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Review article

Towards molecular breeding of reproductive traits in cereal crops

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Summary

The transition from vegetative to reproductive phase, flowering *per se*, floral organ development, panicle structure and morphology, meiosis, pollination and fertilization, cytoplasmic male sterility (CMS) and fertility restoration, and grain development are the main reproductive traits. Unlocking their genetic insights will enable plant breeders to manipulate these traits in cereal germplasm enhancement. Multiple genes or quantitative trait loci (QTLs) affecting flowering (phase transition, photoperiod and vernalization, flowering *per se*), panicle morphology and grain development have been cloned, and gene expression research has provided new information about the nature of complex genetic networks involved in the expression of these traits. Molecular biology is also facilitating the identification of diverse CMS sources in hybrid breeding. Few *Rf* (fertility restorer) genes have been cloned in maize, rice and sorghum. DNA markers are now used to assess the genetic purity of hybrids and their parental lines, and to pyramid *Rf* or *tms* (thermosensitive male sterility) genes in rice. Transgene(s) can be used to create *de novo* CMS trait in cereals. The understanding of reproductive biology facilitated by functional genomics will allow a better manipulation of genes by crop breeders and their potential use across species through genetic transformation.

Keywords: CMS and *Rf* systems, floral organ development model, flowering, gene expression, gene/QTL cloning, inflorescence architecture, MADS-box genes, meiosis, transgenics.

Introduction

Maize, rice and wheat are the major food crops worldwide, and together they contribute 74%–86% of the world's cereal production: from an average of 737 million tons between 1962 and 1966 to 1882 million tons between 2002 and 2006 [Food and Agriculture Organization (FAO), 2006]. The world's population is expected to reach 8.3 billion in 2030; the Earth will have to feed an extra two billion people, 90% of whom will live in developing countries (Bruinsma, 2003). It is therefore crucial to ensure not only that sufficient food is produced to feed this expanding population, but also that it is easily accessible to all. The Green Revolution more than doubled world grain production, thereby averting large-scale famine in the 'developing world'. Crop productivity will need to be raised further to meet the growing demand for food crops.

Hybrid cultivars have made a significant contribution to the world's food supply. In cereals, heterosis has been exploited in maize, rice, sorghum and pearl millet to produce high-yielding hybrids that, by far, dominate the global acreage for each crop. For example, about 95% of corn acreage in the USA is planted to hybrids that exhibit a 15% yield advantage relative to the best open-pollinated cultivars (Duvick, 1999), and more than half of the total rice-growing area in China is planted with hybrid rice cultivars (Wang *et al.*, 2005a). The three- or two-line systems for producing hybrid seeds are well established in cereal crops. Cytoplasmic male sterility (CMS) and fertility restoration systems in three-line hybrids and environmentally sensitive genetic male sterility in two-line

hybrids are used to produce hybrid seeds. Understanding the molecular mechanism of CMS and fertility restorer (*Rf*) genes and the molecular basis of environmentally induced genetic male sterility could improve the efficacy of hybrid technology.

Plants are sessile, and flowering is a key adaptive trait that contributes to their fitness by ensuring that they flower at an optimum time for pollination, seed development and dispersal. In addition to flowering *per se*, flower structure (more specifically male and female reproductive organs), panicle morphology, meiosis, pollination, fertilization and seed development are the major reproductive traits that influence grain yield. The mechanism of meiotic recombination and gamete formation ensures genomic stability and unfolds the genetic variation for targeted alterations in plant genomes. DNA marker-aided analysis of reproductive biology is still an emerging area. This contrasts with the situation for quality traits or resistance to biotic stresses, where considerable knowledge has been generated about genes and quantitative trait loci (QTLs), and DNA markers associated with these traits have been identified (Dwivedi *et al*., 2007, and references cited therein). Genomics can facilitate research on several key issues: unlocking the secret of what makes plants flower, the basis of structural divergence in panicle morphology amongst cereals, whether plants control meiosis, whether or not there are key gene(s) or a complex genetic network involved in the development of male and female organs, pollination and fertilization, and the development of seeds and their nutritional quality.

Global warming as a result of climate change will affect grain yields of cereals, particularly in non-temperate regions. By 2100, average global temperatures could rise by as much as 6 °C under the business-as-usual scenario (http://www.fao.org/docrep/005/y4252e/y4252e15.htm). High temperatures impair plant reproductive processes in particular, and thus may significantly reduce grain yields. For example, grain yield declined by 10% for each 1 °C increase in the growing season minimum temperature in the dry season, whereas the maximum temperature had no significant effect on rice yield (Peng *et al*., 2004).

Recent advances in plant biotechnology can help to address food security concerns. The structure of the cereal genomes and genes contained within them will aid geneticists and molecular biologists to understand cereal biology and help plant breeders to develop better products. Because of the remarkable degree of collinearity amongst grasses, rice can be used as a model plant for cereal genomics. This will greatly facilitate the isolation of agronomically important genes and our understanding of genome evolution. The rice genome has been fully sequenced, and this information can be used to obtain greater insights into the syntenic relationship between rice and the major cereals (Sasaki and Antonio, 2004).

Applied genomics for rice, wheat, maize, barley and pearl millet has provided useful new tools for breeding, and marker-assisted genetic enhancement has led to the development of several improved cultivars and advanced lines that show greater yields, possess good grain quality and minimize damage caused by pests and diseases. The introgression of beneficial genes under the control of specific promoters through transgenic approaches is another targeted approach to crop improvement. Genomic sciences have already identified many genes that have exciting potential for this purpose. Many genes and QTLs for important agronomic traits in cereals have been cloned, and are good candidates for transformation into other cultivars of the same crop, or into other cereals, without additional modification (Dwivedi *et al*., 2007, and references cited therein).

Flowering has been researched in detail in the model plant *Arabidopsis*, and in some grasses (Putterill *et al*., 2004; Corbesier and Coupland, 2006; Roux *et al*., 2006; Cockram *et al*., 2007). Inflorescence branching is a major yield trait in crop plants. It is controlled by the developmental fate of shoot apical meristems, and variation in branching patterns leads to diversity in inflorescences and affects crop yield; a number of mutants with altered inflorescence structure have been used to study the molecular and genetic control of grass inflorescence (Vollbrecht *et al*., 2005; Malcomber *et al*., 2006; Satoh-Nagasawa *et al*., 2006; Kellogg, 2007; Prusinkiewicz *et al*., 2007). A number of mutants defective in several aspects of organ development and meiosis in *Arabidopsis* have been used extensively to study the genetic and molecular basis of plant meiosis (Schwarzacher, 2003; Hamant *et al*., 2006; Ma, 2006). Information derived from this model plant is being used to study meiosis and crossover effects in crop plants including cereals. In contrast with flowering, inflorescence and plant meiosis, to the authors' best knowledge, there have been only a couple of thorough reviews on the development of marker-assisted selection strategies for breeding hybrid rice (Xu, 2003), and on the nature and origins of the genes that determine CMS or plant mitochondrial–nuclear interactions (Chase, 2007), but there have been some recent reports on gene expression for dissecting the molecular basis of heterosis in maize, rice and wheat (Dwivedi *et al*., 2007, and references cited therein).

In this review, brief descriptions are given of the following: the model explaining floral organ development; the molecular basis of plant meiosis; molecular mechanisms regulating inflorescence architecture; mapping and cloning of genes or

QTLs associated with phase transition (vegetative to reproductive growth) and variation in flowering and spike and grain development traits; gene expression with respect to floral organ development, pollination, fertilization and grain development; the molecular basis of CMS and the mapping and cloning of *Rf* genes; DNA markers for maintaining the purity of CMS and maintainer lines and hybrids; marker-assisted selection to pyramid *tms* (thermosensitive male sterility) and *Rf* genes; and transgenic approaches to hybrid breeding in cereals.

Flowering

ABC model and MADS-box genes in flower organ development

Flowers normally consist of sepals, petals, stamens and pistils that arise in four concentric rings or whorls. The ABC model explaining flower development as the combination of different identity factors was postulated in the early 1990s (Bowman *et al*., 1991; Coen and Meyerowitz, 1991). The A signals specify whorl 1 or sepal formation, A + B direct whorl 2 or petals, B + C whorl 3 or stamens, and C whorl 4 or carpel formation (Figure 1). Moreover, A and C functions are mutually repressive (Jack, 2004). By using a mutagenesis approach, the genes responsible for the identity of different whorls have been cloned. For example, in *Arabidopsis*, the A function is triggered by *APETALA1* (*AP1*) and *APETALA2* (*AP2*), the B function by *AP3* and *PISTILLATA* (*PI*) and the C function by *AGAMOUS* (*AG*). Ectopic expression of these genes in flowers is sufficient to trigger differentiation of the individual organs (Jack, 2004). Although *AP2* defines whorls 1 and 2, transcripts accumulate in all the floral whorls (Jofuku *et al*., 1994). This suggests a more complex role for *AP2* in organ determinism. Null mutations in *AP2* induce the formation of reproductive organs in place of petals and sepals (Bowman *et al*., 1991). Ectopic expression of AG in the outer whorls produces a similar phenotype to *AP2* mutants (Mizukami and Ma, 1992). Moreover, loss of function of *AG* induces petal formation instead of stamens, together with additional flower formation in place of carpels (Bowman *et al*., 1991). This suggests that AP2 and AG have an antagonistic effect. Recently, it has been shown that microRNAs play a role in determining floral identity. MicroRNAs induce post-transcriptional degradation of genes by recognizing complementary sequences in the transcripts. For example, miR172 appears to be a negative regulator of *AP2* (Zhao *et al*., 2007). Moreover, in petunia, two members of the miR169 family (BL and FIS) appear to regulate inner whorl identity, as null mutations

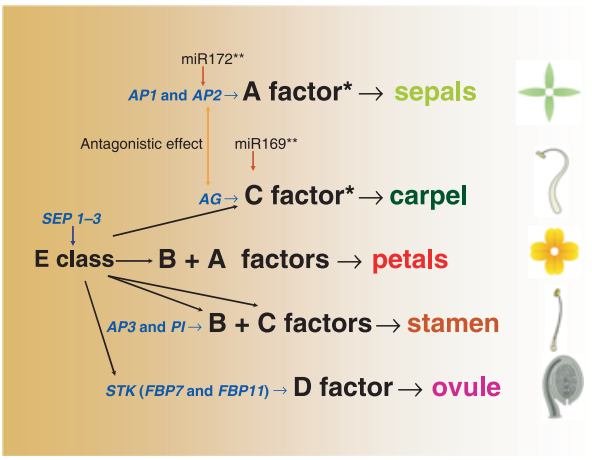

Figure 1 ABC model MADS-box genes in flower organ development. *Mutually repressive. **MicroRNA negative regulators. *AG*, *AGAMOUS*; *AP*, *APETALA*; *PI*, *PISTILLATA*; *SEP*, *SEPALLATA*; *SKT*, *SEEDSTICK*.

increase C-function gene expression (Zhao *et al*., 2007). Future work will probably demonstrate the increasing importance of microRNAs in the regulation of flowering. In addition to the ABC model, a D-function gene, which controls the specific formation of ovules, has been defined (Figure 1). Two D-function genes, *FBP7* (*floral binding protein*) and *FBP11*, specify placenta and ovule identity in petunia, and, when these genes are silenced, ovules fail to develop (Angenent *et al*., 1995). Moreover, ectopic expression of *FBP11* produces ovules on sepals and petals (Colombo *et al*., 1995). In *Arabidopsis*, the D-function gene *SEEDSTICK* (*STK*) is solely expressed in ovules and corresponds to *FBP7* and *FBP11* (Favaro *et al*., 2003).

The latest addition to the ABC model is a fifth set of genes, the E class (Figure 1), necessary for normal flower development: *SEPALLATA* (*SEP*). In *Arabidopsis*, triple mutants in *SEP1–3* produce flowers consisting solely of sepals (Pelaz *et al*., 2001). This suggests that the A function alone is responsible for sepal formation, whereas petals, stamens and carpels also require the E function. This has been confirmed experimentally, given that ectopic expression of *SEP3* in *Arabidopsis* in conjunction with *AP3* and *PI* produces petal-like organs, and over-expression of *AG*, *AP3*, *PI* and *SEP3* produces stamen-like organs (Honma and Goto, 2001). The SEP proteins control organ identity through the formation of multimeric complexes with other MADS-box proteins, such as STK. Genetic evidence for this role has been demonstrated: a decrease in SEP activity led to a loss of ovule development (Favaro *et al*., 2003).

Flower morphology in cereals differs from flower morphology in other species, making comparisons in floral organ development

difficult. Rice spikelets contain a single bisexual floret consisting of the pistil, stamens, two lodicules, palea and lemma. Similarly, maize spikelets have florets, a pistil, stamen, lodicules, palea and lemma (Bommert *et al*., 2005b). The lodicules correspond to whorl 2, the stamens to whorl 3 and the pistil to whorl 4 of *Arabidopsis*. It is not yet clear which structures correspond to whorl 1, although it might be assumed that the lemma/palea structures correspond to the sepals. The MADS-box proteins orthologous to all organ identity classes (ABCD and E) have been found in cereals (Bommert *et al*., 2005b; Zhao *et al*., 2006a).

