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Grass Meristems I: Shoot Apical Meristem Maintenance, Axillary Meristem Determinacy and the Floral Transition

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The vegetative and reproductive shoot architectures displayed by members of the grass family are critical to reproductive success, and thus agronomic yield. Variation in shoot architecture is explained by the maintenance, activity and determinacy of meristems, pools of pluripotent stem cells responsible for post-embryonic plant growth. This review summarizes recent progress in understanding the major properties of grass shoot meristems, focusing on vegetative phase meristems and the floral transition, primarily in rice and maize. Major areas of interest include: the control of meristem homeostasis by the CLAVATA–WUSCHEL pathway and by hormones such as cytokinin; the initiation of axillary meristems and the control of axillary meristem dormancy; and the environmental and endogenous cues that regulate flowering time. In an accompanying paper, Tanaka et al. review subsequent stages of shoot development, including current knowledge of reproductive meristem determinacy and the fate transitions associated with these meristems.

Keywords: Floral transition • Grass • Maize • Meristem maintenance • Rice • Tillering.

Abbreviations: AM, axillary meristem; CLE, CLAVATA3 (CLV3)/ENDOSPERM SURROUNDING REGION (ESR); CLV, CLAVATA; CZ, central zone; FM, floral (flower) meristem; IM, inflorescence meristem; LRR, leucine-rich repeat; OC, organizing center; PZ, peripheral zone; P0, plastochron zero; QTL, quantitative trait locus; RAM, root apical meristem; RR, response regulator; SAM, shoot apical meristem; SL, strigonolactone; ta-siRNA, *trans*-acting small interfering RNA; WOX, WUSCHEL-related homeobox; WUS, WUSCHEL.

Introduction

All post-embryonic plant tissues are derived from meristems, structures that harbor pluripotent stem cells. Shoot structures are created by the shoot apical meristem (SAM), while the root apical meristem (RAM) gives rise to root structures. Shoot development occurs in repeating modules called phytomers, consisting of a leaf, an axillary meristem (AM) and an internode. Plant architecture is largely dictated by the activity and determinacy of the SAM and AMs. For example, the shape of the plant can be determined by spatial and temporal patterns of leaf initiation from the SAM, and by elaboration of secondary shoots from AMs. This review will focus on the genetic networks controlling meristem maintenance and organization during the vegetative phase. It will also cover another major process in meristem biology: the transition of the SAM from vegetative to reproductive fate. The determinacy and fate transitions of reproductive meristems are reviewed in an accompanying paper by Tanaka et al. (2013).

Stem cells in the SAM are continuously self-maintained, and supply cells that will differentiate into lateral organs. The stem cells are located in the upper region of the central zone (CZ) of the meristem, in which cells divide slowly. The progeny produced from the division of the stem cells are used to replenish the stem cells themselves and are also displaced into the peripheral zone (PZ), where they start to divide more rapidly and lateral organs are initiated. Stem cell maintenance is achieved by the balance between self-replacement and organ initiation. The elucidation of the molecular mechanisms of meristem function, including stem cell maintenance, is currently a major area of interest in plant development.

WUS–CLV Negative Feedback Loop in Arabidopsis

In Arabidopsis, the CLAVATA (CLV)–WUSCHEL (WUS) negative feedback loop is a major genetic mechanism to maintain stem cell populations in the meristem (Brand et al. 2000, Schoof et al. 2000; for reviews, see Ha et al. 2010, Aichinger et al. 2012). Mutations in the *CLV* genes, such as *CLV1*, *2* and *3*, cause enlargement of the meristem by an overaccumulation of stem cells, whereas mutation in the *WUS* gene results in premature termination of the meristem. Thus, CLVs and WUS are negative and positive regulators for stem cell maintenance, respectively (**Fig. 1A**). *CLV3* encodes a small protein containing the conserved CLE [CLAVATA3 (CLV3)/ENDOSPERM SURROUNDING

