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FLOWERING NEWSLETTER REVIEW

Flowering and determinacy in maize

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Abstract

All plant organs are produced by meristems, groups of stem cells located in the tips of roots and shoots. Indeterminate meristems make an indefinite number of organs, whereas determinate meristems are consumed after making a specific number of organs. Maize is an ideal system to study the genetic control of meristem fate because of the contribution from determinate and indeterminate meristems to the overall inflorescence. Here, the latest work on meristem maintenance and organ specification in maize is reviewed. Genetic networks, such as the CLAVATA components of meristem maintenance and the ABC programme of flower development, are conserved between grasses and eudicots. Maize and rice appear to have conserved mechanisms of meristem maintenance and organ identity. Other pathways, such as sex determination, are likely to be found only in maize with its separate male and female flowers. A rich genetic history has resulted in a large collection of maize mutants. The advent of genomic tools and synteny across the grasses now permits the isolation of the genes behind inflorescence architecture and the ability to compare function across the Angiosperms.

Key words: Determinacy, flowers, inflorescence, maize, meristem, spikelets.

Introduction

A remarkable aspect of plants is their ability to produce new organs throughout their life. This capacity is achieved by the action of meristems, groups of self-renewing stem cells located at the tips of shoots and roots (Steeves and Sussex, 1989). Divisions in the meristem give rise to cells with different fates. Cells in the centre of the meristem, the central zone, continue to replenish the meristem, maintaining a defined size. Cells in the periphery of the meristem are in the morphogenetic zone from which organs eventually arise. The balance of these two processes, organogenesis and self-perpetuation, guarantees prolonged activity and such a meristem is said to be indeterminate. In contrast, determinate meristems, such as those that produce flowers, are consumed after making a certain number of organs.

The maize inflorescence provides an excellent model to study the developmental control of meristems because it is shaped by both indeterminate and determinate meristems. In addition, maize has a rich genetic history and several mutations affecting discrete stages of inflorescence development have been described (Neuffer *et al*., 1997). These mutants may have abnormal meristem size or misspecification of organ identity, or both. The genetics of inflorescence and flower development in maize and other grasses has been recently reviewed by other authors (McSteen *et al*., 2000; Bommert *et al*., 2005*a*). Current knowledge of grass inflorescence development is briefly summarized here and the latest work is reviewed. The focus is on maize, but some discoveries in rice are also included.

The basic unit of grass inflorescence architecture is the spikelet, a compact axillary branch that consists of two bracts subtending one to several reduced flowers (Clifford, 1987). Maize is a monoecious plant that produces male flowers on a terminal tassel (Fig. 1A) and female flowers on lateral ears (Fig. 1B), which arise in the axils of vegetative leaves. The tassel initiates several long, indeterminate branches at the base while the ear consists of a single spike with no long branches. The tassel's main spike and branches, and the entire ear, produce short branches (spikelet pairs) that bear two spikelets (Figs. 1C, D, 2A–D). The branches and spikelet pairs arise in the axils of small, undeveloped leaves referred to as bracts. In maize, spikelet and spikelet pair meristems are considered determinate because they produce a defined number of organs (Vollbrecht *et al*., 2005).

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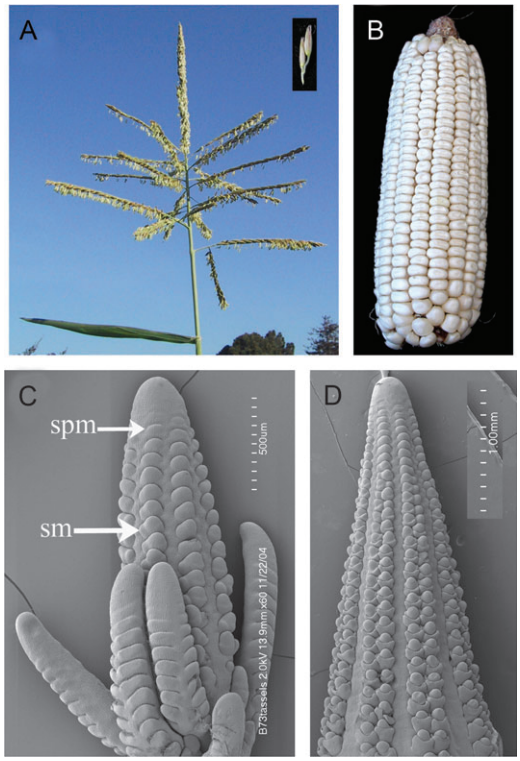