In *Arabidopsis*, the A-class genes responsible for sepal and petal identity include *AP1* and *AP2*. The grass genes belonging to the *AP1* family have been found in maize (*Zap1a* and *Zap1b*), rice (*OsMADS14*, *OsMADS15*, *OsMADS18* and *OsMADS20*) and barley (*BM3* and *BM8*), and the *VRN1* gene complex in wheat (Whipple *et al*., 2004; Zhao *et al*., 2006a). Using RNA profiling, Mena *et al*. (1995) showed that *Zap1a* was expressed in the outer whorls of the maize floret, but not in the stamen and pistil. Similarly, *OsMADS14* expression was not detected in the reproductive organs, but did occur in the palea, lemma and lodicule (Kyozuka *et al*., 2000). Based on sequence homology, at least six A-class proteins have been found in wheat (Zhao *et al*., 2006a). Although there might be some redundancy, the size of this gene family suggests that these proteins could play different roles in monocotyledons than in dicotyledons. A demonstration of this additional complexity is the finding that the *VRN1* gene, a *Triticum AP1* orthologue, is induced by vernalization in winter wheats. As *VRN1* controls flowering time on cold treatment, it appears that this gene in wheat not only defines outer whorl identity, but plays an additional role in floral transition (Yan *et al*., 2003). Similarly, over-expression of *OsMADS18* in rice accelerates flowering time, whereas silencing of the gene produces no visible phenotype (Fornara *et al*., 2004).

Although the A function appears to be conserved between certain cereal genes and *Arabidopsis*, the situation may be more complex. Some *AP1*-like cereal genes do not appear to be involved in whorl 1 identity. This is not unique to cereals: no true A-function protein has been found in *Antirrhinum*, for example (Huijser *et al*., 1992). A better characterization of the numerous *AP1*-like genes is required to establish the presence of a defined A-function class of proteins in cereals.

The B-class genes *AP3* and *PI* are responsible for petals and stamen identity in *Arabidopsis*. *SILKY1* (*SI1*) from maize and *OsMADS16* or *SUPERWOMAN1* (*SPW1*) from rice are *AP3* orthologues (Ambrose *et al*., 2000; Nagasawa *et al*., 2003). These genes are expressed during the early development of lodicules and stamens. Mutations in these genes induce homeotic changes from stamen into carpels and lodicules into lemma/palea-type organs. These data confirm that, in cereals, lodicules correspond to whorl 2 and stamen to whorl 3; the data also suggest that the lemma/palea corresponds to whorl 1. Moreover, the data also suggest that B function is conserved between monocotyledons and dicotyledons.

OsMADS2 and *OsMADS24* from rice and *Zmm16*, *Zmm18* and *Zmm29* from maize appear to be homologues of *PI* (Münster *et al*., 2001; Kater *et al*., 2006). RNA profiling analysis showed that *OsMADS2* is expressed in the inner whorls, whereas *OsMADS24* is present in organs from whorls 2 and 3 (Kyozuka *et al*., 2000; Yadav *et al*., 2007). Antisense co-suppression of *OsMADS4* in rice converts lodicules to lemma/palea and stamens to carpel structures, confirming its role in whorls 2 and 3, and demonstrating a conserved function between the *Arabidopsis* and rice orthologues (Kang *et al*., 1998). Interestingly, when *OsMADS2* was silenced, no modification in stamen development was found, although lodicules were modified into lemma/palea (Prasad and Vijayraghavan, 2003). Wheat has two orthologues of *PI* (*WPI1* and *WPI2*) and one orthologue of *AP3* (*WAP3*) (Zhao *et al*., 2006a). When analysing the expression of the *WPI1* and *WAP3* genes, Hama *et al*. (2004) showed RNA expression in lodicule and stamen primordia. Moreover, by studying alloplasmic wheat lines presenting homeotic changes of stamen into pistil-like structures, they demonstrated the role of these B-class proteins in floral organ identity.

In *Arabidopsis*, the B-class proteins AP3 and PI function as a heterodimer to regulate the transcription of floral genes. Whipple *et al*. (2004) showed that the maize orthologue of AP3 (SI1) formed a heterodimer with Zmm16, an orthologue of PI. In addition, they demonstrated that SI1 or Zmm16 could activate transcription by forming heterodimers with PI and AP3, respectively. *Arabidopsis AP3* and *PI* mutants could also be rescued with the maize orthologues. This finding suggests that the B function in maize and *Arabidopsis* is conserved and grass lodicules correspond to petals.

The stamen and carpel organ identities in *Arabidopsis* are controlled by the C-class gene *AG* (Jack, 2004). Two C-class genes were found in maize: *Zag1* and *Zmm2* (Schmidt *et al*., 1993; Theissen *et al*., 1995). *Zag1* is highly expressed in pistils, whereas *Zmm2* is mainly expressed in stamen. Knockout in *Zag1* induces indeterminate cellular growth in the ovary, but does not modify tassel identity (Mena *et al*., 1996). The lack of a tassel phenotype suggests that *Zmm2* is redundant with *Zag1* in stamen determination. Similar to maize, rice has an orthologue of *Zmm2* (*OsMADS3*) and an orthologue of *Zag1* (*OsMADS58*). RNA profiling has shown that *OsMADS3* is mainly found in the ovule primordia, whereas *OsMADS58* is

expressed in the stamen and carpel (Yamaguchi and Hirano, 2006). Ectopic expression of *OsMADS3* under the control of an actin promoter transformed lodicules into stamen, which is predicted for C-class genes (Kyozuka and Shimamoto, 2002). The C-class nature was confirmed by analysis of transgenic rice expressing antisense *OsMADS3*. These plants had lodicule-like stamens and carpelloid and stamenoid structures instead of carpels (Kang *et al*., 1998). RNA interference (RNAi) knockouts of *OsMADS58* showed a phenotype similar to null mutants of *Zag1*. Floral meristem determinacy and carpel development were affected, but the effect on stamen identity was less severe than in *OsMADS3* mutants (Yamaguchi and Hirano, 2006). Thus, *Zmm2*/*OsMADS3* plays a predominant role in whorl 3 determinism, whereas *Zag1*/*OsMADS58* is mainly responsible for the formation of whorl 4.

Homology searches have shown that rice and maize have homologues of the D-class genes *FBP7* and *FBP11* that control ovule identity in petunia. These genes are *Zag2*, *Zmm1* and *Zmm25* in maize and *OsMADS13* and *OsMADS21* in rice (Kater *et al*., 2006). Expression analysis of *OsMADS13* and *Zag2* showed persistent expression in the ovules (Lopez-Dee *et al*., 1999). It is not clear whether these genes play a role in determining ovule identity, given that ectopic expression of *OsMADS13* in rice and *Arabidopsis* does not induce ovule formation (Favaro *et al*., 2002).

The E function in *Arabidopsis* is regulated by *SEP* genes that appear to work in conjunction with the A, B, C and D MADS-box genes to specify floral organ identity. Numerous *SEP* homologues have been found in cereals. At least 12 *SEP*-like MADS boxes have been found in wheat (Zhao *et al*., 2006a). Characterization of *TaMADS1* transcripts shows accumulation in floral primordia. Moreover, ectopic expression induces early flowering and alterations in floral organ development in *Arabidopsis* (Zhao *et al*., 2006b). Maize has seven E-class MADS-box genes (Whipple and Schmidt, 2006). Expression profiling of *Zmm8* and *Zmm14* shows transcription mainly in the meristems of the upper florets, suggesting a role in floral induction (Cacharrón *et al*., 1999). In rice, at least five *SEP*-like genes (*OsMADS1*, *OsMADS5*, *OsMADS7*, *OsMADS8* and *OsMADS19*) have been found (Kater *et al*., 2006). Null mutations in the *OsMADS1* or *leafy hull sterile 1* (*lhs1*) genes produce leafy lemma and palea. In addition, the lodicules and stamens are also modified into leafy lemma and palea structures (Agrawal *et al*., 2005; Bommert *et al*., 2005b). These observations demonstrate that *OsMADS1*, as well as the *Arabidopsis* SEP proteins, play a role in the E function in rice. Confirming this role of cereal E-class genes, over-expression of *OsMADS8* in tobacco induced early flowering (Kang *et al*., 1997). In contrast, a loss of function of *OsMADS5* does not produce significant disruptions in flower identity (Agrawal *et al*., 2005). These data, in conjunction with the complexity of the *SEP* family in cereals, suggest that these proteins may play additional roles in plant development.

MADS-box genes have been characterized in *Arabidopsis*, petunia and *Antirrhinum*. Recently, more effort has been invested in understanding the function of these genes in cereals. Although the picture may be more complex for the A-class genes, it is now clear that the B and C genes act similarly in monocotyledons and dicotyledons. Current data based on RNA profiling, protein interaction studies and phylogenetic analysis suggest that the D and E functions are also conserved throughout flowering plants, although gene redundancy has complicated the functional characterization of these classes of genes. As flower development is associated with traits such as grain yield and abiotic stress tolerance, a better understanding of the function of MADS-box proteins presents tremendous potential to improve crop yields.

Phase transition from vegetative to reproductive growth

Reproduction is a function of life. The transition from vegetative growth to flowering is essential for survival, and plants normally correlate the onset of flowering with suitable environmental conditions. Flower development and seed set are greatly impeded by stresses, such as drought or frost. The control of flowering is a highly regulated process that entails many environmental and endogenous signals that induce a change of determinism of the stem cells in the shoot apical meristem to give rise to reproductive structures in plants. It has been well documented that a mobile signal produced in the leaves, termed 'florigen', triggers floral transition in the shoot apical meristem (Corbesier and Coupland, 2006). Recently, the nature of this floral stimulus has been elucidated in *Arabidopsis thaliana* (Figure 2) and in rice. *FLOWERING LOCUS T* (*FT*), which encodes a small protein similar to receptor-associated factor (RAF)-kinase inhibitors, has been shown to be expressed in the leaves and then transported to the meristem. In this tissue, *FT*, together with the bZIP transcription factor *FD* expressed solely in the shoot apical meristem, activates floral identity genes, such as *AP1* (Wigge *et al*., 2005). Using FT–green fluorescent protein (GFP) fusions, Corbesier *et al*. (2007) showed that the protein was translocated from the leaves via phloem companion cells to the meristem, and that this movement correlated with flowering. Tamaki *et al*. (2007) have demonstrated that the Hd3a protein, an orthologue of FT, induces flowering by moving from the leaf

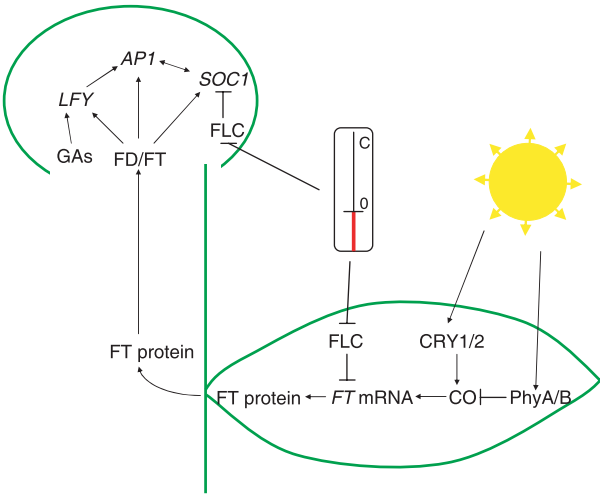

Figure 2 Summary of interactions regulating the phase transition from vegetative to reproductive growth in the model plant *Arabidopsis thaliana* (modified from Kobayashi and Weigel, 2007). Day length regulates flowering by activating *FT* expression via modulation of CO by the phytochromes and the cryptochromes. Cold temperatures induce flowering by activating *FT* expression through repression of FLC. FT is then transported via the phloem to the shoot apex, where it activates expression of *AP1*, *SOC1* and *LFY*, thus triggering flower development. *AP1*, *APETALA 1*; *CO*, *CONSTANS*; CRY1/2, cryptochromes; *FD*, bZIP transcription factor; *FLC*, *FLOWERING LOCUS C*; *FT*, *FLOWERING LOCUS T*; GAs, gibberellins; *LFY*, *LEAFY*; PhyA/B, phytochromes; *SOC1*, *SUPPRESSOR OF OVER-EXPRESSION OF CO1*.

to the shoot apical meristem. Working with Hd3a–GFP fusions, they showed that over-expression of the gene significantly accelerated flowering. Indeed, transgenic rice flowered after about 14–44 days, depending on the promoter upstream of the *Hd3a* genes, whereas wild-type rice usually took more than 50 days to flower in the same conditions. This suggests that the increase in expression of the mobile flowering signal FT induces early flowering, and appears to be a major player in the transition from vegetative to reproductive growth.

FT orthologues have been found in other crops (maize, barley and wheat) and appear to be involved in floral determination (Yan *et al*., 2006). Apart from *FT*, genetic analyses of *Arabidopsis* mutants showing alteration in flowering time have permitted the isolation of numerous genes involved in four basic interlinked pathways in floral transition: photoperiod, vernalization, gibberellin and autonomous pathways (Bernier and Perilleux, 2005).

Photoperiod pathway

The photoperiod pathway promotes flowering in *Arabidopsis* under long days (LD) (Boss *et al*., 2004). The plant perceives the day length through photoreceptors that absorb either red/far-red light for the phytochromes or blue light for the cryptochromes (Lin, 2000; Quail, 2002).

The transcription factor *CONSTANS* (CO) plays a major role in stimulating flowering on LD conditions through the transcriptional activation of *FT* (Samach *et al*., 2000). The expression of *CO* oscillates according to a circadian rhythm and has a peak at the end of the day under LD, which correlates with *FT* expression, and during the night under short days (SD) (Suarez-Lopez *et al*., 2001). Transgenic plants constitutively expressing *CO* flower earlier than wild-type controls and lose photoperiod sensitivity (Onouchi *et al*., 2000). In these plants, *FT* and *SOC1* (*SUPPRESSOR OF OVER-EXPRESSION OF CO1*) are enhanced, demonstrating that *CO* promotes flowering by activating the expression of these genes (Samach *et al*., 2000). Valverde *et al*. (2004) showed that *CO* function was post-transcriptionally regulated through cryptochromes (CRY1 and CRY2) and through phytochromes A and B (phyA and phyB). Under red light and in the mornings, mutations in phyB produced an increase in the CO protein concentration, suggesting that the flowering repression activity of phyB is partly a result of a decrease in CO abundance. In contrast, mutations in the cryptochrome genes (*CRY1* and *CRY2*) reduced the level of CO protein in the morning and under blue light. Thus, these proteins stabilize CO and compete with phyB to induce flowering. During LD and under far-red light, phyA appears to stabilize CO similarly to the cryptochromes, given that *phyA* mutants have less CO (Valverde *et al*., 2004). Thus, it appears that, under SD, CO degradation is enhanced via phyB, whereas, under LD, flowering is induced by the stabilization of CO through the cryptochromes and phyA.

