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Mini Review

Genetics and Evolution of Inflorescence and Flower Development in Grasses

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Inflorescences and flowers in the grass species have characteristic structures that are distinct from those in eudicots. Owing to the availability of genetic tools and their genome sequences, rice and maize have become model plants for the grasses and for the monocots in general. Recent studies have provided much insight into the genetic control of inflorescence and flower development in grasses, especially in rice and maize. Progress in elucidating the developmental mechanisms in each of these plants may contribute greatly to our understanding of the evolution of development in higher plants.

Keywords: Evolutionary development — Grass morphology — Inflorescence and flower development — Maize — Meristem — Rice

Abbreviations: BM, branch meristem; FM, floral meristem; IM, inflorescence meristem; LRR, leucine-rich repeat; QTL, quantitative trait locus; SM, spikelet meristem; SPM, spikelet pair meristem.

Introduction

Much progress has been made in our understanding of the genetic control of inflorescence and flower development in higher plants. A good example is the ABC model, which explains the specification of organ identities in the flower. This model has been derived primarily from molecular genetic studies of eudicots such as *Arabidopsis thaliana* and *Antirrhinum majus* (Coen and Meyerowitz 1991). Subsequent studies analyzing orthologs of the ABC MADS-box genes have revealed that this model is fairly well conserved in the eudicots (reviewed in Theissen et al. 2000). It is also of great interest to elucidate the genetic control of development and morphogenesis of flowers in other plants, such as the grasses, where floral and inflorescence structure is diverse and quite different from the core eudicot model systems.

The grasses, *Poaceae*, constitute a large family containing about 10,000 species in the monocotyledonous plants (Kellogg 2001). The family diverged around 55–70 million years ago and has expanded through two major radiations. The grasses show remarkable diversity in morphological, physiological, genetic and ecological traits. For example, grass inflorescences comprise characteristic structural units called spikelets that can contain from one to 40 florets and can be either determinate or indeterminate depending on the species (Schmidt and Ambrose 1998, McSteen et al. 2000, Goto et al. 2001). The florets do not have obvious sepals and petals, but instead form leaf-like floral organs called palea, lemma and lodicules. Both *Oryza sativa* (rice) and *Zea mays* (maize) are model plants in the grasses and in monocots in general because of genetic resources, molecular tools and increasing information from genome projects.

In the case of maize, genetic developmental studies have been carried out over the past several decades, and important genes have been isolated by the use of transposable elements or by homology cloning. The sequencing of the maize genome is at an advanced stage, so positional cloning is also becoming a suitable method for gene isolation. In contrast, rice does not have a long history of developmental studies, although this situation has changed in the past decade (see articles by Kurata et al. and Itoh et al. in this issue). Compared with other grasses, the genome size of rice is exceptionally small and has been fully sequenced, enabling rice researchers to isolate genes associated with defects in development and morphology by positional cloning strategies. In addition, genetic transformation is relatively easy in rice, providing a crucial advantage for developmental studies. On the one hand, the progress of research in both rice and maize is important, because the analysis of one species can facilitate that of the other, due to the conservation of synteny and developmental strategies. On the other hand, maize and rice are relatively different among the cereals, and understanding the development of each will no doubt facilitate studies of other less tractable but equally important agronomic species such as wheat, barley, the millets and sorghum.

In this article, we review findings from recent developmental studies of rice and maize, focusing on inflorescence and flower development. These studies have revealed novel regulatory pathways and concepts that are relevant to basic developmental biology, as well as increasing our understanding of the evolution of crop plants.

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Inflorescence Development in the Grasses

Inflorescence morphology

The grasses include some of the most important food crops in the world, and inflorescence morphology is one of the major factors for controlling their yield. The dissection of genetic and molecular mechanisms that regulate inflorescence morphology is therefore of paramount importance. Grass inflorescences also have interesting unique features for developmental study, such as the spikelet and other structures not seen in the dicot models. Spikelet determinacy differs by species, for example, in wheat, the spikelet meristems (SMs) are indeterminate (Murai et al. 2002), whereas in maize the degree of SM determinacy is still an open question.

Maize forms two distinct types of inflorescences after the transition to flowering. The shoot apical meristem gives rise to the terminal tassel, which has long branches and develops the male flowers. The ears are derived from axillary shoot meristems, have a prominent axis with no long branches, and develop the female flowers. The inflorescence meristems (IMs) of the tassel and the ear each produce spikelet pair meristems (SPMs). Each SPM forms a short branch, bearing two SMs, which in turn produce a pair of floral meristems (FMs), though in the ear only one of these develops into a fertile flower (Fig. 1B). The interesting morphological differences between the ear and tassel have arisen during the domestication of maize, and remain of great interest to maize breeders.

In rice, the shoot apical and axillary meristems form identical inflorescences (Fig. 1A). Each IM produces primary branches in a spiral phyllotaxy, and these make secondary branches and SMs in a biased distichous phyllotaxy with a divergence angle of about 110° (Ikeda et al. 2004). Both primary and secondary branch meristems (BMs) in rice correspond to SPMs in maize inflorescences, from the viewpoint that they initiate SMs. The rice IM degenerates after making primary BMs (Fig. 1A, 'dp'), and the internodes of both primary and secondary branches elongate to form a panicle architecture, which looks very different from that of maize, though their structural components are essentially the same. In contrast to maize, each SM in rice produces only one fertile floret subtended by two pairs of small bracts called empty glumes and rudimentary glumes, as described in more detail below.

Genes that affect inflorescence development

Many developmental mutants that affect grass inflorescence and floral development have been reported, especially in maize (McSteen et al. 2000). Cloning of the corresponding genes has started to give us more powerful tools and ideas to understand grass inflorescence architecture. Since McSteen et al. (2000) described the maize mutants comprehensively, and similar reports of rice mutants have been published (Ikeda et al. 2004), we focus here on the recent progress in molecular characterization of the genes that control inflorescence architecture and development.