Fig. 1. Wild-type maize inflorescences. (A) Tassel bearing spikelet pairs (inset) on branches and main spike. (B) Ear showing rows of kernels. (C) Scanning electron microscopy of a tassel primordium initiating spikelet pair meristems. (D) Scanning electron microscopy of an ear. Spm: spikelet pair meristem. Sm: spikelet meristem.

Inflorescence meristem size and maintenance

Unlike its ancestor teosinte, which is induced to flower by short days, maize undergoes transition from the vegetative to reproductive phase after producing a fixed number of leaves (Irish and Nelson, 1988). The most important known regulator of the transition to reproductive stage in maize is *indeterminate1* (*id1*). The *id1* gene encodes a zinc-finger protein that is produced in young leaves. ID1 functions non-autonomously to signal to the shoot apical meristem (SAM) for the transition to a reproductive stage. Mutants of *id1* form many more leaves than wild-type maize and show vegetative reversion in the tassel with plantlets arising in male spikelets, often complete with roots (Colasanti *et al*., 1998).

In the eudicots *Antirrhinum* and *Arabidopsis*, the genes *FLORICAULA* (*FLO*) and *LEAFY* (*LFY*) are necessary for the production of flowers (Coen *et al*., 1990; Weigel *et al*., 1992). *flo* mutants produce inflorescence branches in the position of flowers while *lfy* mutants produce flowers with features of the inflorescence. Maize has duplicate orthologues of *FLO*/*LFY*, *zea flo*/*lfy1* (*zfl1*) and *zfl2*. Phenotypic analyses of *zfl1* and *zfl2* mutants shows that their function is somewhat conserved in maize. While single *zfl1* and *zfl2* mutants have mild phenotypes, the double mutants do not undergo normal transition to reproductive development and have abnormal terminal inflorescences. These are described as 'tassel ears' because they are branched inflorescences with female branches enveloped in husk leaves that terminate in a spike of male flowers. Development of spikelets, paleas, and lemmas of *zfl1*/*zfl2* mutants appear to be normal, but flowers show various defects associated with a lack of determinacy and organ identity: normal carpels fail to form and, instead, the female floral meristem produces several 'carpelloid' organs with silks and vegetative outgrowths. Similarly, in the tassel, paleas and lemmas are normal but stamens do not develop and are sometimes replaced by lemma or palea-like organs (Bomblies *et al*., 2003).

One of the key processes in meristem maintenance is the CLAVATA (CLV) pathway, originally described in *Arabidopsis* and named after three genes, *CLV1*, *CLV2*, and *CLV3*. Mutations in these genes cause an enlargement of the shoot and flower meristems, resulting in flowers with extra floral parts (Clark *et al*., 1993; Clark *et al*., 1995, Kayes and Clark, 1998). *CLV1* and *CLV2* belong to a large gene family and both contain a transmembrane domain. *CLV1* is a receptor-like kinase (RLK) with a leucine-rich repeat region (LRR), and *CLV2* is a receptor-like protein (RLP) with an LRR but, unlike *CLV1*, it lacks a cytoplasmic tail and has no kinase function (Jeong *et al*., 1999). *CLV3* encodes an extracellular protein that putatively interacts with *CLV1* and *CLV2* to form a complex that triggers a signalling pathway in the central zone of the SAM resulting in the restriction of stem cell accumulation through the transcription factor *WUSCHEL* (Carles and Fletcher, 2003).