The analysis of the genomic sequence of rice and other cereals has shown that many *Arabidopsis* genes that play a role in the photoperiod pathway and circadian clock have cereal orthologues. This suggests that the molecular mechanisms controlling flowering time in cereals and *Arabidopsis* are similar. Interestingly, barley *CO* shows a diurnal rhythm similar to that of the *Arabidopsis* orthologue (Cockram *et al*., 2007). Moreover, the rice orthologue of *CO*, *Heading date 1* (*Hd1*), appears to play a major role in day length sensitivity (Hayama and Coupland, 2004). In this SD plant, loss of *Hd1* produces an increase in *Hd3a* expression and induces early flowering under LD and delayed flowering under SD (Yano *et al*., 2000). Hayama and Coupland (2004) proposed that, under LD, the HD1 protein is activated by phytochrome and, contrary to *Arabidopsis*, inhibits flowering through inactivation of *Hd3a*. Under SD, in the absence of active phytochrome, *Hd1* is expressed at night and triggers Hd3a expression and flowering. Not all mechanisms involved in the photoperiod

pathway in cereals are clearly understood, but similarities between genes and functions show that data from *Arabidopsis* can be used for enhancement of crops.

Vernalization pathway

Certain plants, such as winter wheat and *Arabidopsis*, require prolonged exposure to low temperatures to flower. In these plants, the vernalization response impedes flowering whilst temperatures are too low, permitting the plant to grow in winter. Several genes involved in the regulation of the vernalization pathway in *Arabidopsis* have been cloned (Sung and Amasino, 2005). The two major players are the MADS-box transcription factor *FLOWERING LOCUS C* (*FLC*) and *FRIGIDA* (*FRI*). FLC is a repressor of flowering and is strongly up-regulated by FRI, a coiled-coil domain protein with unknown biochemical function (Johanson *et al*., 2000). The repression of flowering occurs through the inhibition of *FT* and *SOC1* expression (Mouradov *et al*., 2002). *FLC* is irreversibly down-regulated in a time-dependent manner during cold treatment, and therefore repression of flowering is lifted when warmer temperatures occur (Sheldon *et al*., 2000). The cold-induced decrease in *FLC* expression is stable throughout plant development and remains low even in organs formed at warmer temperatures. One exception is in gametes, where *FLC* repression is reset on sporogenesis or gametogenesis (Mouradov *et al*., 2002).

The analysis of late-flowering *Arabidopsis* mutants on vernalization treatment permitted the isolation of *VERNALIZATION 1* (*VRN1*) and *VERNALIZATION 2* (*VRN2*). The latter codes for a zinc-finger protein, part of the Polycomb (PcG) multimeric protein complex. This complex represses gene expression through the modification of chromatin structure (Sung and Amasino, 2005). To date, no orthologues of *FLC* or *FRI* have been found in cereals. Although PcG proteins are present in grasses, it remains unclear whether these play a role in the regulation of vernalization.

The absence, to date, of cereal orthologues of *FLC* and *FRI* suggests that vernalization in *Arabidopsis* and cereals is controlled through different pathways that converge at *SOC1* and *FT*. The discovery in *Arabidopsis* of an *FLC*-independent vernalization pathway in which *AGAMOUS-LIKE 24* (*AGL24*) plays a key role could provide answers as to how cereals modulate *SOC1* and *FT* expression on cold treatment (Yu *et al*., 2002; Michaels *et al*., 2003). Indeed, based on sequence homology, cereal orthologues of *AGL24* have been found.

In cereals such as wheat and barley, the response to vernalization is regulated by at least three genes, *VRN1*, *VRN2* and *VRN3*, which have no relationship to the *Arabidopsis* genes of the same name (Cockram *et al*., 2007). *VRN1* encodes an AP1-like MADS-box and is an orthologue of *VRN-A*^{m}*1* from *Triticum monococcum* (Yan *et al*., 2003; Shitsukawa *et al*., 2007b). VRN2 is a transcription factor with a zinc finger and CCT (*CO*, *CO-LIKE* and *TIMING OF CAB EXPRESSION 1*) domain (ZCCT domain), also found in CO, and VRN3 is an orthologue of FT (Valverde *et al*., 2004; Yan *et al*., 2004). On prolonged exposure to cold, *VRN1* is up-regulated, thus promoting flowering, whereas *VRN2* is repressed (Yan *et al*., 2004). In spring wheat characterized by dominant *VRN1* alleles, the gene is constitutively expressed in plants with dominant spring alleles, therefore explaining flowering in the absence of cold treatment. In winter wheat, a MADS-box transcription factor, VEGETATIVE TO REPRODUCTIVE TRANSITION 2 (*TaVRT2*), represses *VRN1* transcription by binding to a site in the promoter, the CarG-Box (Kane *et al*., 2007). When vernalization is complete, *TaVRT2* transcripts are down-regulated, permitting the accumulation of VRN1 and flowering. In addition, down-regulation of *VRN2* on vernalization leads to the induction of *VRN1* (Yan *et al*., 2004). This down-regulation can be replaced by SD treatment, demonstrating a link between the photoperiod and vernalization pathways in wheat (Dubcovsky *et al*., 2006). This link was also found in barley grown in LD conditions, where *VRN1* was expressed despite *VRN2* expression (Trevaskis *et al*., 2006). *VRN2* appears to play an integrative role, as its transcription is regulated by day length and by vernalization. Although the *Arabidopsis* gene *FLC* has no orthologues in cereals, *VRN2* might play the same role in vernalization.

Gibberellin pathway

The *Arabidopsis* over-expressing genes involved in the gibberellin biosynthesis pathway are early flowering, independent of photoperiod. In contrast, a decrease in gibberellin levels retards flowering mainly under SD. Although the gibberellin pathway is different from other pathways, it appears to be involved in floral induction, mainly under SD (Boss *et al*., 2004). Gibberellin promotes flowering under SD through the induction of the *LEAFY* (*LFY*) transcription factor (Blazquez and Weigel, 2000). This protein plays a central role in the onset of flowering. *LFY* is expressed in leaf primordia, and a rapid increase in expression is correlated with floral transition in *Arabidopsis* during LD (Araki, 2001). Although *LFY* is not a direct target of *CO*, activation of this protein triggers a rapid increase in expression (Samach *et al*., 2000).

The *Arabidopsis* LFY protein is characterized by a conserved domain found in floricaula/leafy proteins. Although these proteins have been well studied in dicotyledons, not much is known of their function in monocotyledons. Null mutations in *FLORICAULA/LEAFY-like 1* and *2* from maize produced

defects in inflorescence development and structure, demonstrating that the LFY proteins play a conserved role (i.e. behave in the same way) in dicots and monocots (Bomblies *et al*., 2003).

Although the application of bioactive gibberellins accelerates floral initiation in wheat, sorghum, barley and rice, it remains unclear what transductional pathways are involved in this process (King and Evans, 2003).

The Green Revolution in the 1960s occurred as a result of farmers adopting new wheat cultivars that were shorter, photoperiod insensitive, higher yielding and with higher harvest indices. The reduced size came from mutations in genes such as *Reduced height 1–3*, responsible for gibberellin signalling (Peng *et al*., 1999). The importance of gibberellin as an essential regulator of cereal growth has been demonstrated; however, its role in flowering is still not clear.

Autonomous pathway

This pathway was identified in a series of *Arabidopsis* mutants that contained higher levels of *FLC* than wild-type plants and that were later flowering under all photoperiods (Mouradov *et al*., 2002). This delay in flowering is overcome by vernalization, suggesting a link between the vernalization and autonomous pathways. To date, seven proteins are known to be involved in the autonomous pathway in *Arabidopsis* [FCA, FY, FPA, FVE, luminidependens (LD), flowering late KH motif (FLK) and flowering locus D (FLD)]. All seven proteins have orthologues in cereals. Although the mode of action of the RNA-binding protein FCA is unclear, overexpression under the control of a constitutive promoter results in early-flowering *Arabidopsis* lines (Marquardt *et al*., 2006). As FCA physically interacts with FY, a WD repeat polyadenylation factor, it is postulated that the complex regulates *FLC* transcripts through the stabilization of mRNA (Marquardt *et al*., 2006). Constitutive expression of rice *FCA* (*OsFCA*) in *fca Arabidopsis* mutants rescued the late-flowering phenotype (Lee *et al*., 2005a), but no significant effect on *FLC* expression was obtained. Moreover, as no *FLC* orthologue has been found in cereals, *FCA* and the autonomous pathway might play different roles in the regulation of flowering in monocots and dicots.

The genetic and molecular bases of meiosis in plants

Meiosis, a specialized type of cell division, is critical in the life cycle of sexually reproducing organisms. In plants, specialized reproductive cells differentiate from somatic tissue. These cells then undergo a single round of DNA replication, followed by two rounds of chromosome division to produce haploid cells, which then undergo further rounds of mitotic division to produce the pollen grain and embryo sacs (Caryl *et al*., 2003). Chromosome pairing, synapsis and recombination are the major events in meiosis. Synapsis and recombination are tightly linked, and there are complex networks of interactions between them. Homologous chromosomes interact with each other and form bivalents. Chromosome pairing is largely dependent on the initiation and progression of recombination. Recombination is a highly conserved feature of meiosis that results in the formation of crossovers and non-crossover products. Recombination helps to ensure chromosome segregation and promotes allelic diversity. Errors in meiosis often lead to sterility (Pawlowski and Cande, 2005; Mézard *et al*., 2007).

Budding yeast (*Saccharomyces cerevisiae*), *Caenorhabditis elegans* and *Drosophila* are the model organisms used to study meiosis in fungi and animals, whereas *Arabidopsis* and, to some extent, maize are the models for understanding the molecular basis of plant meiosis. A basic knowledge about the *Arabidopsis* genes important for meiotic recombination, and their relationship to pairing and synopsis, meiotic progression, spindle assembly, chromosome separation and meiotic cytokinesis, has been uncovered and characterized. The molecular genetic studies in this model plant are also providing insights into meiosis that have not yet been recognized elsewhere in eukaryotes, including gene functions that might be unique to plants vs. those that are potentially shared with animals and fungi (Caryl *et al*., 2003; Hamant *et al*., 2006; Ma, 2006).

Crossing over is a key process for the accurate segregation of homologous chromosomes during meiosis. It tends to decrease near the centromeres and increase towards the telomeres (Anderson and Stack, 2002). For example, crossover frequency in wheat, maize and barley tends to increase with relative physical distance from the centromere, whereas in Welsh onion (*Allium fistulosum*) it clusters close to the centromeres; in *Arabidopsis* and tomato, the crossover distribution varies between and along chromosome arms, with no apparent rule. Moreover, within chromosome regions (cold and hot, which have significantly low and high crossover frequencies, respectively), crossover rates vary enormously from one kilobase to another in *Arabidopsis*, indicating the presence of several levels of control, each operating at different scales: chromosomal, regional (megabase) or local (kilobase) (Drouaud *et al*., 2007; Mézard *et al*., 2007). Gene-rich regions, for example in wheat, barley and maize, are more recombinationally active than gene-poor regions (Schnable and Wise, 1998). Two pathways of crossover have been identified: interference-sensitive crossover, which inhibits the

occurrence of another crossover in a distance-dependent manner; and interference-insensitive crossover, when both pathways exist in the plant kingdom, including *Arabidopsis* (Mercier *et al*., 2005). The ratio of interference-sensitive to interference-insensitive crossover differs between species, e.g. about 30% of crossovers escape the interference-sensitive mechanism in yeast and tomato, but only 15% escape it in *Arabidopsis*.

Recombination nodules are protein complexes associated with meiotic (pachytene) chromosomes. Studying recombination nodule structure and function provides insights into the processes by which meiotic recombination is regulated in eukaryotes. The two types of recombination nodule identified are early nodules and late nodules, with the former appearing at leptotene and persisting into early pachytene, and the latter appearing in pachytene and remaining into early diplotene. Both can be distinguished by their time of appearance and by characteristics such as shape, size, relative numbers and association with unsynapsed or synapsed chromosomal segments. Early nodule function is not clearly understood, but it may assist in research on DNA homology, synapsis, gene conversion and/or crossing over. Late nodules are well correlated with crossing over (Anderson and Stack, 2005).

Wheat is a disomic hexaploid, i.e. a polyploid that behaves as a diploid during meiosis. Chromosome pairing is restricted to homologous chromosomes, despite the presence of homologues in the nucleus (Sears, 1976). Using the Affymetrix wheat GeneChip®, Crismani *et al*. (2006) identified 1350 transcripts that were temporally regulated during the early stages of meiosis, many of these associated with chromatin condensation, synaptonemal complex formation, recombination and fertility. Thirty transcripts displayed at least an eightfold expression change between and including pre-meiosis and telophase II, with more than 50% of these having no similarities to known sequences in the National Center for Biotechnology Information (NCBI) and Institute for Genomic Research (TIGR) databases that could be used to study the molecular basis of pairing and recombination control in a complex polyploid such as wheat. Furthermore, Crismani *et al*. (2006) detected four transcripts expressed only in early meiotic stages, three of which showed no significant similarities to sequences in the NCBI and TIGR databases. These genes are prime candidates, as they may play a role in co-ordinating early meiotic recombination in wheat. Variations in the time for completion of meiosis have also been reported: meiosis in bread wheat anthers is completed within 24 h, in barley 39 h and in rye 51 h (Crismani *et al*., 2006, and references cited therein). There is also a high degree of asynchrony between male and female meiosis. For example, in *Arabidopsis*, male meiosis is completed before female meiosis reaches prophase 1 (Caryl *et al*., 2003).

