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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 mis-specification 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., 2005a). 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 monococious 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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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 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., 2005b). 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...
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. 2. Maize is a monocious 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.

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). knl 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., 2003a; 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., 2003a).

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 feature 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 distinct 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., 2003b). ids1 mutants also have
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, 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. idsl1 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 Bottriri 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 idsl1 or bd1 mutants (Irish, 1997; G Chuck and S Hake, unpublished results).

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).

silky (sil) is a MADS-box gene related to Arabidopsis APETALA3 and Antirrhinum DEFICIENS (B-class). Mutations in sil 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 whors 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, Dw3 (br2 in maize), and Sbra2 (the orthologue of maize ra2) mapped to two regions with QTL. Dw3, which encodes a P-glycoprotein 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, *tdl*, 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 (Upadayayula 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 now routine in rice biology research. Rice has been limited. The development of new techniques in grasses to unravel the mechanisms behind inflorescence development (Upadayayula et al., 2006). Genomic synteny in the family has been used to localize genes to specific regions of the genome. Some genes identified by mutant phenotypes co-localize to QTL with the notable exception of *ra1* (Vollbrecht et al., 2005). Future experiments will take advantage of the genomic synteny in the family to identify novel genes involved in inflorescence architecture.

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