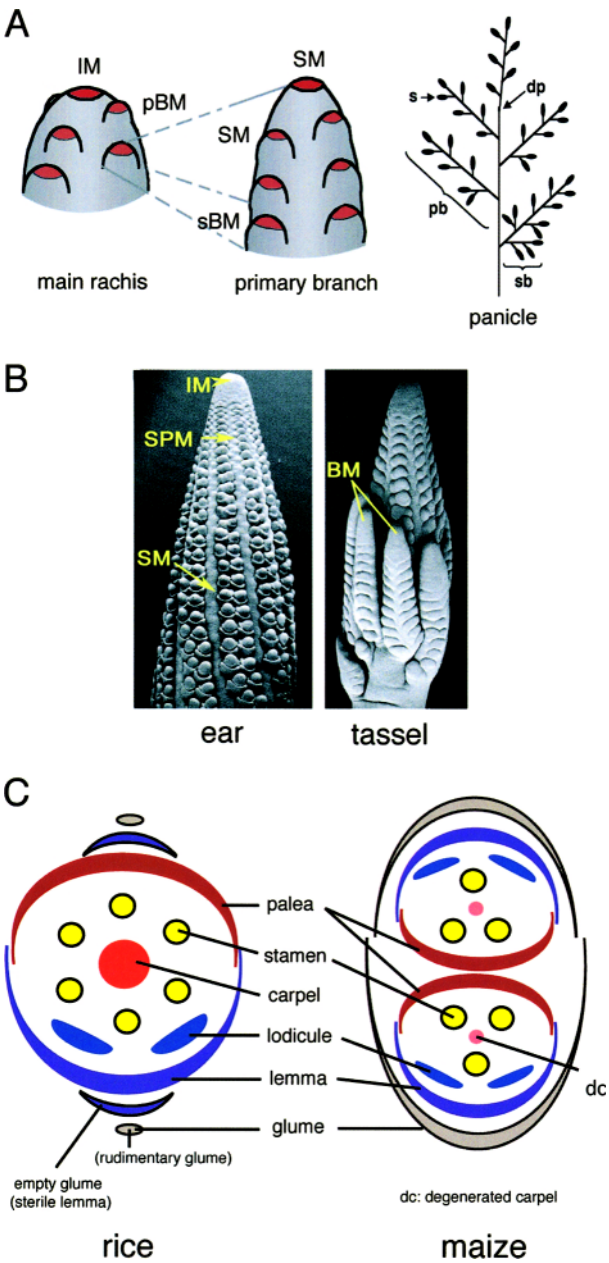

Fig. 1 (A) Rice inflorescence development. The inflorescence meristem (IM) initiates primary branch meristems (BMs) in a spiral phyllotaxy. Primary BMs initiate secondary BMs (sBM) and spikelet meristems (SMs) in a biased distichous phyllotaxy and terminate as an SM. Each meristem is colored in red. dp, degenerate point; s, spikelet; pb, primary branch; sb, secondary branch (modified after M. Komatsu et al. 2003, with permission). (B) Maize inflorescence development. The IM initiates files of spikelet pair meristems (SPMs). Each SPM then produces two SMs. In the tassel, the IM initiates several BMs first and then produces SPMs and SMs in the same way as in the ear. (C) Schematic models of rice and maizema spikelets (see text).

Inflorescence meristem development

The first step in inflorescence development is the transition from vegetative to reproductive state. The *Antirrhinum*

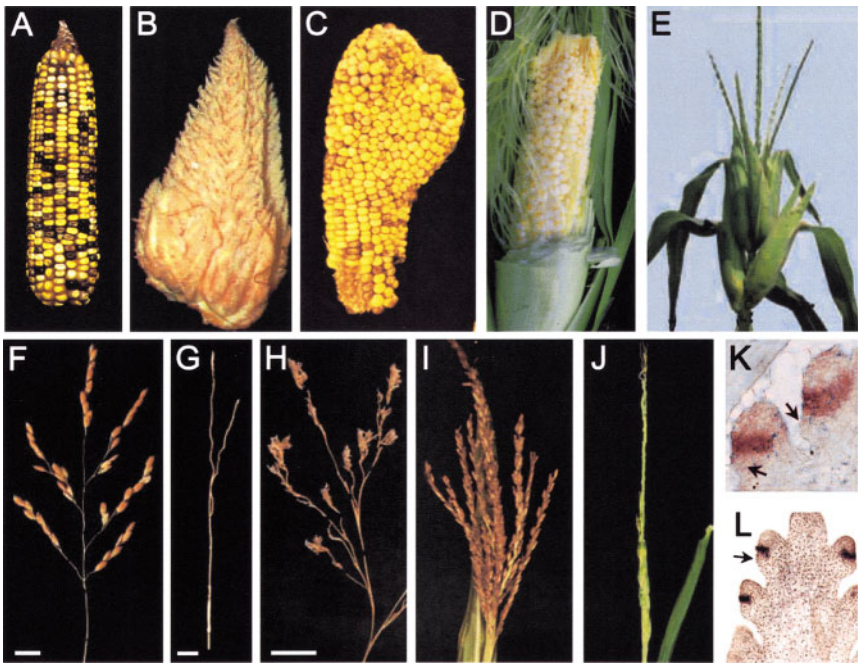

Fig. 2 Developmental mutants of maize and rice, and expression patterns of *FRIZZY PANICLE* (*FPZ*) and *BRANCHED SILKLESS1* (*BD1*). (A) Normal maize ear. (B) Ear of *bd1* (Chuck et al. 2002). (C) Ear of *fasciated ear2* (*fea2*). (D) Ear of *thick tassel dwarf1* (*td1*). (E) Tassel of a *zfl1;zfl2* double mutant plant, showing several 'tassel ears' (Bomblies et al. 2003). (F) Wild-type rice panicle (M. Komatsu et al. 2003). (G) Panicle of *lax panicle* (*lax*). (H) Close-up view of *fzp* panicle (M. Komatsu et al. 2003). (I) Normal maize tassel. (J) Tassel of *barren inflorescence2* (*bif2*) (McSteen and Hake 2001). (K) In situ hybridization showing the *FZP* expression pattern in a wild-type rice panicle (M. Komatsu et al. 2003); arrows indicate rudimentary glume primordial. (L) In situ hybridization showing the *BD1* expression pattern in a wild-type maize tassel (Chuck et al. 2002); the arrow indicates outer glume primordial. Scale bars in (F), (G) and (H) 1 cm. (B) and (L) are reproduced with permission from Chuck et al. (2002); Copyright 2002 AAAS. (E), (F), (H), (J) and (K) are reproduced with permission from the Company of Biologists Ltd. (G) is reproduced with permission from K. Komatsu et al. (2003); Copyright 2003 National Academy of Science, U.S.A.