A number of factors make plants suited to the analysis of gamete development: late germline specification, the non-lethality of mutations affecting gamete development and the large size of their chromosomes. Many genes with roles in gamete development in *Arabidopsis*, principally those for meiosis, recombination and DNA repair, have yielded novel information about the processes of gamete formation in higher plants (Wilson and Yang, 2004). The angiosperm female gametophyte typically consists of one egg cell, two synergid cells, one central cell and three antipodal cells. Each of these four cell types has unique structural features and performs unique functions, essential for reproduction. The gene regulatory networks conferring these four phenotypic states are largely uncharacterized. Using the Affymetrix ATH1 genome array for differential expression, real-time reverse transcriptase-polymerase chain reaction (RT-PCR) and *Arabidopsis* mutant *determinant infertile 1* (*dif1*) ovules, which lack the female gametophyte, Steffen *et al*. (2007) identified 71 genes that exhibit decreased expression in *dif1* ovules; when further validated using promoter–GFP fusions, they detected 11 genes that expressed exclusively in the antipodal cells, another 11 genes that expressed exclusively or predominantly in the central cell, 17 genes that were exclusive to or predominant in the synergid cells, one gene that expressed exclusively in the egg cell, and three genes that expressed strongly in multiple cells of the female gametophyte. These genes offer insights into the molecular processes involved in the female gametophyte, insights that serve as starting points to dissect the gene regulatory networks functioning during the differentiation of the four female gametophyte cell types. Furthermore, Ma *et al*. (2007a) used three male-sterile mutants, lacking a range of normal cell types resulting from a temporal progression of anther failure, in comparison with genotypes having fertile siblings, at four equivalent stages of anther development, to profile gene expression in dissected maize anthers using oligonucleotide arrays. They detected nearly 9200 sense and antisense transcripts, with the most diverse transcripts present at the pre-meiotic stage. By combining data sets from the comparisons between individual sterile and fertile anthers, they assigned candidate genes predicted to play important roles during maize anther development to stages and probable cell types. Comparative analysis with a data set of anther-specific genes from rice highlighted remarkable quantitative similarities in gene expression between these two grasses.

Pairing between wheat homeologous chromosomes is prevented by the expression of the *Ph1* locus on the long arm of chromosome 5B. Suppressors with major effects were mapped as Mendelian loci on the long arms of *Aegilops speltoides* chromosome 3S and 7S, with the former designated as *Su1-Ph1* and the latter as *Su2-Ph1*. A QTL designated as *QPh.ucd-5S*, with a minor effect, was also mapped on the short arm of chromosome 5S. Both *Su1-Ph1* and *Su2-Ph1* increased homeologous chromosome pairing, the former completely epistatic to the latter. The two genes acting together increased homeologous chromosome pairing to the same level as *Su1-Ph1* acting alone. *QPh.ucd-5S* expression was additive to the expression of *Su2-Ph1* for increased homeologous chromosome pairing. Based on these observations, Dvorak *et al*. (2006) hypothesized that the products of *Su1-Ph1* and *Su2-Ph1* affect pairing between homeologous chromosomes by regulating the expression of *Ph1*, but the product of *QPh.ucd-5S* may primarily regulate recombination between homologous chromosomes. Griffiths *et al*. (2006) localized *Ph1* to a 2.5-Mb interstitial region of wheat chromosome 5B, containing a structure consisting of a segment of subtelomeric heterochromatin inserted into a cluster of *cdc2*-related genes. The correlation of the presence of this structure with *Ph1* activity, together with the involvement of heterochromatin with *Ph1* and *cdc2* genes in meiosis, makes the structure a good candidate for the *Ph1* locus. Taken together, the *Ph1* locus prevents recombination between homeologous chromosomes in wheat, thereby furnishing a powerful tool for manipulating alien genes for wheat improvement. Incorporation of a *Ph1* suppressor into wheat would greatly facilitate introgression of alien genes into wheat chromosomes via recombination between homeologous chromosomes, thus paving the way for the introgression of beneficial alleles from distant wheat relatives. In maize, *phs1* is required for pairing to occur between homologous chromosomes (Pawlowski *et al*., 2004). This gene encodes a putative 347-amino-acid protein with a predicted molecular mass of 38 kDa. In rice, it is the *PAIR1* (*HOMOLOGOUS PAIRING ABERRATION IN RICE MEIOSIS1*) gene that plays an essential role in the establishment of homologous chromosome pairing (Nonomura *et al*., 2004). The *PAIR1* gene encodes a 492-amino-acid protein, which contains putative coiled-coil motifs in the middle, two basic regions at both termini and a potential nuclear localization signal at the C-terminus. Using a comparative genetic approach, Sutton *et al*. (2003) identified the rice genomic region syntenous to the region deleted in the wheat chromosome pairing mutant *ph2a*, and detected 218 wheat expressed sequence tags (ESTs) putatively located in the region deleted in *ph2a*.

Genetic gains in plant breeding depend on the generation and selection of new recombinants ensuing from crosses between chosen strains. The genetic variation released in segregating populations depends on the assortment of chromosomes and the amount of recombination within chromosomes. In addition to environmental factors, genotype effects influence meiotic recombination in plants: increased recombination occurs in pollen mother cells of barley, pearl millet and wheat, whereas recombination is greater in egg mother cells in the cases of rye, *Brassica oleracea* and *Brassica nigra* (Guzy-Wróbelska *et al*., 2007, and references cited therein). Differences in male–female recombination frequency can be potentially exploited for the construction of genetic linkage maps, fine mapping, map-based gene cloning or the development of alien substitution lines, as well as to avoid linkage drag.

Mapping and cloning genes or QTLs associated with variation in flowering

There are a number of reports in the literature regarding the identification of putative QTLs for variation in flowering time in barley, maize, rice, sorghum and wheat (Table 1); however, few studies have succeeded in the fine mapping and cloning of these QTLs. For example, *Hd1*, *Hd3a*, *Hd6*, *EHD1* and *Se5* were cloned in rice, with the first four promoting flowering under SD, and the latter involved in rice phytochrome synthesis (chromophore), regulating flowering in response to day length (Cockram *et al.*, 2007). Two major photoperiod loci (*Ppd-H1* and *Ppd-H2*) have been identified in barley, but only *Ppd-H1* has been cloned, whereas none of the three photoperiod loci (*Ppd-A1*, *Ppd-B1* and *Ppd-D1*) identified in wheat have been cloned. Interestingly, the major loci affecting photoperiod response in wheat and barley have been mapped to collinear positions on the short arm of the group 2 chromosomes (Cockram *et al*., 2007, and references cited therein). An understanding of the photoperiod pathway in *Arabidopsis* provides a source of candidate genes for *Ppd* loci in cereals. *Hd1*, *Hd3a* and *Hd6* encode orthologues of *CO* and *FT*, and the α subunit of casein kinase 2 (*CK2*), which are well-characterized factors for flowering or the circadian clock in *Arabidopsis* (Izawa *et al*., 2003; Hayama and Coupland, 2004). However, rice *Hd1* promotes flowering under SD, whereas *Arabidopsis CO* promotes flowering under LD (Izawa *et al*., 2003). Furthermore, 19 of the 62 consensus QTLs in maize are syntenic to rice and *Arabidopsis* flowering time QTLs or genes, whereas *vgt-f7p* is allelic to *vgt1* in maize (Table 1). A sorghum QTL associated with photoperiod sensitivity on linkage group (LG) H is an orthologue to *Hd1*,

Table 1 Quantitative trait loci (QTLs) associated with flowering time in barley, maize, rice, sorghum and wheat from 1967 to 2006

Flowering time QTL	Reference
Barley	
2–5 QTLs for heading, one in two environments	Baum *et al*. (2003)
Two major genes, *eam8* and *eam10*, and two QTLs determine flowering; *eam8* and *eam10* mapped on long arm of *Hordeum* (barley) chromosome 1 (1HL) and 3HL, respectively, whereas QTL on 1HL and short arm of *Hordeum* (barley) chromosome 7 (7HS)	Börner *et al*. (2002a)
Five major genes and eight QTLs	Laurie *et al*. (1995)
Maize	
vgt-f7p mapped (6 cM) on chromosome 8; probably allelic to *vgt1*	Chardon *et al*. (2005)
Eight QTLs for GGD heat units to pollen shedding	Zhang *et al*. (2005b)
Six of the 62 consensus QTLs displaying major effect; 19 QTLs and genes syntenic to rice and *Arabidopsis* flowering	Chardon *et al*. (2004)
Rice	
Seven QTLs for flowering across three environments	Khillare *et al*. (2005)
Nineteen QTLs related to vegetative and reproductive growth mapped on six chromosomes	Zhou *et al*. (2001)
Fourteen QTLs control flowering; *Hd1*, *Hd2*, *Hd3*, *Hd6* and *Hd9* mapped as Mendelian factors; two tightly linked loci, *Hd3a* and *Hd3b*, detected in *Hd3* region	Yano *et al*. (2001)
Sorghum	
Two major QTLs for maturity	Crasta *et al*. (1999)
Six major loci, *Ma1* to *Ma6*, control flowering and maturity	Rooney and Aydin (1999); Quinby (1967)
Ma3 mapped on LG A encoded by phytochrome B1	Childs *et al*. (1997)
A QTL on LG D assigned to *Ma1*	Lin *et al*. (1995)
Wheat	
Eps-A^{m}1 on chromosome 1A^{m}L in *Triticum monococcum* flanked by *VatpC* and *Smp*	Valárik *et al*. (2006)
Four QTLs for intrinsic earliness	Hanocq *et al*. (2004)
Eps-5BL1 and *Eps-5BL2* mapped close to the centromere on 5BL; one homologous to barley on 5H	Tóth *et al*. (2003)
4–8 QTLs for ear emergence and 5–7 for flowering in 11 environments	Börner *et al*. (2002b)
Nse-3A^m and *Nse-5A^m* mapped on chromosome *3A^m* and *5A^m*, respectively; former homologous to *eps3L* in barley and the latter to *Qeet.ocs-5A1* in wheat	Shindo *et al*. (2002)
*QEet.ocs-5A*1 for earliness *per se* on 5AL with little influence on grain yield	Kato *et al*. (2002)
A major QTL on chromosome 2BS for heading, co-segregated with *Ppd-B1*, and another on 7BS corresponds to a QTL for earliness *per se*	Sourdille *et al*. (2000)

Table 2 DNA markers/quantitative trait loci (QTLs) associated with response to variation in photoperiod and vernalization in barley, sorghum and wheat from 2000 to 2004

Marker/QTL information	Reference
Barley	
Six AFLP markers closely linked to *Ppd-H1*	Decousset *et al*. (2000)
Sorghum	
Two QTLs on LG C and H associated with photoperiod sensitivity *sensu stricto*; former close to earliness, *Ef-1*, and the latter orthologue to *Hd1*, a major photoperiod sensitivity gene in rice	Chantereau *et al*. (2001)
Wheat	
Four QTLs each for photoperiod and vernalization; two photoperiod-sensitive QTLs located at the same position as *Ppd-B1* and *Ppd-D1*	Hanocq *et al*. (2004)
Vrn-B1, *Vrn-D1* and *Ppd-B1* on 5B, 5D and 2B, respectively; two types of genes for photoperiod sensitivity are known: one dependent on and the other independent of vernalization; a QTL for narrow-sense earliness close to *Ppd-B1*	Shindo *et al*. (2003)
Vrn-B1 mapped on 5B and homologous to other wheat, rye and barley vernalization response genes	Leonova *et al*. (2003)
Three markers linked to *Vrn-B1* on 5BL; Xgwm408 closest in two populations	Barrett *et al*. (2002)

which is a major photoperiod sensitivity gene in rice. Likewise, photoperiod-sensitive QTLs are located at the same position as the major genes *Ppd-B1* and *Ppd-D1* in wheat, and *Vrn-B1* is homologous to other vernalization response genes in wheat, rye and barley (Table 2). The wheat gene *TaGI1*, which is involved in photoperiodic flowering, is an orthologue of *GIGANTEA* (*GI*) in *Arabidopsis*. *TaGI1* is expressed in leaves in a rhythmic manner under LD and SD conditions, and its rhythmic expression is regulated by photoperiods and circadian clocks (Zhao *et al*., 2005). A 6-bp insertion/

deletion in the *Dwarf8* (*D8idp*) polymorphism is associated with flowering time under LD. In maize, the deletion allele shows an average earlier flowering of 29 degree-days for inbred lines and 145 degree-days for landraces. Thus, *Dwarf8* could be involved in maize climatic adaptation through the diversification of selection of the flowering time (Camus-Kulandaivelu *et al*., 2006).

Earliness *per se* (*Eps*) and 'narrow sense' earliness genes, often detected as QTLs, control flowering time independently of these environmental cues (photoperiod and vernalization induction pathways promote flowering), and are responsible for the fine tuning of flowering time. Several *eps* QTLs and genes have been reported in wheat and barley (Table 1), with some homologous to each other, thereby representing more sources of variation to breed for earliness. Moreover, there may be temperature–*eps* gene interaction, as shown in wheat *Eps-A*^{m}*1* (Appendo and Slafer, 2003), which should be further investigated to eliminate the effect of growing temperature on the expression of *eps* genes, thereby enabling researchers to select for earliness *per se* under any thermal condition.

