

Review article

Sustainable harvest: managing plasticity for resilient crops

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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 \times environment (G \times 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.

Crop plasticity, G \times 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 epigenetics 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 \times environment (G \times 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.

Biological plasticity refers to distinct or overlapping phenomena at different levels of organization, while organismal plasticity may be defined as an individual's response to environmental conditions or to biological and developmental cues. In contrast, phenotypic plasticity refers to the range of phenotypes a single genotype can express as a function of its environment, where adaptive plasticity is a form of the latter that specifically increases the global fitness of a genotype (Nicotra *et al.*, 2010). Meanwhile, developmental plasticity is the capacity of a genotype or an individual's progeny to express phenotypic variation without DNA sequence mutations (Jablonka, 2012).

In the context of crop plants, plasticity plays a key role in adaptation and potential resilience of cultivars to specific or changing growing environments. Phenological plasticity refers to the specific ability of a plant to adjust to seasonal variations during development (Rathcke and Lacey, 1985), although during species divergence, this may not always result in selection of advantageous traits and may limit the ability of a species to invade new habitats (Levin, 2009). However, in the context of generating crops resilient to climate change, such variation may be desirable. In the case of allopolyploid crops such as canola, wheat, oat, cotton and coffee, functional plasticity is the ability of an organism to relocate functions from one tissue to another as a

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 Bruelheide, 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 Palyga, 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 methylome 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 *hobo/Ac/Tam* superfamily of TEs (Alzohairy *et al.*, 2013), *Gary* in a number of cereal genomes (Muehlbauer *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 (SIT1R1) 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 × 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.

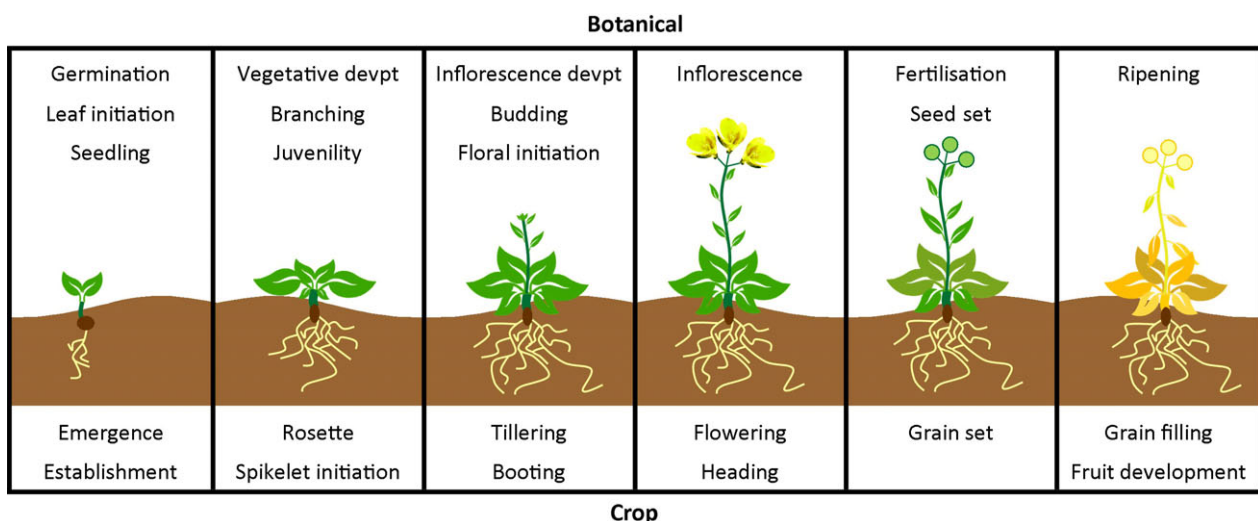


Figure 1 Typical stages within the crop cycle, with corresponding stages of plant development.