In recent years it has become evident that much of the CLV pathway is conserved between *Arabidopsis* and grasses. In maize, the gene *thick tassel dwarf1* encodes an LRR-RLK and is the putative orthologue of *CLV1* (Bommert *et al*., 2005*b*). Another maize gene, *fasciated ear2* encodes an LRR-RLP, similar to *CLV2* (Taguchi-Shiobara *et al*., 2001). The inflorescence phenotypes of *td1* and *fea2* mutants are similar. Mutations result in fasciated ears, an increase in spikelet density in the tassel due to a thicker rachis, and an increase in stamen number in male florets. Ears have increased seed row number and are shorter and fatter than wild type. These phenotypes are consistent with the observed increase in size of all inflorescence meristems of *td1* and *fea2* mutants. A dominant maize mutant that causes fasciation of the ear, *Fasciated ear1* (*Fas1*) (Fig. 3F), has recently been identified and its role in the CLV pathway is being investigated (China Lunde, unpublished results).

Mutations in rice orthologues of *CLV1* and *CLV3* show similar phenotypes to maize *td1* and *fea2* mutants, especially the enlargement of shoot apical and floral meristems. The *FLORAL ORGAN NUMBER1* (*FON1*) gene, which encodes an LRR-RLK similar to *CLV1* and

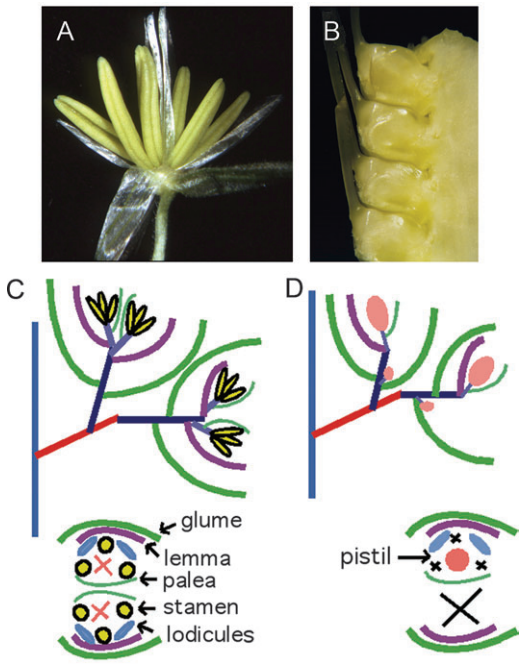

Fig. 2. Maize is a monoecious plant with staminate flowers borne in a tassel and pistillate flowers in ears. (A) A pair of staminate flowers each showing a lemma, a palea, and three stamens (the two lodicules are not seen here). (B) A row of pistillate flowers showing one silk (style) each. (C, D) A schematic representation showing the arrangement of flowering organs in a pair of staminate (C) and pistillate (D) spikelets.

td1, is expressed in vegetative and reproductive meristems and in all floral organ primordia (Suzaki *et al*., 2004). Despite its broad expression pattern, mutations in *FON1* only affect the floral meristems by increasing the numbers of palea, lemma, stamens, and pistils. Mutations in *FON4*, a gene with sequence similarity to *CLV3*, cause enlargement of shoot apical, inflorescence, and floral meristems (Chu *et al*., 2006). Consequently, *FON4* mutants have thicker stems, additional inflorescence branches, and extrafloral organs. *FON4* is expressed in the central zone of vegetative, inflorescence, and floral meristems, similar to *CLV3*. Another rice *CLV3*-like gene, *FON2,* has a broad expression pattern, but its loss of function only affects the specification of flower organ number, while inflorescences are normal (Suzaki *et al*., 2004). This suggests that in vegetative and inflorescence meristems, FON4 acts redundantly with FON2 to limit meristem size, but both are needed in floral meristems for proper flower formation.

An opposite group of maize mutants fail to produce branches and spikelets. *barren inflorescence2* (*bif2*) mutants have few if any branches in both ears and tassels. Bracts are not affected, as demonstrated by a double mutant with *tasselsheath*, which makes enlarged bracts (McSteen and Hake, 2001). *bif2* encodes a serine/threonine protein kinase co-orthologous to *PID* of *Arabidopsis* (P McSteen and S Hake, unpublished data). PID is responsible for the polar localization of the auxin efflux