Szûc *et al*. (2006) mapped six photoperiod response QTLs and determined their positional relationship with respect to the phytochrome and cryptochrome photoreceptor gene families and the vernalization regulatory genes *HvBM5A*, *ZCCT-H* and *HvVRT-2*. Of the six photoreceptors mapped (*HvPhyA* and *HvPhyB* to 4HS, *HvPhyC* to 5HL, *HvCry1a*, *HvCry2*-6HS and *HvCry1b* to 2HL), only *HvPhyC* coincided with a photoperiod response QTL. *HvBM5A*, *ZCCT-H* and *HvVRT-2* are located in chromosome regions determining small photoperiod response QTL effects. Previously, they had mapped candidate genes for the 5HL *VRN-H1* (*HvBM5A*) and 4HL *VRN-H2* (*ZCCT-H*) loci and, in this study, *HvVRT-2*, the barley *TaVRT-2* orthologue (a wheat-flowering repressor regulated by vernalization and photoperiod), to 7HS. *HvBM5A* and *HvPhyC* are closely linked on 5HL, and therefore are positional candidates for the same photoperiod effect. von Zitzewitz *et al*. (2005) had already mapped candidate genes for the 5HL *VRN1* (*HvBM5A*) and 4HL *VRN-H2* (*ZCCT-H*) loci in barley. Phytochromes are a family of red/far-red light-absorbing photoreceptors that control plant development and metabolic processes in response to changes in light. Transgenic rice lines containing *Arabidopsis PhyA*, together with a tissue-specific rice *rbcS* promoter, showed reduced plant height but more panicles per plant, and produced 6%–21% more grain than non-transgenic plants, demonstrating the potential to manipulate light signal transduction pathways to enhance grain productivity (Garg *et al*., 2006a).

The *FT* gene plays a central role in integrating flowering signals in *Arabidopsis*, given that its expression is regulated antagonistically by the photoperiod and vernalization pathways (Boss *et al*., 2004; Jack, 2004; Bäurle and Dean, 2006). *FT* belongs to a family of six genes characterized by a phosphatidylethanolamine-binding protein domain. Thirteen *FT*-like sequences, designated as *OsFTL1–OsFTL13*, have been reported in rice, with *Hd3a* corresponding to *OsFTL2* (Izawa *et al*., 2002; Chardon and Damerval, 2005; Zhang *et al*., 2005a). More recently, Faure *et al*. (2007) found five *FT*-like genes in barley. *HvFT1*, *HvFT2*, *HvFT3* and *HvFT4* are highly homologous to *OsFTL2* (the *Hd3a* QTL), *OsFTL1*, *OsFTL10* and *OsFTL12*, respectively, but there is no rice equivalent for *HvFT5*. *HvFT1* was highly expressed under LD at the time of the morphological switch of the shoot apex from vegetative to reproductive growth, and *HvFT2* and *HvFT4* were expressed later in plant development. *HvFT1* was thus identified as the main barley *FT*-like gene involved in the switch to flowering. Mapping of the *HvFT* genes should therefore provide important sources of flowering time variation in barley. *HvFT1* is a candidate for *VRN-H3*, a dominant mutation giving precocious flowering; *HvFT3*, a candidate for *Ppd-H2*, is a major QTL affecting flowering time under SD in barley. In plants, seasonal changes in day length are perceived in leaves, which initiate long-distance signalling that induces flowering at the shoot apex. Florigen, the mobile signal, moves from an induced leaf to the shoot apex and causes flowering. Understanding the nature of the mobile flowering signal would provide a key insight into the molecular mechanism of floral induction. The *Arabidopsis FT* gene is a candidate for encoding florigen (Corbesier *et al*., 2007), and the protein encoded by *Hd3a*, a rice orthologue of *FT*, moves from the leaf to the shoot apical meristem and induces flowering in rice, suggesting that the Hd3a protein may be the rice florigen (Tamaki *et al*., 2007).

Vernalization, the induction of flowering by prolonged exposure to low temperature, is the major determinant of flowering in wheat and barley. Vernalization-dependent types are commonly called winter wheat and winter barley, whereas vernalization-independent types are called spring wheat and spring barley. *VRN-H1* (*Sh2*, *Sgh2*), *VRN-H2* (*Sh*, *Sgh*) and *VRN-H3* (*Sh3*, *Sgh3*) in barley, *VRN-A*^{m}*1* (*VRN-1*) and *VRN-A*^{m}*2* (*VRN-2*) in diploid einkorn wheat (*Triticum monococcum*), and *VRN-A1* (*Vrn1*), *VRN-B1* (*Vrn2*), *VRN-D1* (*Vrn3*) and *VRN-B3* (*Vrn-B4*) in bread wheat promote flowering after vernalization (Cockram *et al*., 2007, and references cited therein). *VRN-H1*, *VRN-A*^{m}*1*, *VRN-A1*, *VRN-B1* and *VRN-D1* encode MADS-box and AP1-like, *VRN-H2* and *VRN-A*^{m}*2* encode B-box and CCT domain, and *VRN-H3* and *VRN-B3* encode putative kinase inhibitor proteins. *Vrn3* is linked completely to a gene similar to *Arabidopsis FT* (Yan

et al., 2006). FT induction in leaves results in a signal that promotes flowering. Transcript levels of the barley and wheat orthologues, designated as *HvFT* and *TaFT*, respectively, are significantly higher in plants that are homozygous for the dominant *Vrn3* alleles (early flowering) than in plants that are homozygous for the recessive *Vrn3* alleles (late flowering). In wheat, the dominant *Vrn3* allele is associated with the insertion of a retro-element in the *TaFT* promoter, whereas, in barley, mutations in the *HvFT* first intron differentiate plants with dominant and recessive *Vrn3* alleles. Winter wheat plants transformed with the *TaFT* allele carrying the promoter retro-element insertion flower earlier than non-transgenic plants, supporting the identity between *TaFT* and *VRN-B3*. This research confirms that wheat and barley *FT* genes are responsible for natural allelic variation in the vernalization requirement, providing additional sources of adaptive diversity in these crops.

Dubcovsky *et al*. (2006) showed that the vernalization requirement in some of the photoperiod-sensitive winter wheat cultivars can be replaced by interrupting LD by 6 weeks of SD, and that this interruption is associated with SD down-regulation of the *VRN2* flowering repressor. In addition, SD down-regulation of *VRN2* at room temperature is not followed by the up-regulation of the meristem identity gene *VRN1* until plants are transferred to LD, which contrasts with the *VRN1* up-regulation observed after the *VRN2* down-regulation by vernalization, suggesting the existence of a second *VRN* repressor. Further analysis of natural *VRN1* mutants has revealed that the *CArG-box* located in the *VRN1* promoter is the most likely regulatory site for the interaction with this second repressor. Up-regulation of *VRN1* under SD in accessions carrying mutations in the *CArG-box* resulted in an earlier initiation of spike development, compared with other genotypes. However, even the genotypes with *CArG-box* mutations required LD for normal and timely spike development. SD accelerates flowering in photoperiod-sensitive winter cultivars, suggesting that wheat was initially an SD–LD plant, and that strong selection pressures during domestication and breeding resulted in the modification of this dual regulation. The down-regulation of the *VRN2* repressor by SD is probably part of the mechanism associated with the SD–LD regulation of flowering in photoperiod-sensitive winter wheat.

More recently, Kane *et al*. (2007) have shown that a MADS-box transcription factor, *TaVRT2*, in wheat is also associated with the vernalization response in a manner similar to *TaVRN2*. Using transient expression assays in *Nicotiana benthamiana*, they showed that *TaVRT2* acts as a repressor of *TaVRN1* transcription. *TaVRT2* binds the CArG motifs in the *TaVRN1* promoter and represses its activity *in vivo*. In contrast, *TaVRN2* does not bind the *TaVRN1* promoter and has no direct effect on its activity, but can enhance the repression effect of *TaVRT2*, suggesting that a repressor complex regulates the expression of *TaVRN1*. In winter wheat, *TaVRT2*, *TaVRN2* and *TaVRN1* transcripts accumulate in the shoot apical meristem and young leaves, and temporal expression is consistent with *TaVRT2* and *TaVRN2* being repressors of floral transition, whereas *TaVRN1* is an activator. Non-vernalized spring wheat grown under SD accumulates *TaVRT2* and shows a delay in flowering, suggesting that *TaVRT2* is regulated independently by photoperiod and low temperatures. The results demonstrate that *TaVRT2*, in association with *TaVRN2*, represses the transcription of *TaVRN1*.

Vgt1 is a QTL involved in the control of the transition of the apical meristem from the vegetative to the reproductive phase (flowering) in maize. Using positional cloning and association mapping, Salvi *et al*. (2007) resolved *Vgt1* to an approximately 2-kb non-coding region positioned 70 kb upstream of an *Ap2*-like transcription factor involved in flowering time control. *Vgt1* functions as a *cis*-acting regulatory element, as indicated by the correlation of the *Vgt1* alleles with transcript expression levels of the downstream gene. In addition, within *Vgt1*, they identified evolutionary conserved non-coding sequences across the maize–sorghum–rice lineages, supporting the notion that changes in distant *cis*-acting regulatory regions are a key component of plant genetic adaptation throughout breeding and evolution. *WAP1* (wheat *AP1*) is a key gene in the regulatory pathway controlling the transition phase from vegetative to reproductive growth in common wheat, and is an orthologue of *VRN1* in diploid einkorn wheat (Murai *et al*., 2003). More recently, Shitsukawa *et al*. (2007a) identified a mutant in einkorn wheat, *maintained vegetative phase* (*mvp*), which makes it unable to transit from the vegetative to the reproductive phase. This *mvp* mutation resulted from the deletion of the *VRN1* coding and promoter regions, demonstrating that *WAP1/VRN1* is an indispensable gene for phase transition in wheat. Expression analysis of flowering-related genes in *mvp* plants indicated that wheat *GI*, *CO* and *SOC1* genes either act upstream of or in a different pathway from *WAP1/VRN1*. The MADS-box gene *SOC1* is an integrator of flowering pathways in *Arabidopsis*. Shitsukawa *et al*. (2007b) isolated a wheat orthologue of *SOC1*, wheat *SOC1* (*WSOC1*), which is expressed in young spikes, but preferentially expressed in leaves. Expression starts before the phase transition and is maintained during the reproductive growth phase. Over-expression of *WSOC1* in transgenic *Arabidopsis* caused early flowering under SD conditions, suggesting that *WSOC1*

functions as a flowering activator in *Arabidopsis*. *WSOC1* expression is not affected by either vernalization or photoperiod, whereas it is induced by gibberellin at the seedling stage. Moreover, *WOSC1* is expressed in transgenic wheat plants in which *WAP1* expression is co-suppressed, indicating that *WSOC1* acts in a pathway different from the *WAP1*-related vernalization and photoperiod pathways.

The mapping and cloning of the genes associated with flowering in the model plants *Arabidopsis* and rice should enable researchers to alter flowering for the better adaptation of cereal crops to existing environments and to new conditions predicted to emerge as a result of climate change. Some MADS-box genes activate or repress flowering in rice. Using rice *OsMADS* cDNA clones connected to the maize *ubiquitin* promoter in the sense orientation, Jeon *et al*. (2000) introduced the constructs into rice plants by *Agrobacterium*-mediated transformation. The transgenic plants exhibited early flowering and dwarf phenotypes that correlated well with the transcript levels detected in these plants. Interestingly, transgenics containing *OsMADS1* attached with the *nopaline synthase* promoter shortened the heading time, but with a mild reaction on dwarfism without any pleiotropic effects on other agronomic traits. Thus, rice MADS-box genes could be used as sources of early flowering and dwarfing traits in monocots. Tadege *et al*. (2003) identified a *OsSOC1* gene in rice that encodes a MADS-domain protein related to the *Arabidopsis* gene *AtSOC1*, with 97% amino acid similarity in the MADS domain. *OsSOC1* is located on top of the short arm of chromosome 3, tightly linked to the heading date locus *Hd9*. Although it expressed in vegetative tissues, its expression was elevated at the time of floral initiation and remained uniformly high thereafter, similar to the expression pattern of *AtSOC1*. The constitutive expression of *OsSOC1* in *Arabidopsis* results in early flowering, suggesting that the rice gene is a functional equivalent of *AtSOC1*. However, Tadege *et al*. (2003) were not able to identify FLC-like sequences in the rice genome, but found that ectopic expression of the *Arabidopsis FLC* delayed flowering in rice, and the up-regulation of *OsSOC1* at the onset of flowering initiation was delayed in *AtFLC* transgenic lines.

The *CO* gene of *Arabidopsis* plays a key role in the photoperiodic flowering pathway. Nemoto *et al*. (2003) isolated three kinds of *CO/Hd1* (rice orthologue of *CO*) homologues from the A, B and D genomes of hexaploid wheat: *TaHd1-1*, *TaHd1-2* and *TaHd1-3*, respectively. They are highly similar to each other and to *Hd1*, and contain two conserved regions: two zinc-finger motifs and a CCT domain like *CO/Hd1* located on the long arm of the homologous chromosome 6. When the *TaHd1-1* genomic clone was introduced into a rice line deficient in *Hd1* function, the transgene complemented the functions of rice *Hd1*, i.e. it promoted heading under SD conditions and delayed it under LD and natural conditions, indicating that *Hd1* proteins from SD and LD plants share common structures and functions. A floral control gene *LFY* from *Arabidopsis* was introduced into rice using the cauliflower mosaic virus 35S promoter, and caused the transgenic rice plant to flower 26–34 days earlier than wild-type plants, with yield loss and panicle abnormality. This suggests that floral regulatory genes from *Arabidopsis* are useful tools for heading date improvement in cereal crops (Zuhua *et al*., 2000).

The reciprocal recognition and flowering time effects of genes introduced into either *Arabidopsis* or rice suggest that some components of the flowering pathways may be shared. Moreover, the wheat *TaHd1-1* gene can complement rice *Hd1* and function normally in the rice background. These genes thus provide the potential to genetically manipulate the flowering time, employing either well-characterized *Arabidopsis* genes or heterologous genes from other cereals, using comparative genomics in cereals.