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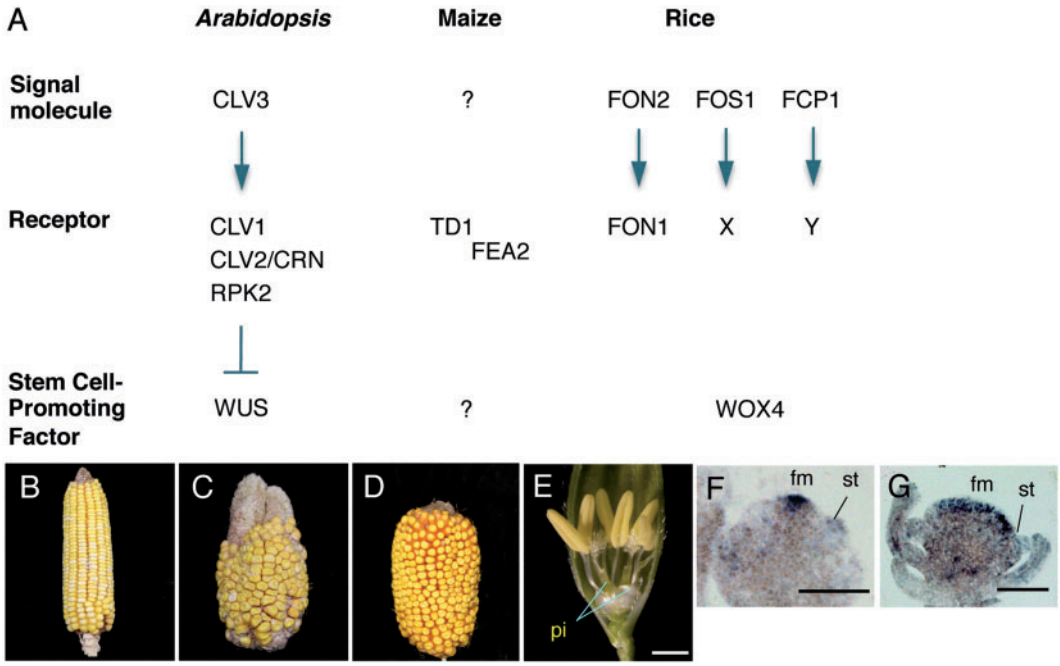

Fig. 1 Genes involved in stem cell maintenance. (A) Models of stem cell maintenance in Arabidopsis, maize and rice. Receptor X and Y are different from FON1, but it is unknown whether X and Y are equivalent. (B–D) Ears of maize in the wild type (B), and fasciated ears of *td1* (C) and *fea2* mutants (D). (E) Flower of the rice *fon1* mutant, showing an increase in the number of floral organs. (F, G) Expression of rice *FON2* in the wild type (F) and the *fon1* mutant (G), showing expansion of the *FON2* domain (images kindly provided by T. Suzaki). fm, flower meristem; pi, pistil; st, stamen. Bars = 1 mm in (E) and 100 μm in (F, G).

REGION (ESR)] domain, while *CLV1* and 2 encode a leucine-rich repeat (LRR)-receptor kinase and an LRR-receptor-like protein, respectively (Clark et al. 1997, Fletcher et al. 1999). CLV3 is processed into a small peptide, followed by chemical modifications such as proline hydroxylation and glycosylation (Kondo et al. 2006, Ogawa et al. 2008, Ohyama et al. 2009). It acts as a mobile signal, which is perceived by numerous receptors including CLV1 and CLV2, which forms a complex with the pseudokinase CORYNE (CRN)/SOL2, and RPK2/TOAD2 (Clark et al. 1997, Miwa et al. 2008, Müller et al. 2008, Kinoshita et al. 2010, Betsuyaku et al. 2011). *WUS* encodes a homeodomain-containing transcription factor (Mayer et al. 1998). *WUS* promotes stem cell identity and the expression of CLV3, while the CLV pathway negatively regulates it by restricting the expression of *WUS* (Schoof et al. 2000). Thus, stem cell maintenance is regulated by the WUS–CLV negative feedback loop, which is associated with communication between different domains of the meristem, the stem cell region where it *CLV* is expressed and the organizing center (OC) where *WUS* is expressed (Mayer et al. 1998, Fletcher et al. 1999). Signaling between these different domains is probably achieved by intercellular movement of the CLV3 peptide and of the WUS transcription factor (Yadav et al. 2011).

CLV-Related Pathway in Grasses

Stem cell maintenance is also studied in grasses, where the framework of meristem maintenance is principally conserved, with some interesting differences (for reviews, see Bommert et al. 2005b, Hirano 2008). Mutations in the maize genes *THICK TASSEL DWARF* (*TD1*) and *FASCIATED EAR2* (*FEA2*) predominantly affect the maintenance of the inflorescence meristems (IMs) (Taguchi-Shiobara et al. 2001, Bommert et al. 2005a). In the tassel, the IM enlarges, resulting in an increased spikelet density and a thicker central spike. In the ear, the inflorescence is fasciated and seed row number is increased (**Fig. 1B–D**). Floral meristems (FMs) are also enlarged, resulting in an increase in the number of floral organs, such as stamens. *TD1* and *FEA2* encode a CLV1-like LRR-receptor kinase and a CLV2-like LRR receptor-like protein, respectively. *td1 fea2* double mutants show an enhanced phenotype relative to each single mutant, suggesting that these two genes function in different genetic pathways (Bommert et al. 2005a). This maize double mutant phenotype initially implied a difference in genetic mechanism between maize and Arabidopsis, since it was once thought that *CLV1* and *CLV2* act in the same genetic pathway (Kayes and Clark 1998). However, recently it has been revealed that CLV2 acts in a signaling pathway independently of CLV1, by forming a receptor complex with CRN, also known as SUPPRESSOR OF LLP2 (SOL2) (Miwa et al. 2008, Müller et al. 2008). Another interesting aspect of the work in maize is the finding that *FEA2* maps to a quantitative trait locus (QTL) for kernel row number, suggesting that natural variation in these genes contributed to crop improvement (Taguchi-Shiobara et al. 2001). This QTL association has been confirmed by the characterization of weak *fea2* alleles that