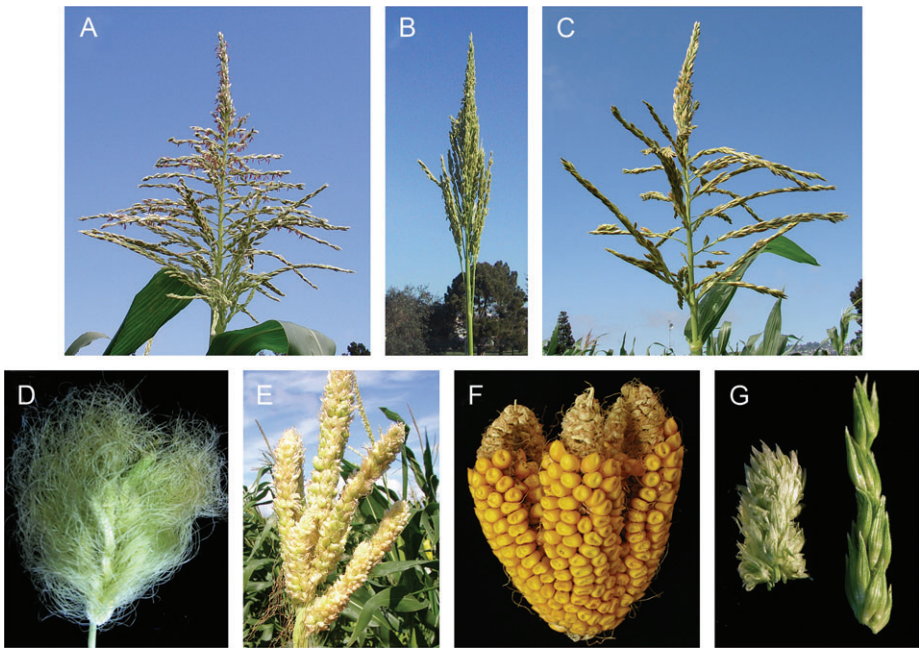

Fig. 3. Maize inflorescence and flowering mutants. (A–C) The *ramosa* mutants have increased indeterminacy of lateral organs, transforming determinate meristems (spikelet pairs) into branches with varying degrees of indeterminacy. (A) *ra1*. (B) *ra2*. (C) *ra3*. (D) *tasselseed4* (*ts4*) is a mutant that fails to abort pistils in tassel spikelets and also shows increased branching. Notice the proliferation of silks due to pistil formation in the tassel (picture courtesy of George Chuck). (E) *Ts6* also has feminization of tassels. In this picture silks have been removed to reveal pistil formation. (F) *Fascicled ear1 (Fas1)*, a mutant with fasciated ear and increased kernel row number (picture courtesy of China Lunde). (G) The *fuzzy tassel* mutant makes extra flowers per spikelet, multiple sterile flowers parts, and lacks normal glumes. Shown is a segment of the mutant tassel rachis on the left compared with the wild type on the right.

carrier PIN proteins (Friml *et al*., 2004), and both *PIN* and *PID* loss-of-function mutants have inflorescences that lack leaves and axillary branches and flowers (Galweiler *et al*., 1998; Christensen *et al*., 2000). *kn1* loss-of-function mutants show a mild barren phenotype. Ears often fail to form and if they do, have few kernels and extra silks. Tassels have fewer branches and fewer spikelet pairs (Kerstetter *et al*., 1997).

Mutants of the rice gene *LAX PANICLE* (*LAX*) and its maize orthologue *barren stalk1* (*ba1*) also show a decrease in production of axillary branches. Although the inflorescence defects are similar, the effect on vegetative branching differs. *ba1* mutant plants fail to produce any tillers while tillering in *lax* mutants is only mildly affected (Komatsu *et al*., 2003*a*; Gallavotti *et al*., 2004). This difference is probably due to redundancy of *LAX* and *SMALL PANICLE* (*SPA*) since the *lax*/*spa* double mutants have a significantly lower numbers of tillers (Komatsu *et al*., 2003*a*).

The pattern of expression of *ra2*, a marker of the very early stages of axillary branching (Bortiri *et al*., 2006), can be used to examine the stage at which a mutant departs from normal development. Expression of *ra2* in *bif2* tassels show that this mutant initiates fewer than normal meristems, but they are of normal size. Consequently, *bif2* inflorescences form some 'escape' axillary branches and spikelet pairs (McSteen and Hake, 2001). On the other hand, *ba1* tassels have a normal distribution of axillary meristems as determined by the domains of *ra2* expression but the size of the meristem anlagen is smaller, indicating that meristems of *ba1* mutants fail to grow because they do not reach a critical size (E Bortiri *et al*., unpublished results).