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 *AtBRAHMA* (*AtBRM*), *BRUSHY1* (*BRU1*)/*MGOUN3* (*MGO3*)/*TONSOKU* (*TSK*), *FASCIATA 1/2* (*FAS1/2*), *MULTICOPY SUPPRESSOR OF IRA 1* (*MS1*) 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 response (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 (Ortiz-Morea *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 axillary 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*, *BRANCHED1* (*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 Gueriot, 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 (Beauclair *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 *S-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

Table 1 Examples of plant genes effected by or involved with epigenetic mechanisms (Table updated from King *et al.*, 2010)

Species	Crop trait	Gene	Gene class	Gene function	Epigenetic mode	References
<i>Arabidopsis</i>	Vernalization	<i>AG</i>	MADS domain type	Reduces H3K27 trimethylation of <i>KNU</i>	–	Ito (2012), Lamesch <i>et al.</i> (2011)
<i>Arabidopsis</i>	Vernalization	<i>AGL19</i>	MADS-box	H3K27 trimethylation, possibly regulated by PRC2	–	Lamesch <i>et al.</i> (2011), Schonrock <i>et al.</i> (2006)
<i>Arabidopsis</i>	Flowering	<i>AP1</i>	MADS domain protein	–	–	Lamesch <i>et al.</i> (2011), Saleh <i>et al.</i> (2008b)
<i>Arabidopsis</i>	Vegetative development and flowering	<i>AtBRM</i>	SWI/SNF chromatin-remodelling ATPase	Involved in chromatin remodelling	–	Jarillo and Pineiro (2011), Lamesch <i>et al.</i> (2011)
<i>Brassica</i>	Flowering and fertilization	<i>BcJMJ30</i>	jmjC domain-containing histone demethylase	Putative histone demethylase regulating cell fate	–	Lamesch <i>et al.</i> (2011), Li <i>et al.</i> (2012c)
<i>Arabidopsis</i>	Plant architecture	<i>BNS</i>	Anaphase-promoting complex	Methylated	Hypermethylation induces by <i>ddm1 dominance and abnormal floral morphology</i>	Saze and Kakutani (2007)
<i>Arabidopsis</i>	Vegetative development	<i>BRU1/ MGO3/TSK</i>	Tetratricopeptide repeat	Putative part of a protein complex involved in chromatin organization	–	Jarillo and Pineiro (2011), Lamesch <i>et al.</i> (2011)
<i>Arabidopsis</i>	–	<i>CMT3</i>	Chromomethylase	DNA methylation maintenance in CHG contexts	–	Lamesch <i>et al.</i> (2011), Law and Jacobsen (2010)
<i>Solanum lycopersicon</i>	Fruit (pericarp) ripening	<i>CNR</i>	MADS TF	Hypomethylated	Hypermethylation	Manning <i>et al.</i> (2006)
<i>Linaria vulgaris</i>	–	<i>CYCLOIDEA</i>	Class II TCP transcription activator	Hypomethylated. Normal floral symmetry	Hypermethylated allele confers irregular floral symmetry	Cubas <i>et al.</i> (1999)
<i>Oryza</i>	Stature	<i>D1</i>	–	–	Transcriptional initiation site differentially hypermethylated in metastable <i>Epi-d1</i>	Miura <i>et al.</i> (2009b)
<i>Arabidopsis</i>	Flowering/ fertilization	<i>DDM1</i>	SWI2/SNF2-like chromatin-remodelling protein	DNA methylation and heterochromatin maintenance	–	Lamesch <i>et al.</i> (2011), Melamed-Bessudo and Levy (2012)
<i>Arabidopsis</i>	–	<i>DME</i>	DNA glycosylase DEMETER	Maternal-allele-specific hypomethylation at the MEDEA (MEA) gene	–	Lamesch <i>et al.</i> (2011)
<i>Arabidopsis</i>	–	<i>DRM2</i>	Dormancy/auxin-associated family protein	DNA methylation maintenance in CHH contexts	–	Law and Jacobsen (2010)
<i>Arabidopsis</i>	–	<i>FAS1/2</i>	Chromatin Assembly Factor-1	<i>De novo</i> nucleosome assembly during DNA replication	Reduced heterochromatin content	Jarillo and Pineiro (2011), Lamesch <i>et al.</i> (2011)
<i>Arabidopsis</i>	Seed development	<i>FIE</i>	Polycomb protein	–	–	Ohad <i>et al.</i> (1996)
<i>Arabidopsis</i>	Seed development	<i>FIS2</i>	TF	Methylated	Mediated by DEMETER	Luo <i>et al.</i> (1999)
<i>Arabidopsis</i>	Vernalization	<i>FLC</i>	Nuclear localized	–	Modified histone derepresses	Bastow <i>et al.</i> (2004), Saleh <i>et al.</i> (2008b)
<i>Arabidopsis, Brassica</i>	Flowering, vernalization	<i>FT</i>	Phosphatidylethanolamine-binding protein	Paralogues independently silenced by 5mC	–	Lamesch <i>et al.</i> (2011)
<i>Arabidopsis thaliana</i>	Seed development	<i>FWA</i>	Homeodomain-containing TF	Hypermethylated and positively regulates flowering	Hypomethylated allele confers late flowering, mediated by DEMETER	Kinoshita <i>et al.</i> (2004), Soppe <i>et al.</i> (2000)