Inflorescence architecture and development

Genetic and molecular mechanisms regulating inflorescence architecture

Plants undergo a series of profound developmental changes throughout their life cycle. They can be broadly grouped into changes occurring from juvenile to adult leaf formation, vegetative to inflorescence development, and inflorescence to floral meristem initiation (Chuck and Hake, 2005). Grass inflorescences and flowers have characteristic structures distinct from those in *Arabidopsis* (Bommert *et al*., 2005b). The major differences are related to changes in the number of branches, the numbers of orders of branches and the amount of axis elongation (Doust and Kellog, 2002). Information on the developmental transition in plants (Chuck and Hake, 2005) and grass inflorescence diversity and genetics (Bommert *et al*., 2005b; Malcomber *et al*., 2006; Doust, 2007; Kellog, 2007) has been published elsewhere. In this section, we highlight only those developmental phenomena and genes involved that, if brought together, might result in substantial improvement in the productivity of the major cereal food crops.

Maize and rice are excellent model systems for studying the genetics and molecular characterization of inflorescence architecture and development in cereals because of the subtle differences in inflorescence, the fact that a large number of mutants affect inflorescence and floral development, the

high density of genetic linkage maps, and the fact that the rice and maize genomes have been fully or partially sequenced (McSteen *et al*., 2000; Vollbrecht *et al*., 2005; Dwivedi *et al*., 2007, and references cited therein). A combination of internal and external environmental signals affect, for example, the transition from vegetative to reproductive stage (see the section on 'Flowering' above), and control the major genetic pathways regulating inflorescence architecture and development. Using mutants with discrete phenotypes and molecular biology tools, a number of maize, rice and sorghum genes regulating the transition from vegetative to reproductive phase, or those related to inflorescence structure and development, have been mapped or cloned, and their molecular functions determined (Table 3). Interestingly, some of the genes associated with inflorescence or panicle architecture traits are known orthologues to *Arabidopsis* genes, i.e. maize *fasciated ear2* (*fea2*) and *thick tassel dwarf1* (*td1*) to *CLAVATA1* (*CLV1*) and *CLAVATA2* (*CLV2*), and rice *floral organ number1* (*FON1*) and *Oryza sativa leucine-rich repeat receptor like protein kinase1* (*OsLRK1*) to *CLV1*. Rice *frizzy panicle* (*FZP*) and *branched floretless1* (*BFL1*) are orthologues to the maize *branched silkless1* (*BD1*) gene. The *ramosa 2* (*ra2*) expression pattern is conserved in rice, barley, sorghum and maize, suggesting that this gene is critical for shaping the initial steps of grass inflorescence architecture (Bortiri *et al*., 2006).

Inflorescence architecture is a key agronomic trait. For example, increasing the number of branches in the tassel increases pollen yield, which influences hybrid seed production and overall yield in maize (Cassani *et al*., 2006). From an applied breeding viewpoint, the inflorescence architecture genes that map in the vicinity of QTLs that harbour beneficial traits are of significant importance. For example, *td1*, *fea2* and *ra* map close to the QTLs reported for seed row number and spikelet density in maize (Taguchi-Shiobara *et al*., 2001; Bommert *et al*., 2005a; Upadyayula *et al*., 2006a). Allelic variation in *ra* (*ra1*, *ra2* and *ra3*) forms part of a network of genes that control the production of tassel lateral branches in maize. Lateral branches in the panicle and spikelet density are also of importance in barley, rice and wheat. It is therefore possible that such genes could be manipulated to improve crop yields. Multiple QTLs control inflorescence branching in foxtail millet (Doust *et al*., 2005), and it would be interesting to determine whether any of the *ra* genes are candidates for these loci.

Mapping and cloning QTLs associated with spike and grain development traits

Understanding the pathways and gene(s) involved in seed development is a major step towards dissecting reproductive trait biology in cereals. Seed development in angiosperms begins with double fertilization, which results in a diploid embryo and a triploid endosperm. Further development is marked by the rapid growth of the endosperm and embryo until seed maturation, which is accompanied by desiccation. Simultaneously, the maternal ovule undergoes regulated growth to accommodate the growing embryo and endosperm. The endosperm in monocots constitutes the major contribution to the volume of the mature seed, in which the ovule integument forms the seed coat. Seed size is the result of three different growth programmes: those of the diploid embryo, the triploid endosperm and the diploid maternal ovule. All of these are genetically regulated, defining the development of the maternal integument, the embryo and the endosperm. For example, when the relative dosages of maternal and paternal genomes are perturbed, endosperm and seed size are affected. Endosperm development is also subject to the differential expression of many genes which are dependent on the parent of origin (see section on 'Gene expression associated with panicle development, pollination, fertilization and developing seeds' below).

Unlike the extensive use of molecular biology to study the genetics of agronomic traits, including resistance to biotic and abiotic stresses, there have been fewer studies dissecting the QTLs for panicle architecture and development in cereals (Table 4). Several QTLs from these studies were identified in regions known to harbour candidate genes, e.g. *fea2*, *td1* and *ramosa1* (*ra1*) in maize, *barren stalk1* (*ba1*), *ra1*, *ramosa2* (*ra2*), *branched silkless1* (*bd1*), *indeterminate spikelet1* (*ids1*), *leafy* (*lfy*), *terminal flower1* (*tfl1*) and *Dwarf3* (*Dw3*) in sorghum, and *Q* in wheat. The genes *Dw3* and *ra2* in sorghum were co-localized precisely with QTLs of large effect for rachis length, number of primary branches and primary branch length.

In rice, the QTLs for grain number (*Gn1a*), grain size (*GS3*), grain weight (*gw3.1* and *gw8.1*) and grains per panicle (*gpa7*) have been cloned, and the molecular function has been determined in some cases (Dwivedi *et al*., 2007, and references cited therein). More recently, Song *et al*. (2007) cloned a new QTL (*GW2*) for rice grain width and weight. It encodes a previously unknown RING-type protein with E3 ubiquitin ligase activity, which is known to function in the degradation of the ubiquitin–proteasome pathway. Loss of *GW2* function increased cell numbers, resulting in a larger (wider) spikelet hull, and accelerated the grain milk-filling rate, resulting in enhanced grain width, weight and yield. This provides an insight into the mechanism of seed development, a potential tool for improving grain yield in crops.

AP2 is best known for its role in the regulation of flower meristem and flower organ identity and development in

Table 3 Genes and their functions associated with inflorescence architecture in maize, rice, sorghum and wheat from 2000 to 2007

Gene	Phenotype associated with the gene	Encoding for	Reference
Maize			
bif2	Axillary meristem and lateral primordia in inflorescence	Co-orthologue of the *PINOID* serine/threonine kinase	McSteen *et al*. (2007)
ra1	Inflorescence architecture	Zinc-finger transcription factor	Cassani *et al*. (2006)
ra2	Increased branching with short branches replaced by long, indeterminate types	LATERAL ORGAN BOUNDARY domain protein	Bortiri *et al*. (2006)
ra3	Inflorescence branching	Trehalose-6-phosphate phosphatase (TPP) enzyme	Satoh-Nagasawa *et al*. (2006)
dLf1	Delays flowering	A leucine zipper protein	Muszynski *et al*. (2006)
td1	Adversely affects male and female inflorescence development	A leucine-rich repeat receptor-like kinase protein, orthologue to *Arabidopsis CLAVATA1*	Bommert *et al*. (2005a)
id	Blocks transition from vegetative to reproductive phase	Zinc-finger transcription factor	Kozaki *et al*. (2004)
ba1	Plants unable to produce tillers, female inflorescence and a tassel	A non-canonical basic helix–loop–helix protein	Gallavotti *et al*. (2004)
Bd1	Forms indeterminate branches instead of spikelets	ERF transcription factor	Chuck *et al*. (2002)
fea2	Overproliferation of ear inflorescence meristem, with modest effect on floral meristem and organ number	A leucine-rich repeat receptor-like kinase protein, related to *CLAVATA2* from *Arabidopsis*	Taguchi-Shiobara *et al*. (2001)
Rice			
fzp-9(*t*)	Transition from the spikelet meristem to floral meristem	Putative protein of 318 amino acids, homologue to maize *bd1*	Yi *et al*. (2005)
FON1	Regulates floral meristem size	A leucine-rich repeat receptor-like kinase, orthologous to *CLV1* of *Arabidopsis*	Suzaki *et al*. (2004)
FZP	Prevents formation of axillary meristem	ERF transcription factor, orthologous to maize *BD1*	Komatsu *et al*. (2003a)
LAX and *SPA*	Axillary meristem formation	Basic helix–loop–helix transcription factor	Komatsu *et al*. (2003b)
OsFOR1	Formation and/or maintenance of floral organ primordia	A protein that contains a leucine-rich repeat domain	Jang *et al*. (2003)
BFL1	Transition from spikelet meristem to floret meristem	Transcription factor protein containing EREBP/AP2 domain, maize orthologue *BD1*	Zhu *et al*. (2003)
OsLRK1	Floral meristem development	Leucine-rich repeat receptor-like protein kinase, similar to Arabidopsis *CLV1*	Kim *et al*. (2000)
Sorghum			
sb-ba1	Primary branch initiation	Basic helix–loop–helix transcription factor	Brown *et al*. (2006)
sb-ra1 and *sb-ra2*	Branch determinacy	EPF-class C2H2 zinc finger, or LOB domain	
Sb-bd1 and *Sb-ids1*	Spikelet determinacy	1 AP2-domain ERF, or 2 AP2-domain ERF	
Sb-lfy and *Sb-tfl1*	Reproductive transition/inflorescence branching	*FLORI-CAULA/LEAFY*, or *TFL1/CEN* (PEBP)	
Dw3	Auxin transport	P-glycoprotein	
Wheat			
TaVRT-1	Transition from vegetative to reproductive phase, responsive to vernalization	A protein homologous to the MADS-box family of transcription factors	Danyluk *et al*. (2003)
WAP1	Activate autonomous phase transition from vegetative to reproductive growth	*APETALA1* (*AP1*)-like MADS-box gene, with large family of transcription factors	Murai et al. (2003)

Arabidopsis (Jofuku *et al*., 1994). A major QTL for seed size and seed weight was mapped on the *Arabidopsis* chromosome 4 region, which bears *AP2* (Alonso-Blanco *et al*., 1999). More recently, Jofuku *et al*. (2005) demonstrated that *AP2* gene sequences can be used to genetically engineer significant increases in *Arabidopsis* seed weight and seed yield. These could serve as useful markers to identify new yield-limiting genes in *Arabidopsis*, which, in turn, may be used in cereal crops.

Gene expression associated with panicle development, pollination, fertilization and developing seeds

Transcription factors are crucial in controlling development. Plants exhibit massive changes in gene expression, as measured by differences in transcriptional profiles, during morpho-physiological and reproductive development, as well as on exposure to a range of biotic and abiotic stresses. This

Table 4 Quantitative trait loci (QTLs) associated with inflorescence and grain development in maize, foxtail millet, rice and wheat from 2000 to 2007

QTL associated with inflorescence structure and grain development	Reference
Maize	
Five QTLs for tassel and nine QTLs for ear traits; a QTL on chromosome 7 for tassel branches near *ra1*, a candidate gene for tassel branches	Upadyayula *et al*. (2006a)
Forty-five QTLs for tassel inflorescence; several in regions with candidate genes *fea2*, *td1* and *ra1*	Upadyayula *et al*. (2006b)
Three QTLs for tassel branch angle (TBA) and six for tassel branch number (TBN), a QTL on chromosome 5 for TBA in the same region as a QTL for TBN	Mickelson *et al*. (2002)
Foxtail millet	
Three QTLs each for primary branches and primary branch density, 6 for spikelets, and 2 for bristle number	Doust *et al*. (2005)
Rice	
Two QTLs associated with increased grain filling independent of spikelets per panicle; QTL on chromosome 12 accelerated grain filling during early filling stage, and QTL on chromosome 8 increased grain filling by translocating non-structural carbohydrate (NSC) from the culm and leaf sheaths to the panicle	Takai *et al*. (2005)
Eight QTLs associated with increased spikelets per panicle	Kobayashi *et al*. (2004)
A major QTL for spikelets	Yagi *et al*. (2001)
Wheat	
Two to six QTLs for five spike-related traits; *Xcfd46-Xwmc702* interval on chromosome 7D related to most traits	Ma *et al*. (2007b)
Thirty QTLs for post-anthesis dry matter accumulation (DMA), flag leaf green (FLG), flag leaf weight (FLW) and grain weight per ear (GWE) mapped on 10 chromosomes; 2–4 QTLs for DMA linked to QTL for FLW and GWE	Su *et al*. (2006)
Yield QTL on 7AL associated with increased biomass at anthesis and maturity; *AINTEGUMENTA* and G-protein subunit genes affecting lateral cell division in leaf, homologous to the wheat 7AL yield QTL	Quarrie *et al*. (2006)
Several QTLs for variation in spike length, spike compactness and spikelet number	Jantasuriyarat *et al*. (2004)
Major QTL for spikelet length and spikelet numbers assigned to A- and B-genome chromosomes	Li *et al*. (2001)
Four to six QTLs for spike length, spikelet number and compactness; several affecting more than one trait; a QTL co-segregated with *Q* involved in ear morphology	Sourdille *et al*. (2000)

variation in transcript abundance can be associated with gene expression using expression quantitative trait loci (eQTLs) analysis (Dwivedi *et al*., 2007, and references cited therein).