Axillary meristem initiation and determinacy

Spikelet pairs are a derived feature, present only in the Andropogoneae tribe, a monophyletic group that includes species such as maize, sorghum, and sugar cane (LeRoux and Kellogg, 1999; Group, 2001). Both spikelet pairs and indeterminate branches originate from axillary meristems; however, unlike other axillary meristems of racemose inflorescences, spikelet pair meristems terminate after the production of two spikelets. For this reason they are considered determinate. The phylogenetic placement of spikelet pairs suggests that a novel genetic programme arose in the Andropogoneae to specify the fate of determinate axillary meristems.

The *ramosa* mutants (*ra1*, *ra2*, *ra3*) provide the starting material to study the molecular basis of the spikelet pair developmental programme. All *ra* mutants have axillary meristems with increased indeterminacy. Ears of strong *ra* mutant alleles make branches and, in tassels, spikelet pairs are replaced by indeterminate branches. The long branches at the base of the tassel show increased degrees of branching (Fig. 3A–C).

ra1 encodes a Cys2-His2 zinc-finger of the plant-specific EPF subclass and it is expressed at the base of the spikelet pair meristem (Vollbrecht *et al*., 2005). *ra2* encodes a plant-specific LOB domain transcription factor containing a cysteine-rich region and a leucine-zipper-like region. RA2 of maize, sorghum, barley, and rice has a conserved C-terminus domain in addition to the LOB domain (Bortiri *et al*., 2006). *ra2* is expressed in the anlagen of indeterminate long branches, spikelet pair meristems, and spikelet meristems. *ra3* encodes a trehalose-6-phosphate phosphatase (TPP) and is expressed at the base of spikelet pair meristems (Satoh *et al*., 2006). Levels of *ra1* transcript are very low in both *ra2* and *ra3* mutant inflorescences and *ra1*/*ra2*, and *ra1*/*ra3* double mutants show an additive phenotype (Vollbrecht *et al*., 2005; Satoh *et al*., 2006). In addition, *ra2* expression is normal in *ra1* and *ra3* mutants (Bortiri *et al*., 2006), and *ra3* transcript levels are not changed in *ra2* and *ra1* mutants (Satoh *et al*., 2006). These data suggest that *ra2* and *ra3* are upstream of *ra1*, but in different pathways, and both are necessary for normal transcription of *ra1*. This finding would explain why *ra1* is not expressed in branch meristems, which have *ra2* but lack *ra3* expression. Orthologues of *ra2* and *ra3* have been found in other grasses, including rice, and they have a similar expression pattern in those grass species (Bortiri *et al*., 2006; Satoh *et al*., 2006). However, a *ra1* orthologue has not been found in rice, or other grasses outside the Andropogoneae (E Vollbrecht, EA Kellogg, and S Malcomber, unpublished results). Judging from the conservation of their sequence and expression patterns, it appears that RA2 and RA3 have been recruited to regulate *ra1*, a gene whose function arose in the Andropogoneae, and the three act together to impose determinate fate to the spikelet pair meristems. The function of *ra2* and *ra3* in other grasses is not yet known, but it is speculated that they modulate the extent of branching.

Other mutants with loss of determinacy in both tassels and ears are *branched silkless1 (bd1), indeterminate spikelet1 (ids1), tassel seed4 (ts4*), *fuzzy tassel*, and the dominant mutant *Tassel seed6 (Ts6*). *bd1* and *ids1* encode proteins containing one or two AP2 domains, respectively, and both affect the spikelet meristem (Chuck *et al*., 1998, 2002), however, the fates of these meristems differ. *bd1* mutants show a very striking phenotype in the ear in which the spikelet is replaced by a sterile, indeterminate branch. Each branch produces spikelet pair meristems, similar to the branches of the tassel. In the tassel, the spikelet meristems are also indeterminate, but produce spikelets in a distichous pattern, eventually producing fertile flowers (Chuck *et al*., 2002). The rice mutant, *frizzy panicle*, is an orthologue of *bd1* with a similar mutant phenotype (Komatsu *et al*., 2003*b*). *ids1* mutants also have

a loss of determinacy in the SM, however, the SM retains its identity, and makes extra flowers and glumes. The ear and tassel are similar, although the ear is not fertile (Chuck *et al*., 1998). The *fuzzy tassel* mutant also makes extra flowers per spikelet and multiple sterile flower parts but, unlike *ids1*, it lacks normal glumes (Fig. 3F).