FLORICAULA (*FLO*) and *Arabidopsis LEAFY* (*LFY*) genes (Coen et al. 1990, Weigel et al. 1992) act upstream in a transcriptional framework regulating this transition and the expression pattern of the floral homeotic ABC genes, as *flo* and *lfy* mutants show a conversion from flowers to leaf-like organs as well as abnormal flowers with altered organ identity (Coen and Meyerowitz 1991, Huala and Sussex 1992, Weigel and Meyerowitz 1994, Parcy et al. 1998). By using a reverse genetics approach, Bomblies et al. (2003) identify duplicate *FLO /LFY* homologs in maize, *ZEA FLO/LFY1* (*ZFL1*) and *ZEA FLO/LFY 2* (*ZFL2*). Analysis of *zfl1; zfl2* double mutants revealed that their function is largely conserved between maize and the dicots. Both genes are expressed in a pattern similar to *FLO* and *LFY* (Coen et al. 1990, Weigel et al. 1992), with an onset at the transition to flowering. They also have a localized expression pattern in SPMs, SMs and FMs, and, as the florets develop, they are expressed in developing floral organ primordia. Whereas single mutants show only very weak phenotypes, the *zfl1; zfl2* double mutant plants produce striking 'tassel ears'; branched reproductive structures bearing a female inflorescence enclosed by husk leaves (Fig. 2E). They also develop secondary ears in husk leaf axils at the base of the main ear, indicating that the transition from the vegetative to the reproductive phase occurs gradually, with vegetative characteristics being maintained after the onset of the reproductive phase.

In addition, *zfl1/ zfl2* mutants show an increased number of spikelets in the tassel and more rows of seeds in the ear. Interestingly, there is a quantitative correlation between these phenotypes and active *ZFL* copy number. In this context, it is worth mentioning that the maize inflorescence evolved from teosinte (Beadle 1980, Doebley 1992). In teosinte, seeds are invariably arranged in single alternating rows (Beadle 1939, Galinat and Naylor 1951), whereas maize shows a polystichious phyllotaxy with seeds arranged in 8–18 rows. Interestingly, both *ZFL* genes map close to quantitative trait loci (QTLs) controlling ear row number; *ZFL2* maps close to strong QTL on chromosome 2 and *ZFL1* to a weak QTL on chromosome 10 (Doebley 1992), implying a possibly role for those genes as being targets during domestication of modern maize lines (Bomblies et al. 2003).

Interestingly, the rice *FLO/LFY* ortholog (*RFL*) shows a divergent expression pattern to that of the maize *ZFL* genes, as it is expressed in epidermal cells of vegetative leaves as well as in the entire developing IM. However, *RFL* is not expressed in floral meristems, suggesting that it might function during vegetative development and not in floral organ patterning (Kyozuka et al. 1998). However, the *RFL* loss-of-function phenotype has to be identified in order to understand its role fully during inflorescence and floral development.

The increase in seed row number in maize might also be explained by modifications of the *CLAVATA* signaling pathway, analogous to the supernumery lateral organs that arise due to increased meristem size in *clavata* (*clv*) mutants of *Arabidopsis*. These mutants (*clv1*, *clv2* and *clv3*) over-accumulate stem cells in the shoot and flower meristems (Clark et al. 1993, Clark et al. 1995, Kayes and Clark 1998). The enlarged meris-

tems result in extra flower organs, club-shaped siliques, and enlarged inflorescence stems, which are often fasciated, indicating a role for the *CLV* genes in restricting the size of the stem cell population. The three CLV protein products probably constitute a single receptor–ligand complex (Clark et al. 1997, Fletcher et al. 1999, Jeong et al. 1999); CLV1 is a trans-membrane leucine-rich repeat (LRR) receptor-like kinase (Clark et al. 1997). CLV2 is structurally similar to CLV1 but lacks a cytoplasmic kinase domain (Jeong et al. 1999), and CLV3 is a small, secreted polypeptide (Rojo et al. 2002). The primary function of the *CLAVATA* signaling pathway is to restrict the expression domain of the stem cell-promoting homeobox gene *WUSCHEL* (*WUS*).

The maize *FASCIATED EAR2* (*FEA2*) gene encodes a *CLV2* homolog, providing the first evidence that the *CLAVATA* signaling pathway is functionally conserved in monocot species. *fea2* mutants plants exhibit severely enlarged inflorescence meristems and an increase in seed row number (Fig. 2C). SPMs, SMs and FMs are also frequently enlarged, with the latter occasionally producing additional floral organs, indicating that FEA2, like CLV2, acts to restrict stem cell proliferation within inflorescence apical and axillary meristems.

Further evidence for the conservation of the *CLAVATA* signaling pathway in maize comes from the cloning of the maize *THICK TASSEL DWARF1* (*TD1*) gene, which encodes an LRR receptor-like kinase with homology to CLV1 (P. Bommert et al. submitted). *td1* mutants also exhibit strong fasciation in the female IM, leading to a dramatic increase in ear row number (Fig. 2D) and, as in *fea2* mutants, SPMs, SMs and FMs are enlarged and the FMs produce additional floral organs. The spikelet density in tassels of *td1* mutants is also significantly increased. Severe fasciation of the male IM, however, has not been observed in *fea2* or *td1* mutants, perhaps due to genetic redundancy.

Positional cloning of the rice *FLORAL ORGAN NUMBER1* (*FON1*) gene showed that it also encodes a *CLV1* homolog (Suzaki et al. 2004). *fon1* mutants share phenotypic similarities with *td1* mutants, most strikingly the formation of additional floral organs. However, the size of the IM in *fon1* mutants is not significantly increased but, similarly to the situation in *td1* mutant tassels, *fon1* mutants produce more primary branches. The severity of *clv*-related mutants specifically on the maize ear strengthens the view that it reflects a unique structure, with a distinct genetic program from the tassel, possibly as a result of the intense selective pressure during domestication.