Table 1 Continued

Species	Crop trait	Gene	Gene class	Gene function	Epigenetic mode	References
<i>Helianthus</i>	Embryogenesis	<i>HaL1L</i>	CCAAT box-binding factor	Differential methylation of CG rich regions	–	Salvini <i>et al.</i> (2012)
<i>Arabidopsis</i>	Floral number	<i>KNU</i>	C2H2-type zinc finger protein	Reduction in H3K27 trimethylation resulting in its derepression	Precocious flowering	Ito and Sun (2009), Lamesch <i>et al.</i> (2011), Sun <i>et al.</i> (2009)
<i>Arabidopsis</i>	Seed development	<i>MEA</i>	Polycomb protein	Methylated	Mediated by DEMETER	Grossniklaus <i>et al.</i> (1998)
<i>Zea mays</i>	Seed development	<i>MEG1</i>	Cys-rich protein	Biallelic at later stages	Maternal parent-of-origin expression during early stages of endosperm; development	Gutierrez-Marcos <i>et al.</i> (2004)
<i>Arabidopsis</i>	Vegetative development, seed set, ripening	<i>MET1</i>	Bromo adjacent homology (BAH) domain, C-5 cytosine methyltransferase	Maternal hypomethylation patterning and transgenerational epigenetic inheritance	Perturbation of auxin gradients in embryos	Lamesch <i>et al.</i> (2011), Law and Jacobsen (2010), Paszkowski and Grossniklaus (2011)
<i>Arabidopsis</i>	Seed development	<i>MPC</i>	Poly(A)-binding protein	–	–	Tiwari <i>et al.</i> (2008)
<i>Arabidopsis</i>	–	<i>MSI1</i>	WD-40 repeat-containing protein	Involved in <i>de novo</i> nucleosome assembly	–	Jarillo and Pineiro (2011), Lamesch <i>et al.</i> (2011)
<i>Oryza</i>	Vegetative and reproductive development	<i>OsLEC1</i>	CCAAT box-binding factor	Stimulates histone post-translational modification	–	Kawahara <i>et al.</i> (2013), Sakai <i>et al.</i> (2013)
<i>Oryza</i>	Sexual reproduction	<i>OsMADS1</i>	MADS-box TF	Methylated promoter region	–	Kawahara <i>et al.</i> (2013), Sakai <i>et al.</i> (2013), Zhang and Xue (2013)
<i>Arabidopsis</i>	–	<i>PAI2</i>	Phosphoribosylanthranilate isomerase	Unmethylated. Does not fluoresce under UV light	Methylated allele leads to fluorescent shoots under UV light	Bender and Fink (1995)
<i>Arabidopsis</i>	Seed development	<i>PHERES1</i>	MADS TF	–	–	Kohler and Makarevich (2006)
<i>Zea mays</i>	Grain colour	<i>P1</i>	DNA binding, similar to <i>MYB oncogenes</i>	Unmethylated allele <i>P-rr</i> confers uniform pigmentation of pericarp	Methylated alleles of <i>P-pr-1</i> and <i>P-pr-2</i> give variegated pigmentation of pericarp	Das and Messing (1994)
<i>Arabidopsis</i> , <i>Brassica</i>	Nucleolar dominance	<i>rDNA</i>	Ribosomal RNA	–	Nucleolar dominance	Preuss and Pikaard (2007)
<i>Arabidopsis</i>	Establishment	<i>SKP2B</i>	F-box	Represses lateral root formation	–	Lamesch <i>et al.</i> (2011), Manzano <i>et al.</i> (2012)
<i>Brassica</i>	Self-incompatibility	<i>SP11</i>	Cys-rich protein	Promoter methylated	Demethylation leads to transcription	Shiba <i>et al.</i> (2006)
<i>Arabidopsis</i>	Male appendages	<i>SUPERMAN</i>	Zinc finger protein	Unmethylated. Normal flower development	Hypermethylated allele results in excessive staminoid organs	Jacobsen and Meyerowitz (1997)
<i>Arabidopsis</i>	–	<i>SYD</i>	SWI2/SNF2-like protein	–	–	Jarillo and Pineiro (2011), Lamesch <i>et al.</i> (2011)
<i>Arabidopsis</i>	Vernalization	<i>VRN1/VIN3</i>	TF	Reduces H3K9 acetylation and dimethylation of <i>FLC</i>	–	Bastow <i>et al.</i> (2004), Lamesch <i>et al.</i> (2011), Sung and Amasino (2004)