bd1 is expressed only in ears and tassels in a very narrow domain at the flank of spikelet meristems (Chuck *et al*., 2002). The expression of *bd1* is seen as the spikelet pair meristem divides to produce a spikelet meristem. The expression appears first at the base of one spikelet meristem, then at the base of the other. The expression marks a position between glume and spikelet meristem. *ids1* is expressed more broadly, although it has a narrow domain of action. It is expressed in SPM and SM and in palea, lemma, and stamen initials. Expression is not seen in the carpel and glumes (Chuck *et al*., 1998).

Ts6 and *ts4* have similar phenotypes (Fig. 3D, E). They both have feminized tassels (see discussion below of sex determination), but can be male fertile depending on inbred background (E Bortiri and S Hake, personal observations). Meristem determinacy is affected at different stages of inflorescence development in these two mutants. Analysis by Erin Irish shows that in *ts4,* spikelet pair meristems are transformed into indeterminate branches bearing additional spikelet pairs, while in *Ts6* the pedicellate spikelet meristems makes more flowers (Irish, 1997). SEM analysis suggests that the branching patterns in *ts4* are not as regular as seen in *ids1* or *bd1* mutants (Irish, 1997; G Chuck and S Hake, unpublished results).

Sex determination in maize flowers

All maize flowers initiate a palea, lemma, two lodicules, three stamens, and three carpels, which fuse to make a single pistil. After initiation, pistil primordia in tassel flowers abort, and stamen primordia in the ear show cell-cycle arrest (Dellaporta and Calderon-Urrea, 1994). In addition, the lower floret of the ear also arrests. As a result, tassel spikelets bear two functional staminate flowers, but in the ear only one pistillate flower develops to maturity.

Several mutants have been found that alter sex determination of either male or female flowers. A special class of dwarf plants is andromonoecious, with male flowers in the tassel and perfect flowers in the ear. Most andromonoecious dwarfs are defective in GA biosynthesis (Phinney, 1956), although the dominant mutant, *D8* is defective in GA response (Harberd and Freeling, 1989). *D8* is homologous to *GAI* of *Arabidopsis* and contains an N-terminal deletion of the DELLA domain (Peng *et al*., 1999). An understanding of how GA regulates sex determination is not known, but the finding that GA levels are 100-fold lower in developing tassel spikelets suggests that low GA levels are required for staminate flower development and higher levels trigger stamen abortion (Rood and Pharis, 1980). An additional effect of GA-deficient mutants in maize is a reduction in tassel branch number. This is most obvious in *anther ear1*, which encodes an ent-kaurene synthase, an enzyme that catalyses an early step in the GA biosynthesis (Bensen *et al*., 1995). Thus GA may regulate not only stamen abortion in the ear, but also tassel branching.

tassel seed1 (ts1) and *ts2* have completely feminized tassels independent of background. In addition, the lower floret of the ear fails to abort. *ts2* encodes a short-chain alcohol dehydrogenase that is presumed to lead to pistil abortion (DeLong *et al*., 1993). Expression of *ts2* is not seen in *ts1* mutants, thus *ts1* is thought to operate upstream of *ts2* (Calderon-Urrea and Dellaporta, 1999). *ts2* is expressed in all pistil primordia including those of the ear, thus Calderon-Urrea and Dellaporta propose that the upper floret of the ear is protected from the TS2 imposed pistil cell death post-transcriptionally (Calderon-Urrea and Dellaporta, 1999). *silkless1* (*sk*) has an opposite phenotype to *ts1* and *ts2;* the tassel is normal, but the ears are without pistils and are thus sterile. Double mutants with *ts2* show that *ts2* is epistatic to *sk* (Jones, 1932; Veit *et al*., 1991; Irish *et al*., 1994; Calderon-Urrea and Dellaporta, 1999). These results suggest that SK negatively regulates TS2 in the upper floret of the ear, thus only this floret is protected from the cell death mediated by TS2. Double mutants between *ts2* and *D8-Mp1* show an additive phenotype with perfect flowers (stamens and pistils) in both ear and tassel (Veit *et al*., 1991; Irish *et al*., 1994). This results shows that the TS2 and GA pathways operate independently and the pistil development in the tassel is not dependent on the loss of stamens.