Potential differences between *CLV* signaling in monocots and dicots were revealed by expression studies. Unlike *CLV1*, which is expressed predominantly in the L3 layer of FMs (Clark et al. 1997), *TD1* and *FON1* are expressed in all three layers of the FM as well as in floral organ primordia. In addition, the fact that *TD1* and *FON1* transcripts can be detected in all shoot meristems, but the mutants do not have phenotypic effects in the vegetative shoot meristem, provides additional support for the existence of functional redundant factors, masking the effect of the *td1* and *fon1* mutations during vegetative development.

As was true for the *ZFL* genes, both *FEA2* and *TD1* map to QTLs controlling inflorescence traits such as seed row number. *TD1* also maps to QTLs controlling tassel spikelet density and plant height (Doebley 1992, Veldboom et al. 1994, Taguchi-Shiobara et al. 2001, P. Bommert et al. submitted). As mentioned previously, given that the increase of seed row number in maize is one of the major acquired domestication characters, we hypothesize that changes in inflorescence architecture result from changes in IM size by modification of the *CLAVATA* signaling pathway.

The functional characterization of members of the *CLAVATA* signaling pathway and *LEAFY* homologs implies that fundamental mechanisms such as regulation of meristem size, flowering time and inflorescence development are conserved between dicot and monocot species. Their association with QTLs for crop yield is a unique finding arising from the studies in the grasses, and awaits confirmation based on transgenic or other molecular approaches such as association analysis.

Spikelet pair and branch meristem development

There is incredible diversity in inflorescence architectures in the grasses. Kellogg (2000) proposed a dynamic model to describe this complex morphological variation. In this model, developmental switches account for the decisions of axes to terminate in spikelets or to continue to be (lateral) meristems, the number of lateral meristems produced, the extent of internode or bract elongation and the phyllotaxy. The diversity in inflorescence architectures can be explained by differential action of these developmental switches, which are controlled by the spatial, temporal and quantitative variation of gene expression. Below we describe the molecular analyses of genes that give support to this model.

BARREN INFLORESCENCE2 (*BIF2*) and *BARREN STALK1* (*BA1*) in maize, and *LAX PANICLE* (*LAX*) in rice control early developmental switches involved in the initiation of axillary meristems. *bif2* mutant tassels make fewer or no branches and spikelets, and the ears have fewer or no spikelets (McSteen and Hake 2001) (Fig. 2J). Since the BMs, SPMs, SMs and FMs in weak *bif2* mutants are all defective, it appears that *BIF2* is required for initiation and maintenance of all types of axillary meristems. *ba1* mutants lack vegetative branches and ears and have unbranched tassels also lacking spikelets (Gallavotti et al. 2004). In rice *lax* mutants, the number of primary branches and spikelets is also strongly reduced (Komatsu et al. 2001) (Fig. 2G). These mutant phenotypes indicate that both *BA1* and *LAX* are required to initiate inflorescence axillary meristems. They encode orthologous basic helix–loop–helix transcription factors, and are expressed at the boundaries between pre-existing and newly initiated meristems, such as the shoot apical and axillary meristems, IM and primary BMs, primary BMs and SMs, SPMs and SMs, upper FMs and lower

FMs, and so on (K. Komatsu et al. 2003, Gallavotti et al. 2004). These localized expression patterns support the functions of *LAX* and *BA1* specifically in the production of axillary meristems, and suggest that these gene functions are strongly conserved between rice and maize.

Very few mutants that affect inflorescence branch phyllotaxy have been isolated; *aberrant panicle organization1* (*apo1*) in rice and *abphyl1* (*abph1*) and *zfl* in maize are perhaps the only examples. *APO1* regulates rice inflorescence meristem organization, and the mutants have defective primary branch phyllotaxy (Ikeda et al. 2000, Ikeda et al. 2002). Tassel branch phyllotaxy is also abnormal in maize *abph1* mutants, where they are generated in a decussate pattern (Jackson and Hake 1999). *ABPH1* encodes a cytokinin-inducible response regulator and also regulates leaf phyllotaxy in the vegetative phase (Giulini et al. 2004).

Spikelet meristem development

After axillary meristems are induced by genes such as *BIF2*, *BA1* and *LAX*, they acquire new identities. *FRIZZY PANICLE* (*FZP*) in rice and *BRANCHED SILKLESS1* (*BD1*) in maize function to regulate meristem identity at the transition from SMs to FMs (Colombo et al. 1998, Chuck et al. 2002, M. Komatsu et al. 2003) (Fig. 2B, H). The fact that *fzp* and *bd1* mutants produce branching structures without making flowers indicates that these genes are required to regulate the determinacy of SMs and to establish the identity of FMs. *FZP* and *BD1* are orthologs, and encode members of the ethylene-responsive element-binding factor class of transcription factors. They are expressed in analogous patterns at the junction of SMs and rudimentary glumes in rice, and SMs and inner/outer glumes in maize (Fig. 2K, L). These studies reiterate the point that some genes that regulate inflorescence architecture in rice and maize are strongly conserved in function and expression pattern.

Other genes regulating SM determinacy include the maize *REVERSED GERM ORIENTATION1* (*RGO1*), *INDETERMINATE SPIKELET1* (*IDS1*) and *INDETERMINATE FLORAL APEX1* (*IFA1*) genes (Chuck et al. 1998, Laudencia-Chingcuanco and Hake 2002, Kaplinsky and Freeling 2003). In these mutants, the SMs become more indeterminate, and produce extra flowers. *rgo1* mutants show non-allelic non-complementation and have a synergistic double mutant phenotype with *ids1* mutants, but not with *ifa1* mutants. On the other hand, *ids1* and *ifa1* mutants have a synergistic interaction. These results suggest that *RGO1* and *IDS1* interact closely, such as in the same complex, whereas *IFA1* has a distinctive function and interacts with *IDS1* but not with *RGO1.*

The degree of SPM and SM determinacy is one of the characteristic variables in grass inflorescence architecture, and differs significantly between rice and maize, as described above. There are two hypotheses to explain the developmental origins of the SMs and FMs: the conversion hypothesis and the lateral branching hypothesis. In the conversion hypothesis, the SM first initiates an FM laterally, and then converts into the second FM (Irish 1997a, Irish 1997b, Irish 1998). In the lateral branching hypothesis, both FMs are lateral products of the SM. In this case, the SM should still be present, though it is not normally visible in maize (Chuck et al. 1998). This problem is controversial (Irish 1997a, Irish 1997b, Irish 1998, Chuck et al. 1998, Cacharron et al. 1999, Kaplinsky and Freeling 2003); however, the analysis of *rgo1* mutants supports the conversion hypothesis since the *ids1 rgo1* double mutant phenotype cannot be explained by the lateral branching hypothesis (Kaplinsky and Freeling 2003).

