosperm transfer cell-specific gene with a maternal parent-of-origin pattern of expression. *Plant Cell, 16*, 1288–1301.

Gutierrez-Marcos, J.F., Constancia, M. and Burton, G.J. (2012) Maternal to offspring resource allocation in plants and mammals. *Placenta, 33*(Suppl. 2), e3–e10.

Guz-Wrobeliska, J., Filek, M., Kaliciak, A., Szarejko, I., Machackova, I., Krekule, J. and Barciszewska, M. (2013) Vernalization and photoperiod-related changes in the DNA methylation state in winter and spring rapspe. *Acta Physiol. Plant. 35*, 817–827.

Hammond, J.P., Mayes, S., Bowen, H.C., Graham, N.S., Hayden, R.M., Love, C.G., Spracklen, W.P., Wang, J., Welham, S.J., White, P.J., King, G.J. and Broadley, M.R. (2011) Regulatory hotspots are associated with plant gene expression under varying soil phosphorus supply in *Brassica rapa*. *Plant Physiol. 156*, 1230–1241.

Hauben, M., Haesendonckx, B., Standaert, E., Van Der Kelen, K., Azmi, A., Akpo, H., Van Breusegem, F., Guisez, Y., Bots, M., Lambert, B., Laga, B. and De Block, M. (2009) Energy use efficiency is characterized by an epigenetic component that can be directed through artifical selection to increase yield. *Proc. Natl Acad. Sci. USA, 106*, 20109–20114.

He, G.M., Elling, A.A. and Deng, X.W. (2011) The epigenome and plant development. In *Annual Review of Plant Biology*, Vol. 62 (Merchant, S.S., Briggs, W.R. and Ort, D., eds), pp. 411–435. Palo Alto, CA: Annual Reviews.

Henderson, I.R. (2012) Control of meiotic recombination frequency in plant genomes. *Curr. Opin. Plant Biol. 15*, 556–561.

Henderson, I.R. and Jacobsen, S.E. (2007) Epigenetic inheritance in plants. *Nature, 447*, 418–424.

Hisamatsu, T., King, R.W., Helliwell, C.A. and Koshibako, M. (2005) The involvement of gibberelin 20-oxidase genes in phytochrome-regulated petiole elongation of *Arabidopsis*. *Plant Physiol. 138*, 1106–1116.

Hodge, A. (2004) The plastic plant: root responses to heterogenous supplies of nutrients. *New Phytol. 162*, 9–24.

Hofmann, N.R. (2013) A new function for BRC1 in auxilary buds: suppression of floral identity. *Plant Cell, 25*, 1191.

Hisieh, L.C., Lin, S.I., Shih, A.C.C., Chen, J.W., Lin, W.Y., Tseng, C.Y., Li, W.H. and Chiou, T.J. (2009) Uncovering small RNA-mediated responses to phosphate deficiency in *Arabidopsis* by deep sequencing. *Plant Physiol. 151*, 2120–2132.

Ikeda, M., Mitsuda, N. and Ohme-Takagi, M. (2009) *Arabidopsis* WUSCHEL is a bifunctional transcription factor that acts as a repressor in stem cell regulation and as an activator in floral patterning. *Plant Cell, 21*, 3493–3505.

Ito, H. (2012) Small RNAs and transposon silencing in plants. *Dev. Growth Differ. 54*, 100–107.

Ito, T. and Sun, B. (2009) Epigenetic regulation of developmental timing in floral stem cells. *Epigenetics, 4*, 564–567.
and epigenetic regulation of SKP2B, an F-Box that represses lateral root formation. Plant Physiol. 160, 749–762.

Marfil, C.F., Asurmendi, S. and MasueUi, R.W. (2012) Changes in micro RNA expression in a wild tuber-bearing Solanum species induced by S-Azacytidine treatment. Plant Cell Rep. 31, 1449–1461.

Marin-Gonzalez, E. and Suarez-Lopez, P. (2012) ‘‘And yet it moves’’: cell-to-cell and long-distance signaling by plant microRNAs. Plant Sci. 196, 18–30.