Maize floral organ specification

The ABC model of flower development was originally described for the eudicots *Arabidopsis* and *Antirrhinum*. This model holds that A-class genes specify sepal fate in the first flower whorl, A plus B genes specify petals in the second whorl, B plus C genes give rise to stamens, and C genes alone are needed for carpel development in the fourth whorl (Coen and Meyerowitz, 1991). This model has been expanded recently to incorporate D class genes, responsible for the development of ovules, and E-class genes, which are necessary for normal expression of all the above-mentioned genes. With the exception of the A-class gene *APETALA2*, all of those genes are members of the MADS-box family of transcription factors and they act by forming dimers and complexes of higher order (de Folter *et al*., 2005).

silky1 (*si1*) is a MADS-box gene related to *Arabidopsis APETALA3* and *Antirrhinum DEFICIENS* (B-class). Mutations in *si1* transform lodicules into bract-like organs

reminiscent of paleas or lemmas (Ambrose *et al*., 2000), and stamens into pistils. This phenotype is similar to a loss of function of B-class genes in eudicots. *si1* is expressed in the centre of the floral meristem at the time that the lemma and palea are produced. Later, expression is restricted to the region of the floral meristem that will give rise to lodicules and stamens. The finding that SILKY1 has biochemical properties of B-class proteins and can rescue an *Arabidopsis ap3* mutant shows that B-class function is conserved between grasses and *Arabidopsis* (Whipple *et al*., 2004).

AGAMOUS and *PLENA*, the *Arabidopsis* and *Antirrhinum* C-class genes, specify stamen and carpel identity in the third and fourth whorls and also confer floral meristem determinacy. In *ag* and *ple* mutants, flowers produce sepals and petals in a reiterative fashion (Yanofsky *et al*., 1990; Bradley *et al*., 1993). Maize and rice have duplicate *AG*-like genes and they appear to have evolved partial subfunctionalization. Mutations in *zag1* cause indeterminate growth of pistil primordia giving rise to more than one silk and undifferentiated masses of tissue inside the ovary (Mena *et al*., 1996). In the tassel some silks occasionally develop, indicating that pistil abortion is not complete, but the stamens are normal. The lack of effect on stamen identity has been explained by the presence of *zmm2*, another MADS box gene highly similar to *AG* and *PLE*. The expression patterns of *zag1* and *zmm2* are largely non-overlapping because *zag1* transcript levels are higher in pistils while *zmm2* is expressed in stamens, suggesting a sex organ specialization that explains the lack of phenotype in tassel flowers of *zag1* (Mena *et al*., 1996).

A similar finding has been described in rice. Both *OsMADS3*, the orthologue of *zmm2*, and *OSMADS58*, the orthologue of *zag1*, are expressed at the site of stamen and pistil initiation. Mutations in *OSMADS3* and *OSMADS58* have consequences for organ specification, i.e. transformation of stamens into lodicules, and increased number of carpels. However, *OSMADS58* appears to have a role in floral meristem determinacy because mutants consistently had indeterminate organ development. In addition, the effects of *OSMADS3* mutations on stamen identities are more severe than those of *OSMADS58* (Yamaguchi *et al*., 2006). Although mutations in *zmm2* have not yet been isolated, there is now evidence indicating that while *zmm2*/*OSMADS3* and *zag1*/*OSMADS58* contribute to stamen and carpel specification, their contributions are unequal, with the former being more important for stamen identity and the latter for proper carpel development and floral meristem determinacy.