enhance kernel number without causing fasciation (Bommert et al. 2013).

In rice, *floral organ number* (*fon*) mutants have also contributed to understanding stem cell maintenance (Nagasawa et al. 1996). The FM enlarges in both *fon1* and *fon2* mutants, resulting in an increase in the number of floral organs, such as stamens and carpels (**Fig. 1E**) (Nagasawa et al. 1996, Suzaki et al. 2004, Suzaki et al. 2006). Molecular cloning has revealed that *FON1* encodes a gene orthologous to *CLV1* and maize *TD1*, whereas *FON2* encodes a CLE protein related to Arabidopsis CLV3. The independently isolated *fon4* mutant is allelic to *fon2* (Chu et al. 2006). *FON1*, like maize *TD1*, is expressed throughout the meristem, whereas *FON2* is expressed in the apical region of the meristem (Suzaki et al. 2004, Chu et al. 2006, Suzaki et al. 2006). The expression domain of *FON2* is highly expanded in the enlarged floral meristem of the *fon1* mutant (**Fig. 1F, G**) (Suzaki et al. 2006), reminiscent of *CLV3* behavior in Arabidopsis (Fletcher et al. 1999, Brand et al. 2000).

The phenotype of *fon1 fon2* double mutants resembles that of each single mutant, indicating that *FON1* and *FON2* function in the same genetic pathway (Suzaki et al. 2006). Overexpression of *FON2* causes severe reduction in the number of floral organs, probably because of a decrease in size of the floral meristem. This overexpression effect is not observed in the *fon1* mutant background, suggesting that FON2 acts through the putative receptor encoded by *FON1* (Suzaki et al. 2006). Thus, the genetic relationship and molecular function of *FON1* and *FON2* in rice are very similar to those of *CLV1* and *CLV3*.

These studies in both maize and rice suggest that the CLV pathway that negatively regulates stem cell maintenance is conserved in grasses. Despite a common mechanism, there are differences in the mutant phenotypes between maize and rice: the inflorescence meristem is severely affected in both maize *td1* and *fea2* mutants, whereas such defects are not evident in rice *fon1* and *fon2* mutants. These differences may be due to genetic redundancy, or to a high sensitivity of the maize IM to these mutations owing to selection for an increase in the number of rows of seeds on the ear during maize domestication (Taguchi-Shiobara et al. 2001, Brown et al. 2011).

In rice, the *FON2 SPARE1* (*FOS1*) gene was identified as a modifier of the *fon2* mutation; the floral phenotype of *fon2* is suppressed when *FOS1* from *indica* is present (Suzaki et al. 2009). *FOS1* encodes a CLE protein like FON2, but the protein encoded by the *japonica* allele is likely to have no or weak function due to a defect in a putative processing site of the signal peptide. Thus, FON2 and FOS1 are likely to act redundantly in the maintenance of the FM in *indica*, and an enlargement of the FM in the original *fon2* mutant (*japonica* background) results from mutations occurring in both the *FON2* and *FOS1* genes. The mutant allele of *FOS1* is distributed in all *japonica* strains examined, whereas all *indica* strains and wild rice species examined have wild-type *FOS1* (Suzaki et al. 2009). Therefore, the FM is robustly maintained by parallel redundant signaling pathways in rice (the genus *Oryza*) in general, whereas a mutation might have occurred in *FOS1* during domestication of *japonica* rice.