Elucidating the regulatory mechanisms of plant organ development is an important component of plant developmental biology, and will be useful for crop improvement. Plant organ formation, or organogenesis, is a well-orchestrated series of events by which a group of primordial cells differentiates into an organ. The stamen is the male reproductive organ, consisting of an anther, in which the male gametophyte develops, and a filament, which provides water and nutrients to the anther. Anther development occurs in two phases. In phase I, the anther structure is established, including the differentiation of cell types and meiosis of pollen mother cells. In phase II, the microspores develop into pollen grains and the anthers dehisce to release pollen grains (Zhao *et al*., 2002). Using organ-specific gene expression profiling, Lu *et al*. (2006) detected 26 genes that were preferentially up-regulated during early stamen development, and clustered into two distinct clades, suggesting that early stamen development involves two distinct phases of pattern formation and cellular differentiation. Both gibberellic acid (GA_3) and jasmonic acid (JA) play important roles in anther development and pollen fertility. Using a 10K cDNA microarray with probes derived from seedlings, meiotic anthers, mature anthers and GA_3- or JA-treated suspension cells of rice, Wang *et al*. (2005b) detected expression level changes in 2155 genes in anthers, compared with those in seedlings. Forty-seven genes with potential functions in cell cycle and cell structure regulation, hormone response, photosynthesis, stress resistance and metabolism were differentially expressed in meiotic and mature anthers. Of the 314 genes that responded to either GA_3 or JA applications, 24 GA_3- and 82 JA-responsive genes showed significant changes in expression between meiosis and the mature anther stage, with the gene *y656d05* not only highly expressed in meiotic anthers but also induced by GA_3. These reports identified a number of candidate genes likely to be involved in both pollination and fertilization. Their detailed characterization is expected to provide a better understanding of the genetic programmes controlling pollination and fertilization in cereal crops.

The basic structure of the rice inflorescence (the panicle) is determined by the pattern of branch formation, which is established at the early stage of panicle development. Young panicle organs (YPOs) in cereals correspond to the onset of

meiosis and mark the transition from the vegetative to the reproductive phase, and therefore make a great contribution to grain yield. By comparing gene expression profiling of YPOs with that of rice aerial vegetative organs (AVOs), it is possible to gain further molecular insight into this developmentally and functionally important period. Comparative analysis of rice ESTs between YPOs and AVOs revealed nearly 20 000 unigenes differentially expressed in YPOs and AVOs, and about 10 000 mRNAs specifically expressed in YPOs (Tang *et al*., 2005). Using a cDNA microarray containing 10 000 unique rice genes, Lan *et al*. (2004) analysed gene expression in the pistil, which revealed that the anther has a gene expression profile more similar to that of the roots than to that of the pistil, and most pistil preferentially expressed genes respond to pollination or fertilization. A total of 253 ESTs exhibited differential expression during pollination and fertilization, and about 70% of these were assigned to a putative function. Furthermore, 136 pollination-related genes and 57 fertilization-related genes of the 253 genes of these types were also regulated by dehydration and wounding, respectively. Nearly half of the genes expressed preferentially in non-pollinated pistils were responsive to dehydration, which suggests that the genetic programmes regulating them are probably related. In addition, 100 of the 253 genes do not appear to be regulated by stress treatments, which indicates that additional genetic networks are involved in pollination and fertilization. Taken together, these observations reveal that the genetic networks regulating photosynthesis, starch metabolism, gibberellin and defence responses are involved in pollination and fertilization (Lan *et al*., 2005).

Furutani *et al*. (2005) conducted global transcriptome profiling to obtain a comprehensive view of gene expression in the early stages of rice panicle development from phase transition to floral organ differentiation. They detected 357 genes expressed differentially in the early stages of panicle development, clustered into seven groups on the basis of the temporal expression patterns. Interestingly, a small number of these genes extensively rich in transcription factors were up-regulated in the shoot apical meristems immediately after phase transition, when each gene exhibits a unique and interesting localization of mRNA. Duan *et al*. (2005) used a cDNA chip containing 325 rice cDNA clones, encoding known or putative transcription factors belonging to 12 different families, to study gene expression at eight continuous seed developmental stages in rice. They detected 135 transcription factor genes preferentially transcribed in seeds, grouped into 12 clusters. Each cluster contained transcription factor genes that peaked and waned at different stages, and 49 seed preferential genes playing major roles in distinct stages of seed development were detected. Many of these seed preferential transcription factors are also involved in hormone and abiotic stress effects, suggesting the existence of uncharacterized transcriptional networks, or crosstalk, between hormone and abiotic stress signalling and seed development. Dof proteins play essential roles in the hierarchical regulation of gene expression during rice seed development.

The caryopsis is the fruit of grasses in which the pericarp is fused to the seed coat at maturity, referred to as the grain in cereals. The pericarp consists of three major structures, the embryo, endosperm and seed coat, with the endosperm being the tissue of economic value. Understanding the development of the cereal caryopsis holds the future of metabolic engineering to enhance global food production. McIntosh *et al*. (2007) developed LongSAGE (Serial Analysis of Gene Expression) libraries at five time points post-anthesis that coincide with key processes in caryopsis development in wheat, and identified 29 261 unique tag sequences across all five libraries. The 500 most abundant tags spanned development, which highlights the array of functional groups being expressed during grain development. Furthermore, differential expression profiles of abundant tags from each library revealed the co-ordinated expression of genes responsible for the cellular events constituting caryopsis development. These provided novel sequence and expression information, including the identification of potentially useful promoter activities.

Expression analysis using the Affymetrix GeneChip® Wheat Genome Array on mRNA from developing seeds of double haploid lines, grown at two locations under field conditions, identified 1455 common probe sets differing in intensity between lines in both locations; 542 eQTLs were detected that each mapped to a single chromosome interval (with a few exceptions in which eQTLs clustered), suggesting regulatory control for many genes in small chromosome intervals. This may constitute a major gene eQTL for developing seed in wheat. Comparison of expression mapping data with physical mapping of wheat ESTs confirmed the presence of both *cis*- and *trans*-acting eQTLs. Many of the eQTL clusters were coincident with QTLs controlling dough, bread-making and seed weight traits, which are based entirely on mature seed composition (Jordan *et al*., 2007). Thus, by mapping patterns of gene expression as eQTLs controlling complex traits, key regulatory regions may be identified and used in molecular plant breeding. A knowledge of the genes regulated by these eQTLs could provide insight into the biochemical nature of the traits, assist in map-based cloning of the regulatory elements and help associate genotype with phenotype.

Table 5 Nuclear fertility restorer (*Rf*) genes, cytoplasmic male sterility (CMS) sources and DNA markers associated with *Rf* in barley, maize, rice, sorghum and wheat from 1994 to 2006

Rf	CMS source	DNA markers associated with *Rf*	Reference
Barley			
Rfm1	msm1 and msm2	e34m2, e46m19 and e48m17 on chromosome 6; the closest e34m2 and e46m19	Murakami *et al*. (2005)
	msm1	CMNB-07/800, OPT-02/700 and MWG2218 on chromosome 6H	Matsui *et al*. (2004)
Maize			
Rf3	S	*Rf3* on chromosome 2; closest marker E7P6, E12M7 and E3P1 from *Rf3*	Zhang *et al*. (2006)
Rf4 and *Rf5* and *Rf-I*	C	*Rf4* restores fertility in all C lines, and *Rf5* in C lines lacking *Rf-I*, mapped on chromosome 7 between umc2326 and umc2327	Hu *et al*. (2006)
rf1 and *rf2*	T	*rf1* between umc97 and umc92 on chromosome 3 and *rf2* between umc153 and sus1 on chromosome 9	Wise and Schnable (1994)
Rice			
Rf4		RM6737, RM304, RM171, RM5841 and RM6737 on chromosome 10; RM171 and RM6737 flanking markers	Ahmadikhah and Karlov (2006)
Rfcw	CW	*Rfcw* on chromosome 4 between AT10.5-1 and RM3866	Fujii and Toriyama (2005)
Rf5 and *Rf6*(*t*)	HL	*Rf5* and *Rf6*(*t*) on chromosome 10; *Rf5* co-segregates with RM3150 and flanked by RM118 and RM5373, whereas *Rf6*(*t*) co-segregates with RM5373 and flanked by RM6737 and SBD07	Liu *et al*. (2004)
Rf1	D1	*Rf1* on chromosome 10 between RM171 and RM6100	Tao *et al*. (2004)
Rf-D1(*t*)	D1	*Rf-D1*(*t*) on chromosome 10 between OSR33 and RM228	Tan *et al*. (2004)
Rf3	WA	OPKO5-800, OPU10-1100, OPW01-350, RG532, RG140 and RG458 on chromosome 1	Zhang *et al*. (1997)
Sorghum			
rf4	A3	LW7 and LW8 mapped to *rf4*, whereas LW9 on the flanking side of *rf4*	Wen *et al*. (2002)
rf1	A1	*rf1* on LG H close to Xtxa2582, whereas Xtxp18 and Xtxp250 flank the locus	Klein *et al*. (2001)
Wheat			
D^2Rf1	Yi 4060	E09-SCAR$_{865}$ mapped to the *D^2Rf1* locus, whereas Xgwm11 and Xgwm18 co-segregate with E09-SCAR$_{865}$	Li *et al*. (2005)
Rf3	Timopheevii-based CMS	Xbarc207, Xgwm131 and Xbarc61 close to Rf3 on 1B and two minor QTLs on 5A and 7D	Zhou et al. (2005)

Male sterility and fertility restoration in hybrid breeding

Mapping and cloning nuclear *Rf* genes

CMS is a maternally inherited trait characterized by the inability to produce functional pollen, often associated with unusual open reading frames (ORFs) in the mitochondrial genome. Male fertility can be restored by *Rf* genes (Schnable and Wise, 1998). Thus, CMS/*Rf* systems are ideal models for studying the genetic interaction and function of mitochondrial and nuclear genomes in plants. Several CMS systems, in addition to normal male-fertile cytoplasm, which yields fertile plants in all known nuclear backgrounds, have been reported in maize (S, C and T) (Backett, 1971), pearl millet (A_1, A_2, A_3, A_4, A_5, Av and gero) (Chandra-Shekara *et al*., 2007), rice (WA, DA, GAM, HL and DIS in indica, and D and BO in japonica backgrounds) (Tao *et al*., 2004, and references cited therein) and sorghum (A_1, A_2, A_3, A_4, A_5, A_6 and 9E) (Schertz, 1994). They can be differentiated by *Rf* gene(s) that suppress their associated male-sterile phenotype, allowing normal pollen development. To date, few CMS and *Rf* systems have been extensively exploited in hybrid breeding: for example, A_1 (Tift23A) in pearl millet (Rai *et al*., 2001), A_1 (milo) in sorghum (Moran and Rooney, 2003), T in maize (Ullstrup, 1972), and D and BO in japonica rice and WA, DA, GAM, DIS and HL in indica rice (Tao *et al*., 2004).

DNA markers associated with *Rf* gene(s) in barley (*Rfm1*), maize (*rf1*, *rf2*, *Rf3*, *Rf4* and *Rf5*), rice [*Rf1*, *Rf3*, *Rf4*, *Rf5*, *Rf6*(*t*) and *Rf-D1*(*t*)], sorghum (*rf1* and *rf4*) and wheat (*D2Rf1* and *Rf3*) (Table 5), and those associated with thermosensitive genetic male sterility (TGMS) gene(s) in maize (*tms3*), rice [*rtms1*, *tms4*(*t*), *tms5* and *tms6*] and wheat (*wtms1*), photoperiod-sensitive genetic male sterility (PGMS) gene in rice (*pms3*) and thermo-photoperiod-sensitive genetic male sterility (TPGMS) genes in wheat (*wptms1* and *wptms2*) (Table 6) have been mapped to respective chromosome regions of each species. These DNA markers can be used to transfer *Rf* or *tms* alleles to new genotypes.

To date, only *rf2* in maize (Cui *et al*., 1996), *Rf1* in rice (Akagi *et al*., 2004; Komori *et al*., 2004) and *Rf1* in sorghum (Klein *et al*., 2005) have been cloned. Maize *rf2* encodes an

Table 6 DNA markers associated with thermo-, photoperiod- and thermo-photoperiod-sensitive genetic male sterility in maize, rice and wheat from 1997 to 2006

Male sterility gene	Source material	DNA markers associated with male sterility	Reference
Thermosensitive genetic male sterility (TGMS)			
Maize			
tms3	Qiong68ms	*tms3* on chromosome 2 between umc2129 and umc1041	Tang *et al*. (2006)
Rice			
tms6	Sokcho-MS	*tms6* on chromosome 5 between RM3351 and E60663	Lee *et al*. (2005b)
tms6(*t*)	0A15-1	*tms6*(*t*) on chromosome 3, close to centromere, linked to S187770	Wang *et al*. (2004)
tms5	AnnongS-1	*tms5* on chromosome 2 between C365-1 and G227-1	Wang *et al*. (2003)
rtms1	J207S	*rtms1* on chromosome 10 between RM222 and RG257	Jia *et al*. (2001)
tms4(*t*)	TGMS-VN1	*tms4*(*t*) on chromosome 2, E5/M12-600 the closest	Dong *et al*. (2000)
tms2	Norin PL12	*tms2* on chromosome 2 between R643 and R1440	Yamaguchi *et al*. (1997)
tms3(*t*)	IR32364TGMS	$OPF18_{2600}$, $OPB19_{750}$, $OPAA7_{550}$, and $OPAC3_{640}$ linked to *tms3*(*t*)	Subudhi *et al*. (1997)
Wheat			
wtms1	BNY-S	*wtms1* on chromosome 2B between Xgwm374 and $E:AAG/M:CTA_{163}$	Xing *et al*. (2003)
Photoperiod-sensitive genetic male sterility (PGMS)			
Rice			
pms3	Nongken 58	*pms3* on chromosome 12, localized to 28.4-kb DNA fragment surrounded by 15 RFLP markers	Lu *et al*. (2005)
Thermo-photoperiod-sensitive genetic male sterility (TPGMS)			
Wheat			
wptms1 and wptms2	337S	wptms1 on chromosome 5B and wptms2 on 2B; wptms1 between Xgwm335 and Xgwm371, and wptms2 between Xgwm374 and Xgwm120	Guo et al. (2006)

aldehyde dehydrogenase that restores male fertility in T cytoplasm (Liu *et al*., 2001). Rice *Rf1*, delimited to a 22.4-kb region, encodes a mitochondrially targeted protein containing 16 repeats of the 35-amino-acid pentatricopeptide repeat (PPR) motif. Klein *et al*. (2005) cloned *Rf1* of sorghum, which they resolved to a 32-kb region spanning four ORFs: a plasma membrane Ca^{2+}-ATPase, a cyclin D-1, an unknown protein and a PPR13. The first three were completely conserved between fertile and sterile plants. In the approximately 7-kb region spanning PPR13, they identified 19 sequence polymorphisms that co-segregated with the fertility restoration phenotype. PPR13 encodes a mitochondrial-targeted protein containing a single exon with 14 PPR repeats, not present in rice, and a candidate gene for *Rf1* in sorghum. More recently, Wang *et al*. (2006) demonstrated in rice with BO cytoplasm that an abnormal mitochondrial ORF, *Orf79*, is co-transcribed with the duplicated *atp6* (*B-atp6*) gene and encodes a cytotoxic peptide. Two *Rf* genes at the *Rf* locus, *Rf1a* and *Rf1b* within an approximately 105-kb region, are members of a multigene cluster encoding PPR proteins. Both target mitochondria and restore male fertility by blocking *Orf79* production via endonucleolytic cleavage or degradation of dicistronic B-*atp6*/*orf79* mRNA.