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 SDG2-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 phenology 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 regulation that ensures individuals are coordinated in reaching reproductive maturity. The passing of winter perceived as the vernalization signal enables promotion of the flowering programme (Ausin *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/VIN3*; 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 transmission 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 (Fujii *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 quantity and quality (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 (Ausin *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 modulation in rice (Wang *et al.*, 2013) as well as transcriptional, post-transcriptional and post-translational regulation in *Arabidopsis* (Ausin *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 able 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-dependant 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 competence 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.*,

1998). It has long been recognized that epigenetics plays a major role in regulation of the plasticity associated with relative stability and immunity 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 regeneration 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 (Danilevskaya 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 floral timing 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 (Arana 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 dwarfism (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 such 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 (Klinteras et al., 2012). However, *FT/TERMINAL 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 (Klinteras et al., 2012).

The *FT* gene encodes the transmissible 'florigen', a phosphatidylethanolamine-binding protein (PEBP; Klinteras 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.*, 2013c). 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 pollination (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 (Paszowski 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 TEs requires additional epigenetic controls.

Diploid *Brassica* crops are able to limit self-fertilization via the sporophytic self-incompatibility system, with the *SP11* locus in anther 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*, *BcJMJ30* (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* (*HaL1L*) is involved in early stages of zygotic and somatic embryogenesis, with multiplexed transcriptional regulation by DNA methylation, TFs, 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 EXPRESSOR 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* (*PHERES1*) 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*, *Solyc07g052960* 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 important in breeding programme. Notably, this epiallelic variation is within genes having little available genetic variation and so are potential targets for crop improvement via epiallelic screening (Zhong *et al.*, 2013).

COLOURLESS NONRIPENING targets *AP2*, a major regulator of tomato fruit ripening (Karlova *et al.*, 2011), and cultivar-specific variation in the pattern of 5mC in the *CNR* promoter region affects the rate of ripening (Table 1). *CNR* is also targeted by miR156/157 (Moxon *et al.*, 2008; Zuo *et al.*, 2012), although there is only partial overlap of expression between miR156 and *CNR*, with the consequence of suppressing *CNR* in specific cell

types (Zuo *et al.*, 2012). A wider range of miRNAs target key TFs and hormonal regulators of tomato fruit development (Karlova *et al.*, 2013).

Concluding remarks

In this review, we have explored the conventional understanding of crop plant G × E interactions and plasticity and outlined the extent to which epigenetic mechanisms contribute to adaptive plasticity. We have mapped key stages of plant development onto the corresponding crop phases and described many transitions and responses modulated by epigenetic marks and processes. We note that while the model plant *Arabidopsis* has provided startling insights into vegetative and reproductive development, it often is unable to provide a viable model for studying many aspects of crop responses to field growing environments (Seymour *et al.*, 2013b).

The domestication of crop plants has involved selection of a wide range of phenotypes adapted to human requirements (Ross-Ibarra *et al.*, 2007; Vaughan *et al.*, 2007). This selection is characterized by strong pressure for stability of key 'domestication traits' associated with the crop products such as food and fibre. In many cases, the value and popularity of a crop in one location has stimulated radiation to other eco-agronomic regions, with a requirement for a wider range of adaptations to local growing environments. While the genetic canalization associated with crop domestication is well characterized, the extent to which breeding germplasm has inadvertently been selected for epiallelic variation has yet to be established (Amoah *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 miRNA 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 5mC 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.

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