Martin-Trillo, M., Grandio, E.G., Serra, F., Marcel, F., Rodriguez-Buey, M.L., Schmitz, G., Theres, K., Bendahmane, A., Dopazo, H. and Cubas, P. (2011) Role of tomato BRANCHED1-like genes in the control of shoot branching. Plant Cell 23, 701–717.

Matsoukas, J.G., Masiash, A.J. and Thomas, B. (2012) Florigenic and antiflorogenic signaling in plants. Plant Cell Physiol. 53, 1827–1842.

Matzke, M., Kanno, T., Huettel, B., Daxinger, L. and Matzke, A.J.M. (2007) Targets of RNA-directed DNA methylation. Curr. Opin. Plant Biol. 10, 512–519.

May, O. (2010) DNA methylation: fingerprints of the (epi)genome. In Muhlhausen, A., Lenser, T., Mummenhoff, K. and Theissen, G. (2013) Evidence for a global change in the control of valve margin identity genes. Plant J. 73, 824–835.

Nagasaki, H., Itoh, J.J., Hayashi, K., Hiba, K., Sato-Nagasawa, N., Nosaka, M., Mukouhata, M., Asahiki, M., Kitano, H., Matsuoka, M., Nagato, Y. and Sato, Y. (2007) The small interfering RNA production pathway is required for shoot meristem initiation in rice. Proc. Natl Acad. Sci. USA, 104, 14867–14871.

Nakashima, K. and Yamaguchi-Shinozaki, K. (2013) ABA signaling in stress-response and seed development. Plant Cell Rep. 32, 959–970.

Nicotra, A.B., Atkin, O.K., Borser, S.P., Davidson, A.M., Finnegan, E.J., Mathews, U., Poot, P., Parungganan, M.D., Richards, C.L., Vallades, F. and van Kleunen, M. (2010) Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15, 684–692.

Niwa, M., Iaino, Y., Kurutani, K-I., Higo, A., Pruneda-Paz, J.L., Breton, G., Mitsuda, N., Kay, S.A., Ohme-Takagi, M., Endo, M. and Araki, T. (2013) BRANCHED1 interacts with FLOWERING LOCUS T to repress the floral transition in Arabidopsis. Plant Cell, 25, 1228–1242.

Oh, M., Lee, H., Kim, Y.K., Nam, J.W., Rhee, J.K., Zhang, B.T., Kim, V.N. and Lee, I. (2007) Identification and characterization of small RNAs from vernalized Arabidopsis thaliana. J. Plant Biol. 50, 562–572.

Ohad, N., Margossian, H., Yu, Y.C., Williams, C., Repetti, P. and Fischer, R.L. (1996) A mutation that allows endosperm development without fertilization. Proc. Natl Acad. Sci. USA, 93, 5319–5324.

Ortiz-MorenO, F.A., VicenDini, R., Silva, G.F.F., Silva, E.M., Carrer, H., Rodrigues, A.P. and Nogueira, F.T.S. (2013) Global analysis of the sugarcane microsyrnaptome reveals a unique composition of small RNAs associated with axillary bud outgrowth. J. Exp. Bot. 64, 2307–2320.

Osborn, T.C., Chris Pires, J., Birchler, J.A., Aufer, D.L., Jeffery Chen, Z., Lee, H.-S., Comai, L., Madlung, A., Doerge, R.W., CoLoT, V. and Martienssen, R.A. (2003) Understanding mechanisms of novel gene expression in polyploids. Trends Genet. 19, 141–147.

Pan, Y.J., Wang, W.S., Zhao, X.Q., Zhou, L.H., Fu, B.Y. and Li, Z.K. (2011) DNA methylation alterations of rice in response to cold stress. Plant OMICS, 4, 364–376.

Pazokiwski, J. and Grossniklaus, U. (2011) Selected aspects of transgenerational epigenetic inheritance and resetting in plants. Curr. Opin. Plant Biol. 14, 195–203.