There are more obvious mutants affected in spikelet determinacy in maize than in rice, which may be due to the different nature of determinacy in the maize inflorescence architecture. On the other hand, rice may be useful to identify mutants that have a loss of indeterminacy in BMs.

Comparative studies

Clearly more genes and mutants involved in inflorescence architecture need to be identified to understand this important developmental and agronomic process, which is one of the most divergent characters in the grasses. Comparative analyses are also useful to understand the molecular basis of variation in inflorescence morphology. Some fundamental processes are likely to be conserved, for example the analyses of *BD1* and *FZP* indicate that the genetic control of spikelet determinacy is similar in rice, sorghum and maize (Chuck et al. 2002, M. Komatsu et al. 2003). Similarly the analyses of *BA1* and *LAX* suggest that gene functions are conserved in axillary meristem initation. However, there are also important differences between rice and maize. The observation that the *bd1* tassel initiates FMs and fertile flowers, whereas *bd1* ears or *fzp* inflorescences do not, suggests the existence of tassel-specific factors contributing to genetic redundancy in maize. The comparison between *bd1* and *fzp* phenotypes also confirms that the 'rudimentary glumes' in rice are homologous to the glumes in other grasses, whereas the 'empty glumes' correspond to sterile lemmas and subtending sterile florets (Fig. 1C). *ba1* and *lax* mutants also show interesting differences. For example, *lax* mutations have little effect on the initiation of vegetative axillary meristems, while *ba1* mutants do not produce any vegetative axillary structures. Molecularly, this difference might be controlled by *SMALL PANICLE*, a partner of *LAX* which acts in the vegetative phase to make axillary shoot meristems (K. Komatsu et al. 2003). Clearly, the comparative analyses are extremely powerful, and should be extended to include other members of the grasses.

The combination of phylogenetic and developmental information should allow us to understand the genetic regulation of phenotypic change over evolutionary time. Doust and Kellogg (2002) presented an excellent example of this in the *Paniceae*, a group that includes several millets and is a sister clade of maize and sorghum in the Panicoid linage. They explained the variation of inflorescence morphology by a relatively small number of characteristics, including the number of

BMs, the orders of branching, the extent of elongation of each axis, and bristle (slender sterile branch) initiation. The combination of phylogenetic, devolpmental and gene expression analyses also provides clues about the impact of developmental genes on evolution. For example, expression studies of *LEAFY HULL STERILE1* (*LHS1*), a rice MADS-box gene conserved in many grasses (Jeon et al. 2000, Malcomber and Kellogg 2004), showed that its expression pattern is also conserved in several grass species and suggest that it might function as a selector gene to specify the upper floret in some species. An additional tool to investigate the genetic basis of morphological diversity in grasses in which there are few classical mutants is QTL analysis. Doust et al. (2004) showed that inflorescence characteristics that differentiate two millet species, such as primary branch number, primary branch density and spikelet number, are each controlled by a small number of loci. Interestingly, inflorescence architecture genes identified from maize map to some of these QTLs. For example, *ZFL1* maps close to a QTL for primary branch number and density. These results offer hope that it will be possible to identify the genes responsible for quantitative variation in inflorescence morphology in diverse grass species.

Flower Development in the Grasses

Spikelets and florets—structural units characteristic of grass inflorescences

First, we describe the structure of rice spikelets and the organs contained within the spikelets. The spikelet contains a single functional floret, which is bisexual and consists of a pistil, six stamens, two lodicules, a palea and a lemma (Fig. 1C). Outside the lemma, there are two empty glumes (or sterile lemma), which are considered to be vestiges of two lower florets. Then, two rudimentary glumes, which are highly reduced, subtend three florets: one fertile and two strongly reduced and sterile ones.

In maize spikelets, two florets are initiated, but only the upper one is functional in the ear spikelets. Male and female florets initiate one pistil, three stamens, two lodicules, a palea and a lemma (Fig. 1C). Carpel primordia in male florets and stamen primordia in female florets initiate but abort during early stages of flower development to produce unisexual florets.

The lodicule, palea and lemma are organs characteristic of the grass family. Lodicules are considered to be homologous to petals in eudicots, and play a role in opening the florets. The palea and lemma structures are thought to be similar to a prophyll and a bract, respectively (Kellogg 2001). A prophyll is a leaf formed at the base of a shoot, while a bract is a leaf-like structure associated with an inflorescence or flower. In this review, we refer to the regions where lodicules, stamens and a pistil develop in rice and maize as whorl 2, whorl 3 and whorl 4, respectively, in line with the definition of regions in *Arabidopsis*. [Because the identities of petal and lemma are controversial at present (see below), we avoid defining whorl 1 here.]

ABC model and MADS-box genes in grasses

Molecular and genetic studies in two model eudicots, *Arabidopsis* and *Antirrhinum*, have led to establishment of the ABC model for the determination of floral organ identities (Coen and Meyerowitz 1991, Ng and Yanofsky 2001, Lohmann and Weigel 2002). This model proposes that each class of floral homeotic gene, termed A, B and C, works in two adjacent whorls, and combinatorial activities of these genes specify four types of floral organs: sepal, petal, stamen and carpel. In *Arabidopsis*, sepals are specified by the A class genes *APETALA1* (*AP1*) and *APETALA2* (*AP2*), and petals are specified by a combination of the class A genes and the class B genes *APETALA3* (*AP3*) and *PISTILLATA* (*PI*). Stamens are specified by class B genes together with a class C gene, *AGAMOUS* (*AG*). Carpels are specified by the class C gene alone. The functions of the class A and class C genes are mutually antagonistic such that loss of the class A gene results in C activity in all four whorls, and vice versa. These homeotic genes encode MADS domain proteins that function as transcriptional regulators, except for *AP2*, which encodes an AP2 domain protein. The MADS-box genes are expressed in restricted domains in floral primordia, where they function.