Of the several TGMS genes reported in rice, Zhou *et al*. (2006) cloned *OsAPT2*, located on chromosome 4, which encodes a putative adenine phosphoribosyl transferase. This is associated with *tms5* in rice, and the *OsAPT2* transcript in the young panicle is down-regulated at 29 °C, the critical temperature for induction of fertility conversion in the TGMS mutant 'Annong S-1'.

Molecular basis of CMS

Mitochondrial function depends on the co-ordinated action of the nuclear and mitochondrial genomes. CMS in plants is determined by the mitochondrial genome, such that the pollen sterility phenotype can be suppressed or counteracted by *Rf* genes. The origin of the genes that determine CMS and insights into plant mitochondrial–nuclear communication and molecular cloning of *Rf* genes identified PPR proteins as key regulators of plant mitochondrial gene expression (Chase, 2007).

Mitochondrial *orf79*, associated with CMS Boro rice, encodes a cytotoxic peptide responsible for CMS. PPR proteins encoded by *Rf1* block the production of cytotoxic peptide in this rice, and expression of *orf79* in CMS lines and transgenic rice plants causes gametophytic male sterility (Wang *et al*., 2006).

Mitochondrial DNA in T cytoplasm of maize contains an *ORF13* that produces a 13-kDa polypeptide unique to T-type

sterility (Dewey *et al*., 1987). CMS S-type cytoplasm of maize is associated with the expression of *orf355-orf77* in the R region of mitochondrial DNA, such that *Rf3* can regulate nuclear and mitochondrial gene expression and shows pleiotropic effects on the transcriptional level. Using a cDNA microarray and suppression subtractive hybridization, Zhang *et al*. (2005c) studied the global expression profile caused by *Rf3* substitution of *rf3* in S cytoplasm during pollen development in a set of *Rf3*/*rf3* near-isogenic line (NIL). They identified 137 tentative unique genes and differential expression amongst S-(*Rf3*) and S-(*rf3*). For example, in S-(*Rf3*), the expression patterns of genes associated with electron or H^+ conduction and of anti-apoptosis genes were distinctly different from those of S-(*rf3*). *Rf3* may therefore regulate the accumulation of nuclear and mitochondrial gene transcripts directly or indirectly to inhibit multiple programmed cell death pathways in S-type cytoplasm, allowing the normal development pathways to unfold. Allen *et al*. (2007) sequenced five distinct mitochondrial genomes in maize – two fertile (NA and NB) and three cytoplasmic male-sterile (CMS-C, CMS-S, CMS-T) cytotypes that ranged from 535 825 bp in CMS-T to 739 719 bp in CMS-C, with large duplications accounting for most size differences. Plastid DNA accounts for 2.3%–4.6% of each mitochondrial genome. The genomes share a minimum of 51 genes for 33 conserved proteins, three rRNAs and 15 tRNAs. Duplicate genes and plastid-derived tRNAs vary amongst cytotypes; however, known CMS-associated ORFs were detected in CMS-S and CMS-T, but not in CMS-C.

Male-sterile sorghum carrying A_3 cytoplasm (IS1112C) represents an unusual example of aberrant microgametogenesis, wherein microspores develop into non-viable pollen that remains physically intact until anther exsertion. Using cDNA amplified fragment length polymorphism (AFLP) transcript profiling and male-fertile and male-sterile NILs at three different stages of pollen development, Pring and Tang (2004) discovered that transition from early to late stages is characterized by changes in abundance of nearly 33% of shared transcripts, and early- or late-specific expression of about 10% of transcripts. Male-sterile plants exhibit extensive changes in regulatory patterns from those characteristic of fertile plants, including premature expression of late-specific and prolonged expression of early-specific transcripts. Furthermore, genome-wide transcriptome patterns indicate the expression of an estimated 12 000 genes in early–mid-microspores, and the abundance of at least 15% of these transcripts is altered in male-sterile plants. NIL restored to male fertility is characterized by the apparent normalized expression of most of these transcripts. The development of the microgametophyte is thus characterized by dynamic programmed changes in gene expression, and the expression of male sterility compounds these changes in a complex manner. Pring *et al*. (2006) examined gene expression and the abundance of protein products from the selected mitochondrial genes in near-isogenic male-sterile, fertility-restored and normal cytoplasm lines in two genetic backgrounds, in addition to recombinant inbred lines differing at two fertility loci. They characterized seven transcript-derived fragments (TDFs) unique to a BC_7F_3 fertility-restored line, four of which were eliminated in a marker-selected $BC_{11}F_3$ line, whereas the remaining three TDFs were detected in all lines examined, indicating that these unique fragments represent alleles derived from the non-recurrent male parent, in which some of the TDFs may be linked to *Rf* alleles. The male-sterile microspore mitochondria contained elevated levels of the nuclear-encoded alternative oxidase protein, potentially associating mitochondrial dysfunction with failed pollen development. The relative abundance of mitochondrial-encoded ATPA, ATP6 and cyclo-oxygenase II proteins and nuclear-encoded manganese superoxide dismutase, cytochrome *c* and aldehyde dehydrogenase proteins, in contrast, did not vary with cytoplasm or fertility status at the microspore stage.

Assessing the genetic purity of hybrids, CMS and maintainer lines

Ensuring the genetic purity of parental lines and hybrids is a prerequisite to realizing the full potential of the hybrids. It is estimated that every 1% impurity of female line seed in rice hybrid seed reduces the yield by 100 kg/ha (Mao *et al*., 1996). One of the common admixtures in hybrid seed production is that of maintainer lines with CMS lines. Given that both are isonuclear lines, it is not possible to distinguish between them until they flower. The purity of hybrid seed lots is normally assayed by a grow-out test on a representative sample of the seed to be marketed (Verma, 1996). The grow-out test involves growing plants to maturity, and assessing the morphological and floral characteristics that distinguish the hybrids, thus precluding the immediate cultivation of the hybrid seed produced. The grow-out test is costly and subject to high genotype–environment interaction. DNA-based markers can be used to assess more quickly and precisely the genetic purity of hybrids and their parental lines. For example, several PCR-based markers have been reported in rice that not only discriminate between CMS lines and their cognate maintainer lines, but also serve to assess the genetic purity of the hybrids (Table 7). More research is needed to develop such marker systems in other crops in which three-line hybrids are used.

Table 7 DNA-based markers for distinguishing between A and B lines and for testing the genetic purity of hybrid seed in rice from 2002 to 2007

Diagnostic marker	Marker differentiating hybrid and its parental lines	Reference
Drrcms	Distinguishes CMS lines from their cognate maintainers	Rajendrakumar *et al*. (2007a)
BF-STS-401 and BF-STS-420	Differentiates CMS lines from their corresponding maintainer lines	Rajendran *et al*. (2007b)
RM258	Differentiates CMS and restorer lines from hybrid	Garg *et al*. (2006b)
RM9	RM9386 differentiates CMS lines and their hybrids but not their cognate maintainer lines	Yashitola *et al*. (2004)
M1, M2 and M3	Differentiates from each other japonica hybrids and their parental lines	Komori and Nitta (2004)
RM#206, 216, 258 and 263	Differentiates 11 rice hybrids grouped into three clusters, hybrids within cluster share a common CMS source	Nandakumar *et al*. (2004)
E-AAC/M-CTC	A fragment with six base pair (Leu-tRNA gene) difference in cpDNA differentiates five CMS lines from their corresponding maintainer lines	He *et al*. (2003)
RM 164 and pTA248	Detects polymorphism between CMS, hybrid and restorer lines	Yashitola *et al*. (2002)

Mitochondrial DNA sequence variation is also useful for fingerprinting male sterility-inducing cytoplasm, determining cytoplasmic diversity amongst germplasm accessions and identifying new sources of cytoplasm that induces male sterility (Xu *et al*., 1995).

Engineering CMS for hybrid breeding

Several mechanisms have been reported to create a *de novo* CMS trait in a species lacking CMS, or to eliminate the flaws in an existing CMS system in plants, mostly affecting tapetum and pollen development (Yui *et al*., 2003; Zheng *et al*., 2003). Severe phenotypic alterations as a result of interference with plant metabolism and development have precluded their use in agriculture (Goetz *et al*., 2001). Mitochondria and plastids are maternally inherited in most plant species. Transformation of chloroplasts with genes interfering in the plastid metabolic pathway essential for pollen development is the most exciting prospect for the development of new forms of CMS. Ruiz and Daniell (2005) were the first to report CMS in *Nicotiana tabacum* through the transformation of the chloroplast genome with a single gene, β-ketothiolase (*phaA*). The transgenic lines were normal except for the male-sterile phenotype, which lacked pollen. Abnormal thickening of the outer wall, enlarged endothecium and vacuolation affected pollen grains, and resulted in an irregular shape or collapsed phenotype. More importantly, reversibility of the male-sterile phenotype under continuous illumination resulted in viable pollen and a copious amount of seeds. This approach opens up a totally new route for the engineering and testing of new CMS systems in crops. Technical issues related to the use of this approach, including problems associated with plastid transformation, the design of restorer genes, stability of the trait, possible negative effects of the introduced gene (causing male sterility) on agronomic traits, and biosafety and social acceptance concerns, must be addressed before this technique may be widely used (Pelletier and Budar, 2007).

The stability of the mitochondrial genome is controlled by nuclear loci, and nuclear genes suppress mitochondrial DNA rearrangements during plant development. One such nuclear gene is *Msh1*. To test that *Msh1* disruption leads to the type of mitochondrial DNA rearrangements associated with naturally occurring CMS in plants, Sandhu *et al*. (2007) used a transgenic approach for RNAi to modulate the expression of *Msh1* in tobacco and tomato. This resulted in reproducible mitochondrial DNA rearrangements and a condition of male sterility (non-reversible) that was heritable, associated with normal female fertility, and maternal in its inheritance, providing a means to develop novel non-genetically modified organisms or transgenic CMS lines.

Male fertility in flowering plants is dependent on the production of viable pollen grains within the anther. Genes expressed exclusively in the anther are likely to include those that control male fertility. *Bcp1*, an anther-specific gene from *Brassica campestris*, is essential for pollen development. Inhibition of its expression in either tapetum or microspores prevents the production of fertile pollen in transgenic *Arabidopsis* plants (Xu *et al*., 1995). Using differential screening of a cDNA library from rice panicles, Luo *et al*. (2006) isolated a tapetum-specific gene, *RTS*, which encodes a putative polypeptide of 91 amino acids with a hydrophobic N-terminal region. *RTS* is predominantly expressed in the anther's tapetum during meiosis. Down-regulation of its expression leads to pollen abortion, and therefore male sterility, in transgenic rice plants. The promoter region of *RTS*, when fused to the *Bacillus amyloliquefaciens* ribonuclease gene, *barnase*, or the antisense of the *RTS* gene, is able to drive tissue-specific expression of both genes in rice, creeping bentgrass (*Agrostis stolonifera* L.) and *Arabidopsis*, conferring male sterility to the transgenic plants. When fertilized with

wild-type pollen, these transgenic plants produce normal seed sets, confirming no adverse effect on female fertility. Thus, *Bcp1* or *RTS* and its promoter have great potential for engineering male sterility in other crop plants.

Pyramiding TGMS and *Rf* genes

Using simple sequence repeat (SSR)-linked markers and TGMS donors, each possessing different genes, Nas *et al*. (2005) developed two-gene and three-gene pyramids (IR80775-46 with *tms2* and *tms5*, and IR80775-21 with *tms2*, *tgms* and *tms5*) possessing the RM11 allele of Norin PL 12 (*tms2*), the RM257 allele of SA2 (*tgms*) and the RM174 allele of DQ200047-21 (*tms5*), which expressed as male sterile under sterility-inducing conditions. In addition, rice SF21 is a candidate *tms5* because of its complete linkage (0.0 cM) with RM174. SF21 is a putative pollen-specific protein (IRGSP) because of its high degree of amino acid sequence alignment to known pollen proteins in *Arabidopsis* and sunflower.

Sattari *et al*. (2007) used two sequence-tagged site (STS) markers (RG140/*Pvu*II and S10019/*Bst*UI) to select for two major *Rf* genes (*Rf3* and *Rf4*) governing fertility restoration of CMS in rice. The combined use of markers associated with these two loci improved the efficiency of screening for putative restorer lines from a set of elite lines. Breeders, in general, identify restorers by test crossing prospective lines with available CMS lines and evaluating F_1 progenies for pollen and spikelet fertility. Lines with progenies showing an excess of pollen and spikelet fertility are designated as restorers. The development of PCR-based, marker-aided selection involving *Rf* genes would significantly reduce the time and resources needed to make and evaluate test crosses in hybrid breeding programmes.

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