Paterson, A.H., Bowers, J.E., Bruggmann, R., Dubchak, I., Grimwood, J., Gundlach, H., Haberer, G., Hellsten, U., Mitos, T., Poliakov, A., Schmutz, J., Spannagl, M., Tang, H.B., Wang, X.Y., Wicker, T., Bhat, A.K., Chapman, J., Feltus, F.A., Gowik, U., Grigoriev, I.V., Lyons, E., Maher, C.A., Martis, M., Narechania, A., O’Toile, R.P., Penning, B.W., Salamow, A.A., Wang, Y., Zhang, L.F., Carpita, N.C., Freeling, M., Gingle, A.R., Hash, C.T., Keler, B., Klein, P., Kressei, M., Mccann, M.C., Ming, R., Peterson, D.G., Melhobou, R., Ware, D., Westhoff, P., Mayer, K.F.X., Messing, J. and Rokhsar, D.S. (2009) The Sorghum bicolor genome and the diversification of grasses. Nature, 457, 551–556.

Pattanayak, D., Solanke, A.U. and Kumar, P.A. (2013) Plant RNA interference pathways: diversity in function, similarity in action. Plant Mol. Biol. Rep. 31, 493–506.

Pauli, A., Rinn, J.L. and Schier, A.F. (2011) Non-coding RNAs as regulators of embryogenesis. Nat. Rev. Genet. 12, 136–149.

Pautler, M., Tanaka, W., Hirano, H.-Y. and Jackson, D. (2013) Grass meristems exhibit shoot branching. Plant Cell Physiol. 54, 302–312.

Poethig, R.S. (2003) Phase change and the regulation of developmental timing in Arabidopsis. Nature, 426, 283–286.

Preuss, S. and Pikaard, C.S. (2007) RNA gene silencing and nucleolar dominance: insights into a chromosome-scale epigenetic on/off switch. Biochim. Biophys. Acta, 1769, 383–392.

Punta, M., Coggill, P.C., Eberhardt, R.Y., Mistry, J., Tate, J., Boursnell, C., Pang, N., spider, L., Cerut, G., Clements, J., Verger, A., Holm, L. Sonhammer, E.L.L., Eddy, S.R., Bateman, A. and Finn, R.D. (2012) The Pfam protein families database. Nucleic Acids Res. 40, D290–D301.

Rathcke, B. and Lacey, E. (1985) Phenological patterns of terrestrial plants. Annu. Rev. Ecol. Syst. 16, 179–214.

Rausch, C. and Bucher, M. (2002) Molecular mechanisms of phosphate transport in plants. Planta, 216, 23–37.