Double mutant analysis of *si1* and *zag1* show the expected phenotype for a BC double mutant, i.e. loss of lodicules and stamen identity and, instead, formation of several whorls of lemma/palea-like organs, indicating the loss of floral meristem determinacy as well as organ identity defects (Ambrose *et al*., 2000).

The origin of the sterile floral parts of grasses has been a mystery for many years. In the last few years it has become evident that the ABC model of flower development applies, with some modifications, to maize and rice. For example, the phenotypes of mutations in maize B- and C-class genes, and their orthologues in rice (Nagasawa *et al*., 2003), indicates that lodicules and petals share a common ancestor and develop in equivalent whorls of grass and eudicot flowers, respectively (Irish, 2000). The interpretation of lemma and palea, however, is more difficult because homeotic transformations in maize B- and C-class mutants generate leaf-like organs that have characteristics of both (Ambrose *et al*., 2000), although, in rice, mutations in *SUPERWOMAN1* (*SPW1*) transform lodicules into palea-like organs (Nagasawa *et al*., 2003). One hypothesis suggests that the lemma arose from reductions and fusions of bracts that formed outside the flower in the common ancestor of grasses and sister lineages (Whipple and Schmidt, 2006).

Quantitative trait loci controlling inflorescence development

Much of the natural variation in inflorescence shape observed in maize and other grass species are actually due to the cumulative effect of several loci. Therefore, and because of the economical importance of maize and grasses in general, the study of quantitative trait loci (QTL) is an important field of cereal genetics aimed at yield improvement. Quantitative studies have been energized recently by the advancement of genomic tools such as the sequencing of the rice genome and the rapid development of very dense genetic maps in several grass species. As a consequence, QTL mapping with greatly improved resolution power is now a powerful tool to uncover genes that control important traits. Recently, two reports have characterized the contribution of QTL to inflorescence architecture in grasses. Using two sorghum inbred lines with different inflorescences, Brown *et al*. (2006) mapped QTL for number of branches of first to third order, branch length, and rachis diameter, among others traits. Their findings suggest that branches of different orders are under the control of different loci. Two genes, *Dwr3* (*br2* in maize), and *Sbra2* (the orthologue of maize *ra2*) mapped to two regions with QTL. *Dw3*, which encodes a P-glyocoprotein responsible for auxin transport (Multani *et al*., 2003), mapped to QTL for plant height, and rachis and branch length. The *Sbra2* gene closely co-localized to one of two QTL detected for primary branch number.

Using maize tassels, Upadyayula and colleagues identified two QTL for higher branch number, five for spikelet pair density on the central spike, and two for spikelet pair density on the branches (Upadyayula *et al*., 2006). It is interesting that the latter two sets of QTL (spikelet pairs on

the central spike versus that on primary branches) are non-overlapping, again indicating that different loci have prominent roles at different stages of development. In ears, QTL were found that control kernel number per row, kernel density, row number per ear, ear diameter, and ear weight. Some genes identified by mutant phenotypes co-localize to QTL. These include *ra1*, which maps closely to a QTL for branch number, *td1*, which is in the same region as QTL that control ear weight, tassel branch angle, and spikelet pair density on primary branches, *ra2* which maps to the region with a QTL for kernel number per row, and *fea2*, which localizes to a region with a QTL for branch number. Some QTL were found in regions with no known genes, indicating that QTL mapping can help to identify novel genes involved in inflorescence development (Upadyayula *et al*., 2006).

Conclusions

Grasses are the most important crop worldwide, but research to understand the mechanisms of organogenesis has been limited. The development of new techniques in combination with the power of maize genetics has unleashed a new era in grass biology research. Rice has a fully sequenced genome and maize and sorghum are being sequenced. Transformation is now routine in rice and a new organism, *Brachypodium distachyon*, with a very short life-cycle and small genome, will be fully sequenced shortly (Draper *et al*., 2001; Vogel *et al*., 2005). Genomic synteny in the family has been used successfully to clone genes in maize and wheat. Most of the genetic networks of meristem determinacy and organ specification are conserved between maize and rice, with the notable exception of *ra1* (Vollbrecht *et al*., 2005). Future experiments will take advantage of the synteny in the grasses to unravel the mechanisms behind the variation in inflorescence architecture.

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