ABC class MADS-box genes have been isolated from several grass species, such as rice, maize, wheat and barley, by homology cloning (Schmidt et al. 1993, Chung et al. 1995, Kang et al. 1998, Mena et al. 1995, Theissen et al. 1995, Ambrose et al. 2000, Kyozuka et al. 2000, Münster et al. 2001, Meguro et al. 2002, Lee et al. 2003b, Murai et al. 2003, Nagasawa et al. 2003, Hama et al. 2004). The spatial expression patterns of these genes are almost similar to the pattern that is expected from the ABC model (Schmidt et al. 1993, Chung et al. 1995, Ambrose et al. 2000, Kyozuka et al. 2000, Münster et al. 2001, Nagasawa et al. 2003, Hama et al. 2004). However, there has been little genetic analysis using mutants of the corresponding MADS genes, except for a few studies (Mena et al. 1996, Ambrose et al. 2000, Nagasawa et al. 2003).

Class B gene function in grasses

Two studies using floral homeotic mutants in rice and maize have shown that the function of class B genes is conserved in grasses. In *silky1* (*si1*) mutants of maize, stamens are replaced by carpels, and lodicules are replaced by bracts that resemble palea/lemma (Ambrose et al. 2000). Similarly, the flowers in the *superwoman1* (*spw1*) mutant of rice show a homeotic transformation of stamens and lodicules into carpels and palea-like organs, respectively (Nagasawa et al. 2003). These homeotic mutations are similar to those caused by mutations in class B genes in *Arabidopsis* and *Antirrhinum* (Coen and Meyerowitz 1991). Molecular cloning has revealed that *SI1* and *SPW1* encode AP3-like proteins in maize and rice, respectively. *SI1* and *SPW1* are expressed in the primordia of stamens and lodicules from the initiation of development of both organs. Whipple et al. (2004) also showed the conserva-

tion of the B-class gene function at the protein level between *Arabidopsis* and maize.

These results clearly indicate that the B function that specifies the identity of petal/lodicule and stamen is conserved in grass flower development. A homeotic transformation of stamens to pistil-like structures, called 'pistillody', has been found in alloplasmic lines of *Triticum aestivum* (bread wheat), which have the cytoplasm of a wild relative, *Aegilops crassa* (Murai et al. 2002). Although the gene responsible for this mutation has not yet been identified, *WPI1*, an ortholog of *PI* in wheat that is normally expressed in stamen primordia, is not expressed in the organs produced in whorl 3 of the pistillody line (Hama et al. 2004). Together with the analysis of maize *PI* orthologs (Whipple et al. 2004), this work also suggests that the two class B genes are responsible for stamen development in the grasses, as is the case in dicots.

The rice genome contains two *PI* orthologs, *OsMADS2* and *OsMADS4*, although it has only one *AP3* ortholog. Northern blot analyses have shown that *OsMADS4* is expressed in whorl 2 and whorl 3 organs, whereas *OsMADS2* is expressed in the inner three whorls (Lee et al. 2003a). In transgenic plants where *OsMADS4* expression is reduced by antisense suppression, lodicules are changed to palea/lemma-like structures and stamens are changed to carpel-like structures, suggesting functional conservation of the *PI* ortholog in rice compared with *Arabidopsis* (Kang et al. 1998). In contrast, silencing of *OsMADS2* by RNA inerference (RNAi) affects only the identity of lodicules, whereas stamen development is normal (Prasad and Vijayraghavan 2003). In *Arabidopsis*, AP3 and PI form heterodimers and are thought to act as a transcriptional regulator (Goto and Meyerowitz 1994). The rice OsMADS16 protein interacts with OsMADS4 in the yeast two-hybrid system, but not with OsMADS2 (Lee et al. 2003a). It is therefore plausible that dimer formation of OsMADS2 and OsMADS4 with OsMADS16 may contribute to the difference in the phenotypes observed in the suppression lines for each gene. The expression of *OsMADS4* is enhanced in the transgenic plants that ectopically express *OsMADS16*, suggesting the partial conservation of autoregulation of class B genes in rice, similar to *AP3* and *PI* in *Arabidopsis* (Jack et al. 1992). In contrast, *OsMADS2* is not up-regulated by ectopic *OsMADS16*. Taken together, these functional differences in *OsMADS2* and *OsMADS4* suggest diversification of gene function after duplication of the *PI* ortholog in rice.

Carpel specification in grasses

In contrast to class B genes, the function of class C genes seems to have diversified in grasses. In *Arabidopsis*, *AG* specifies carpels and negatively regulates the expression of class A genes (Coen and Meyerowitz 1991, reviewed in Ng and Yanofsky 2001, Lohmann and Weigel 2002). Because carpel primordia consume the floral meristem, *AG* also positively regulates determinacy of the floral meristem. Loss-of-function mutants of *AG* produce flowers in which stamens are replaced by petals in whorl 3, and *ag* flowers (sepal–petal–petal) are produced indeterminately in whorl 4.

Maize has two class C genes, *ZAG1* and *ZMM2*, which are closely related to each other, and *ZAG1* is expressed in whorl 3 and whorl 4 like *Arabidopsis AG* (Schmidt et al. 1993, Theissen et al. 1995). A loss-of-function mutant of *ZAG1*, however, shows no defects in organ identity, although floral determinacy is lost (Mena et al. 1996). It is hypothesized that the effect of *zag1* mutation on carpel identity is masked by the redundant functions of *ZMM2*. Alternatively, the two class C genes might have diversified with separate functions: *ZMM2* may be responsible for organ identity, whereas *ZAG1* may be involved in the regulation of floral determinacy. In rice, antisense suppression of the *AG* ortholog *OsMADS3* produces flowers with abnormal carpels but does not give rise to a clear homeotic change in the carpels (Kang et al. 1998).