© 2014 The Authors. Plant Biotechnology Journal published by Society for Experimental Biology and The Association of Applied Biologists and John Wiley & Sons Ltd., 12, 517–533.
Rouached, H., Arpat, A.B. and Poirier, Y. (2010) Regulation of phosphate...in mosaic Arabidopsis thaliana. Plant J. 73, 37–49.
Roueher-Branchat, M., Ripoll, J.J., Yanofsky, M.F. and Pelaz, S. (2013) The WOX13 homeobox gene promotes reprogramming formation in the Arabidopsis thaliana fruit. Plant J. 73, 37–49.
Rouse, A., Alvarez-venegas, R. and Avramova, Z. (2008b) An efficient chromatin immunoprecipitation (ChIP) protocol for studying histone modifications in Arabidopsis. Methods Mol. Biol. 404, 161–170.
Rouach, H., Arpat, A.B. and Poirier, Y. (2010) Regulation of phosphate starvation responses in plants: signaling players and cross-talks. Mol. Plant. 3, 288–299.
Ruz-Garcia, L., Cervera, M.T. and Martinez-Zapater, J.M. (2005) DNA methylation increases throughout Arabidopsis development. Planta, 222, 301–306.
Russo, V.E.A., Martienssen, R.A. and Riggs, A.D. (1996) Epigenetic Mechanisms of Gene Regulation. New York, NY, USA: Cold Spring Harbor Laboratory Press.
Saini, S., Sharma, I., Kaur, N. and Pali, P.K. (2013) Auxin: a master regulator in regulating Arabidopsis. New York, NY, USA: Cold Spring Harbor Laboratory Press.
Salmela, M., Sainio, T., Peltomaki, P., Knuutila, S. and Pukkala, E. (2008) DNA methylation and transposon immobilization in mosaic Arabidopsis. Mol. Cell. 30, 622–629.
Sales, A., Alvarez-Venegas, R. and Avramova, Z. (2008a) Dynamic and stable histone H3 methylation patterns at the Arabidopsis FLC and AP1 loci. Gene, 423, 43–47.
Sales, A., Alvarez-Venegas, R. and Avramova, Z. (2008b) An efficient chromatin immunoprecipitation (ChIP) protocol for studying histone modifications in Arabidopsis plants. Nat. Protoc. 3, 1018–1025.
Salminen, J., Sainio, T., Peltomaki, P., Knuutila, S. and Pukkala, E. (2008) DNA methylation and transposon immobilization in mosaic Arabidopsis. Mol. Cell. 30, 622–629.
Sarmach, A. and Smith, H.M. (2013) Rejuvenation of mature native Tea Tree (Melaleuca alternifolia (Maiden & Betche) Cheelt) for vegetative propagation. Propagation of Ornamental Plants, 13, 107–111.
Sawhney, J., Tandem, L. and Ross, H. (2002) Vernalization-induced changes of the DNA methylation pattern in winter wheat. Genes, 45, 253–260.
Shepherd, M., Rose, T. and Raymond, C. (2013) Rejuvenation of mature native Tea Tree (Melaleuca alternifolia (Maiden & Betche) Cheelt) for vegetative propagation. Propagation of Ornamental Plants, 13, 107–111.
Schnott, S. (2010) Genomic imprinting in plant embryos. Epigenetics, 5, 455–459.
Schnecko, M., Bouvetet, R., Leroy, O., Borghi, L., Kohler, C., Gruissem, W. and Hennig, L. (2006) Polycomb-group proteins repress the floral activator AGL19 in the FLC-independent vernalization pathway. Genes Dev. 20, 1667–1678.
Seymour, G., Poole, M., Manning, K. and King, G.J. (2008) Genetics and epigenetics of fruit development and ripening. Curr. Opin. Plant Biol. 11, 269–278.
Seymour, G.B., Ostergaard, L., Chapman, N.H., Knapp, S. and Martin, C. (2013b) Fruit development and ripening. In Annual Review of Plant Biology, Vol. 64 (Merchant, S.S. ed.), pp. 219–241. Palo Alto, CA: Annual Reviews.
Sheldon, C.C., Finneghan, E.J., Peacock, W.J. and Dennis, E.S. (2009) Mechanisms of gene repression by vernalization in Arabidopsis. Plant J. 59, 488–498.
Shepherd, M., Rose, T. and Raymond, C. (2013) Rejuvenation of mature native Tea Tree (Melaleuca alternifolia (Maiden & Betche) Cheelt) for vegetative propagation. Propagation of Ornamental Plants, 13, 107–111.
Singer, J. and Yarden, I. (2001) Growth factor-mediated receptor activation: a matter of life or death. Nat. Rev. Mol. Cell Biol. 2, 763–773.
Xiao, J., Swain, S.M. (2006) Genetics of flower initiation and development in annual and perennial plants. *Physiol. Plant.* **128**, 8–17.

Thanananta, T., Pongtankam, P., Thongpan, A., Kaweeta, L. and Peychokangril, S. (2006) Effect of short day photoperiod on DNA methylation and expression of a gene in rice *KOQL105*. *Afr. J. Biotechnol.* **5**, 1375–1382.

Thomas, H. (2013) Senescence, ageing and death of the whole plant. *New Phytol.* **197**, 696–711.

Tiwari, S., Schulz, R., Ikeda, Y., Dytham, L., Bravo, J., Mathers, L., Spelman, M., Guzman, P., Oakley, R.J., Kinoshita, T. and Scott, R.J. (2008) MATERNALLY EXPRESSED FAB C-TERMINAL, a novel imprinted gene in *Arabidopsis*, encodes the conserved C-terminal domain of polyadenylate binding proteins. *Plant Cell* **20**, 2387–2398.

Troein, C., Locke, J.C.W., Turner, M.S. and Millar, A.J. (2009) Weather and seasons together demand complex biological clocks. *Curr. Biol.* **19**, 1961–1964.

Tsuchiya, T. and Eulgem, T. (2013) Mutations in EDM2 selectively affect modification of chromatin. *Curr. Biol.* **23**, 170–175.

Wang, J., Hopkins, C.J., Hou, J.N., Zou, X.X., Wang, C.N., Long, Y., Kurup, S., King, A., Pech, J.-C., Fernie, A.R. and Bouzayen, M. (2009) Regulatory features and their consequences. *Plant Physiol.* **150**, 1016–1028.

Wollenberg, A.C. and Amasino, R.M. (2012) Natural variation in the requirement of histone acetyltransferases HAM1 and HAM2 for epigenetic modification of *a*-glucan. *Science* **335**, 1218–1221.

Vu, T.M., Nakamura, M., Calarco, J.P., Susaki, D., Lim, P.Q., Kinoshita, T., Higashiyama, T., Martienssen, R.A. and Berger, F. (2013) RNA-directed DNA methylation regulates parental genomic imprinting at several loci in *Arabidopsis*. *Development*, **140**, 2953–2960.

Waddington, C. and Kacser, H. (1957) The Strategy of Genes. London: Allen & Unwin.

Walbot, V. and Evans, M.M.S. (2003) Unique features of the plant life cycle and their consequences. *Nat. Rev. Genet.* **4**, 369–379.

Wang, H., Schauer, N., Usadel, B., Frasse, P., Zouine, M., Hernandez, M., Latche, A., Pech, J.-C., Fernie, A.R. and Bouzayen, M. (2009) Regulatory features underlying pollination-dependent and -independent tomato fruit set revealed by transcript and primary metabolite profiling. *Plant Cell* **21**, 1428–1452.

Wang, J., Hopkins, C.J., Hou, J.N., Zou, X.X., Wang, C.N., Long, Y., Kurup, S., King, G.J. and Meng, J.L. (2012) Promoter variation and transcript divergence in brassicaceae lineages of *FLOWERING LOCUS T*. *PLoS ONE* **7**, 1–11.

Wang, J., Hu, J., Qian, Q. and Xue, H.W. (2013) LC2 and OsVIL2 promote rice embryogenesis and seed viability. *J. Plant Physiol.* **169**, 867–877.

Xia, X.Y., Kim, D.H. and Huang, I. (2013) ABA homeostasis and signaling involving multiple subcellular compartments and multiple receptors. *Plant Cell Rep.* **32**, 807–813.

Yaish, M., Guevara, D., El-Kareamy, A. and Rothstein, S. (2010) *Plant Developmental Biology—Biotechnological Perspectives*, Vols 1 & 2. Berlin, Heidelberg: Springer-Verlag.

Yamaguchi, A. and Abe, M. (2012) Regulation of reproductive development by non-coding RNA in *Arabidopsis*: to flower or not to flower. *J. Plant. Res.** **125**, 693–704.

Yao, X.Z., Feng, H.Y., Yu, Y., Dong, A.W. and Shen, W.H. (2013) SDG2-mediated H3K4 methylation is required for proper *Arabidopsis* root growth and development. *PLoS ONE* **8**, 1–11.

You, W.H., Lorkovic, Z.J., Matzke, A.J.M. and Matzke, M. (2013) Interplay among RNA polymerases I, IV and V in RNA-directed DNA methylation at a low copy transgene locus in *Arabidopsis thaliana*. *Plant Mol. Biol.* **82**, 85–96.

Zemach, A., Kim, M.Y., Silva, P., Rodrigues, I.A., Dotson, B., Brooks, M.D. and Zilberman, D. (2010) Local DNA hypomethylation activates genes in rice endosperm. *Proc. Natl Acad. Sci. USA* **107**, 18729–18734.