The dilemma about regulation of carpel identity arising from these results is likely to be explained in large part by the isolation of the *DROOPING LEAF* (*DL*) gene, which has been shown to regulate carpel specification in rice (Yamaguchi et al. 2004). The *dl* mutant was isolated initially as a mutant in which the leaves did not stand erect as in normal rice, but instead drooped. The floral homeotic phenotypes, in which carpels are replaced by stamens, were subsequently identified. This floral defect is always associated with the drooping leaf phenotype. Genetic analysis revealed that mutations that cause a drooping phenotype alone are allelic to mutations that cause both floral homeotic and drooping phenotypes (Nagasawa et al. 2003).

In flowers of severe *dl* mutants, carpels are homeotically and completely converted into stamens (Nagasawa et al. 2003, Yamaguchi et al. 2004). Defects in the flower are restricted to whorl 4. This homeotic transformation in rice *dl* strongly contrasts with the usual floral homeotic mutants of *Arabidopsis*, in which defects always occur in two adjacent whorls. Molecular cloning of *DL* revealed that it encodes a YABBY protein, a putative transcription factor that is specific to plants (Yamaguchi et al. 2004). *DL* is expressed in the presumptive region (the carpel anlagen) from which the carpel primordia initiate. Shortly after this expression, the carpel primordia begin to form and *DL* continues to be expressed in the carpel primordia. Thus, phenotype and expression analyses both indicate that *DL* is necessary for carpel specification. This is the first finding that a *YABBY* gene controls organ specification in the flower, similar to the MADS-box genes.

DL has an additional function as it is required for the normal development of rice leaves (Nagasawa et al. 2003, Yamaguchi et al. 2004). The drooping leaf is caused by a failure in formation of the midrib—a strong structure that enables the leaves to stand erect. *DL* is expressed in the central region of leaf primordia, and seems to promote cell proliferation along the adaxial–abaxial axis (Yamaguchi et al. 2004). This cell proliferation may be required to produce a sufficient number of cells for construction of the midrib structure. This hypothesis is supported by constitutive expression of *DL*. In these plants, the

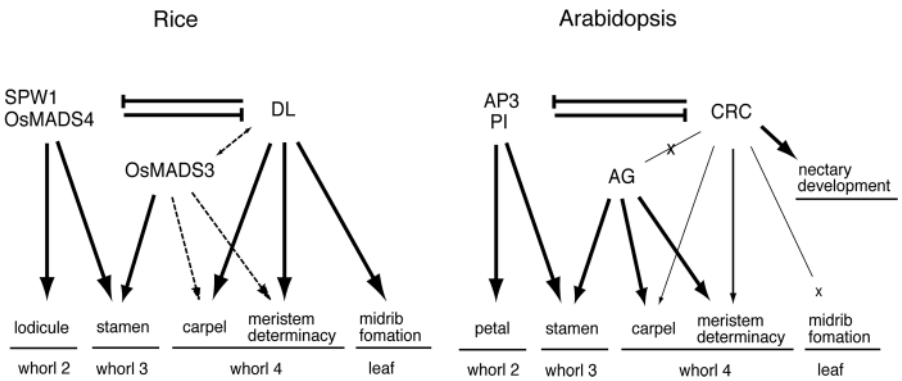

Fig. 3 Comparison of genetic frameworks for floral organ identity and midrib formation in rice and *Arabidopsis*. Unbroken lines show the gene functions that have been revealed so far; dashed lines show actions that remain to be elucidated. Thin arrows mean a weak contribution of gene function; 'Xs' indicate that the gene has no function. Note that rice flowers do not produce a nectary. *OsMADS2* is not included in this model because suppression of this gene does not cause any homeotic changes.

lateral regions, as well as the central region, of the leaves are thickened by cell proliferation along the adaxial–abaxial axis. Subsequently, midrib-like structures are formed in the lateral regions. Thus, it can be concluded that the normal function of *DL* is to regulate formation of the midrib by promoting specific cell proliferation in the central region of the leaf primordia.

Mutants that have defects in both carpel identity and midrib formation have also been reported in other grass species, such as *Pennisetum americanum* (pearl millet) and *Panicum aestivum* (Rao et al. 1988, Fladung et al. 1991). The phenotypes of these mutants are similar to those of the rice *dl* mutants. *DL* orthologs from maize and barley are also expressed both in carpel primordia and in the central region of leaf primordia, with expression patterns similar to those of *DL* (Ishikawa and Y. Hirano, in preparation). These results suggest that the functions of *DL* that regulate carpel specification and midrib development are conserved in the grass family. *DL* is most closely related to the *CRABS CLAW* (*CRC*) gene from the *Arabidopsis YABBY* gene family (Bowman and Smyth 1999). The *crc* mutant has partial defects in carpel identity, but shows no homeotic changes in the flower and no defects in the leaves. Therefore, *DL* may have been recruited to acquire novel critical functions to specify carpel identity and to form the midrib during evolution of the grasses (Fig. 3).

In *dl* mutants, carpels are replaced by ectopic stamens, suggesting that class B genes are ectopically expressed in whorl 4. Conversely, stamens are replaced by ectopic carpels in mutants of the *spw1* mutants, suggesting that *DL* is expressed in whorl 3. These predictions have been confirmed by the spatial expression pattern of both genes in the mutants, i.e. *DL* and *SPW1* are ectopically expressed in whorl 3 of *spw1* and in whorl 4 of *dl*, respectively (Nagasawa et al. 2003, Yamaguchi et al. 2004). These results indicate that *DL* and *SPW1* antagonistically regulate each others' expression. The ectopic expression of *OsMADS16* (*SPW1*) causes a transformation of carpels into stamens, or the loss of carpel development in whorl 4 (Lee et al. 2003a). This result also supports the above idea that *DL* is repressed by the ectopic expression of *OsMADS16* in whorl 4 of the transgenic lines. The mutual negative regulation of *CRC* and class B genes in *Arabidopsis* has been also indicated directly or inferred by analyzing mutants (Alvarez and Smyth 1999, Bowman and Smyth 1999). A comparison of the genes that specify the floral organs in rice and *Arabidopsis* is shown schematically in Fig. 3.