Zeng, Y. (2006) Principles of micro-RNA production and maturation. *Oncogene*, **25**, 6156–6162.

Zeng, H.Q., Wang, G.P., Hu, X.Y., Wang, H.Z., Du, L.Q. and Zhu, Y.Y. (2014) Role of micro-RNAs in plant responses to nutrient stress. *Plant Soil*, **372**, 1005–1021.

Zhang, J.J. and Xue, H.W. (2013) *OsLTC1/OsHAP3E* participates in the determination of meristem identity in both vegetative and reproductive developments of rice. *J. Integr. Plant Biol.* **55**, 232–249.

Zhang, Q.F., Shen, B.Z., Dai, X.K., Mei, M.H., Maroof, M.A.S. and Li, Z.B. (1994) Using bulked extremes and recessive class to map genes for photoperiod-sensitive genic male sterility in rice. *Proc. Natl Acad. Sci. USA*, **91**, 8675–8679.

Zhang, X.Y., Yazaki, J., Sundaresan, A., Cokus, S., Chan, S.W.L., Chen, H.M., Henderson, J.R., Shinn, P., Pellegrini, M., Jacobsen, S.E. and Ecker, J.R. (2006) Genome-wide high-resolution mapping and functional analysis of DNA methylation in *Arabidopsis*. *Cell* **126**, 1189–1201.

Zhang, H., Chaudhury, A. and Wu, X. (2013a) imprinting in plants and its underlying mechanisms. *J. Genet. Genomics*, **40**, 239–247.

Zhang, Y.Y., Fischer, M., Colot, V. and Bosdorff, O. (2013b) Epigenetic variation creates potential for evolution of plant phenotypic plasticity. *New Phytol.* **197**, 314–322.

Zhao, X.Y., Yu, X.H., Foo, E., Symons, G.M., Lopez, J., Endehakkalu, K.T., Xiang, J., Weller, J.L., Liu, X.M., Reid, J.B. and Lin, C.T. (2007) A study of gibberellic homeostasis and chromosome-mediated blue light inhibition of hypocotyl elongation. *Plant Physiol.* **145**, 106–118.

Zhao, N., Zhu, B., Li, M., Wang, L., Xu, L., Zhang, H., Zheng, S., Qi, B., Han, F. and Lu, B. (2011) Extensive and heritable epigenetic remodeling and genetic stability accompany allohexaploidization of wheat. *Genetics*, **188**, 499–510.

Zhong, S.L., Lei, Z.J., Chen, Y.R., Zheng, Y., Huang, M.Y., Vrebalov, J., McQuinn, R., Gapper, N., Liu, B., Xiang, J., Shao, Y. and Giovannoni, J.J. (2013) Single-base resolution methylomes of tomato fruit development reveal epigenome modifications associated with ripening. *Nat. Biotechnol.* **31**, 154–159.

Zhou, M. and Luo, H. (2013) MicroRNA-mediated gene regulation: potential applications for plant genetic engineering. *Plant Mol. Biol.* **83**, 59–75.

Zhou, H., Liu, Q.J., Li, J., Jiang, D.G., Zhou, L.Y., Wu, L., Lu, J., Su, F., Zhu, L.Y., Liu, Z.L., Chen, L.T., Liu, Y.G. and Zhuang, C.X. (2012) Photoperiod- and thermo-sensitive genic male sterility in rice are caused by a point mutation in a novel noncoding RNA that produces a small RNA. *Cell Res.* **22**, 649–660.

Zhu, B. and Reinberg, D. (2011) Epigenetic inheritance: uncontested? *Cell Res.* **21**, 435–441.

Zuo, J.H., Zhou, B.Z., Fu, D.Q., Zhu, Y., Ma, Y.Z., Chi, L.H., Ju, Z., Wang, Y.X., Zhai, B.Q. and Luo, Y.B. (2012) Sculpting the maturation, softening and ethylene pathway: the influences of microRNAs on tomato fruits. *BMC Genomics*, **13**, 1–12.