Antisense suppression and ectopic expression of *OsMADS3* indicate that negative regulation of class A genes and stamen specification in combination with class B genes are also conserved in the rice class C genes (Kang et al. 1998, Kyozuka and Shimamoto 2002). The rice genome has another *AG* ortholog in addition to *OsMADS3* (T. Yamaguchi and Y. Hirano, in preparation). Therefore, to reveal the whole contribution of class C genes to carpel specification in rice, a knockout of both class C genes will be required.

Identity of lodicules and the palea/lemma

The lodicule, a floral organ that is characteristic of grass flowers, has been regarded from anatomical studies as being homologous to petals in eudicots. Recent molecular genetic studies confirm this idea. Petal identity is determined by the combinatorial functions of class A and class B genes in *Arabidopsis*. Likewise, lodicules are replaced by other organs in the class B mutants in grasses, *si1* of maize and *spw1* of rice, and both *SPW1* and *SI1* are expressed in lodicule primordia in wild-type plants (Ambrose et al. 2000, Nagasawa et al. 2003). Other class B genes such as *OsMADS2* and *OsMADS4* are also expressed in the lodicules, together with the class A gene *RAP1A* (*OsMADS15*) (Kyozuka et al. 2000, Lee et al. 2003a). In addition, ectopic expression of the class C gene *OsMADS3* results in the transformation of lodicules into stamen-like structures or into chimeric organs composed of lodicules and stamens in whorl 2. This phenotypic alteration is similar to the transformation of petals into staminoid petals in transgenic *Arabidopsis* plants that ectopically express *AG* (Mizukami and Ma 1992). Taken together, these observations support the idea that lodicules in grasses are homologous to petals in eudicots.

In contrast, the identities of the palea and lemma are controversial (Goto et al. 2001). Comparative morphological studies suggest that the palea is a prophyll-like structure and the lemma is a bract-like structure (reviewed in Kellogg 2001). Genetic analysis, however, has shown that lodicules are transformed into palea/lemma-like structures in *si1* and *spw1* mutants in maize and rice, respectively, as described above

(Ambrose et al. 2000, Nagasawa et al. 2003). Ambrose and colleagues argue that this homeotic transformation implies that the palea and lemma correspond to sepals in grasses, inferred from the analogy of the class B mutants in *Arabidopsis* and *Antirrhinum* (Ambrose et al. 2000, Ng and Yanofsky 2001). Nagasawa et al. (2003) proposed the alternative possibility that the organs formed in whorl 2 of *spw1* may not correspond to palea, but instead correspond to sepal-like structures that do not develop in normal flowers but arise only in the mutants owing to the removal of class B activity (Nagasawa et al. 2003). Unlike ectopic expression of *AG*, which affects the identities of both sepals and petals (Mizukami and Ma 1992), ectopic expression of *OsMADS3* shows no morphological alterations in the palea and lemma, whereas lodicules are transformed into stamen-like structures (Kyozuka and Shimamoto 2002). This finding supports the idea that the palea and lemma in grasses are distinct from sepals in eudicots. Thus, the identities of the palea and lemma remain unsolved. To clarify the situation, it will be necessary to identify mutants and the corresponding genes in which the structure of palea/lemma is disrupted.

SEPALLATA (SEP) genes in grasses

Because the *SEP* genes have diversified in the grass family—for example, there are at least five *SEP* genes present in rice and eight in maize (Lee et al. 2003b, Malcomber and Kellogg 2004)—their function has not been elucidated in detail so far. The only *SEP* genes that have been partially characterized are the *LEAFY HULL STERILE1* (*LHS1*) gene in rice and its orthologs. Inhibition of *OsMADS1* gives rise to floral phenotypes similar to those of the *lhs1* mutants, and molecular analysis has shown that the mutation in *lhs1* is caused by an amino acid substitution in *OsMADS1* (Jeon et al. 2000). Both the *lhs1* mutant and transgenic rice expressing a putative dominant-negative form of *OsMADS1* result in alterations in floret morphology that vary from floret to floret. The palea and lemma are leafy and elongated, lodicules become leafy palea/lemma-like structures, and stamens are reduced in number. In some cases, the florets produce extra florets, including extreme florets in which palea/lemma-like structures are repeated several times (Jeon et al. 2000). *LHS1* is expressed in the floral meristems at an early stage and in the primordia of palea and lemma. Ectopic expression of *OsMADS1* results in the transformation of empty glumes (sterile lemma) into palea/lemma-like organs (Jeon et al. 2000, Prasad et al. 2001) (Note that here we use the term 'empty glume' in place of the terms 'glumes', 'rudimentary glumes' and 'outer glumes' used in the original publications.) In addition, inner floral organs, especially carpels, are reduced or aborted in the *OsMADS1*-ectopic expression lines, suggesting an increase in floral meristem determinacy. Thus, *LHS1* seems to regulate, at the least, palea/lemma identity and determinacy of the floral meristem in rice.

In maize, the *LHS1* orthologs *ZMM8* and *ZMM14* are expressed throughout in the meristems of the upper florets, as is rice *LHS1* (Cacharron et al. 1999). Unlike in rice, however, both genes are expressed in all floral organs of the upper florets in maize. Interestingly, transcripts of both genes are not detected either in the meristems or in any floral organs of the lower florets. Spatial expression patterns of the *LHS1* orthologs in developing florets have been examined in several grass species that are phylogenetically disparate (Malcomber and Kellogg 2004). Although the expression patterns are heterogeneous among species, the authors propose a hypothesis for the general function of the *LHS1* genes; to specify determinacy of the spikelet meristems and to determine the identity of the palea and lemma. To confirm this hypothesis, genetic analysis may be required.

Concluding Remarks

Studies on the genetic control of development in rice and maize are rapidly growing. Elucidating the genetic control of these plants is important not only for our fundamental understanding of grass developmental biology per se but also for aiding evolutionary studies of monocots, angiosperms or seed plants. In addition, the grass family contains many argronomically and economically important crops, and characters of inflorescences and flowers are closely associated with traits for grain yield. Thus, the outcomes of these studies may contribute to applied fields by improving crops.

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