Unlike the *clv* mutants in Arabidopsis, no obvious abnormalities have been described in the vegetative meristems in the grass mutants described above. In addition to *FOS1*, *FON2-LIKE CLE PROTEIN1* (*FCP1*), a gene that encodes a protein containing the CLE domain with high similarity to that of *FON2*, is likely to be involved in the maintenance of the rice vegetative SAM (Suzaki et al. 2008). Constitutive expression of either *FCP1* or *FOS1* causes termination of the vegetative SAM in shoots regenerated from calli (Suzaki et al. 2008, Suzaki et al. 2009). In contrast, *FON2* overexpression causes no abnormality in the vegetative SAM, although the FM is severely affected, as described above (Suzaki et al. 2006). Therefore, *FCP1* and *FOS1* negatively regulate the maintenance of the vegetative SAM, whereas *FON2* function is restricted to reproductive meristems (IMs and FMs). In addition, FCP1 and FOS1 probably act through a receptor other than FON1, because constitutive expression of either *FCP1* or *FOS1* shows a similar effect on shoot regeneration in the *fon1* mutant to that observed in the wild type (Suzaki et al. 2008, Suzaki et al. 2009). These observations demonstrate that stem cell maintenance is likely to be regulated by at least three related negative pathways in rice, and each pathway seems to contribute differently to this regulation depending on the type of meristem.

Genes that Promote Stem Cell Identity

In contrast to negative pathways in meristem maintenance, current understanding of factors that promote stem cell identity is still lacking. It is probable that *WUS* orthologs, or *WUSCHEL RELATED HOMEOBOX* (*WOX*) genes, may also have such function in grasses. Although a few studies concerning the expression patterns of *WOX* genes have been published, no genetic or functional analysis has been reported in grasses. However, the presence of two *WUS* paralogs, *ZmWUS1* and *ZmWUS2*, with different expression patterns, suggests that some degree of subfunctionalization has occurred (Nardmann and Werr 2006). Functional identification of stem cell-promoting factors, such as *WUS*, would be helpful to elucidate the genetic mechanism that regulates stem cell maintenance in grasses. A recent study reports that *WOX4*, a distinct member of the rice *WOX* gene family, acts as a positive factor in shoot meristem maintenance and is negatively regulated by *FCP1* in rice (Ohmori et al. 2013).

Cytokinin action in the meristem

One of the first indications of the role of cytokinin in meristem maintenance came from the maize mutant *aberrant phyllotaxy1* (*abph1*), which has a defect in phyllotaxy and the geometric pattern of leaf initiation, and an enlarged meristem (Jackson and Hake 1999). The *ABPH1* gene encodes a type-A response regulator functioning in cytokinin signaling (Giulini et al. 2004). Cytokinin signal transduction is regulated by a

two-component feedback system where cytokinin-inducible B-type response regulators (RRs) activate the expression of a set of cytokinin-responsive genes, including A-type RRs, which inhibit cytokinin signaling (for a review, see Argueso et al. 2010). In Arabidopsis, WUS promotes cytokinin signaling by repressing the A-type genes *ARABIDOPSIS RESPONSE REGULATOR7* (*ARR7*) and *ARR15*, whereas cytokinin positively regulates the expression of *WUS* (Leibfried et al. 2005, Gordon et al. 2009).

In rice, the *lonely guy* (*log*) mutant produces small panicles with a reduced number of branches and spikelets (Kurakawa et al. 2007). Analysis of *LOG* function provided an important breakthrough, since it was revealed that *LOG* encodes an enzyme that catalyzes the final step of cytokinin biosynthesis, which had not been found by biochemical studies. *LOG* is expressed in the tip of the reproductive meristem, and the expression of cytokinin-inducible genes is dramatically reduced in the meristem of severe *log-1* mutants. Maintenance of the meristem is compromised, especially in the reproductive phase; expression of the meristem marker *Oryza sativa HOMEOBOX GENE1* (*OSH1*) is highly reduced in the FM, and the shape of the FM is altered. A severe reduction in the number of floral organs, especially in the inner whorls, is observed in *log-1*. In a weak allele, *log-3*, the ovule does not develop, due to a failure to maintain the FM after carpel initiation (Yamaki et al. 2011). The floral phenotype of *log-1* resembles that of the *FON2*-overexpressing plant, whereas a *fon1* mutation suppresses the *log-3* phenotype (Suzaki et al. 2006, Kurakawa et al. 2007, Yamaki et al. 2011). These observations suggest involvement of cytokinin action in FON signaling. The importance of *LOG* function in meristem organization has been recently reported in Arabidopsis. The biologically active form of cytokinin, which is probably catalyzed by *LOG4* expression in the SAM epidermis, acts as a positional cue for patterning the *WUS* expression domain (Chickarmane et al. 2012).

KNOX genes promote meristem identity

Another important layer of regulation in the SAM is imposed by the homeobox-containing transcription factor KNOTTED1 (KN1) and related KNOTTED1-like homeodomain (KNOX) proteins. Originally identified as a dominant gain-of-function mutation in maize with knotted protrusions on vegetative leaves, *KN1* is required for maintenance of the SAM, as loss-of-function alleles cause meristem termination in a background-dependent manner (Kerstetter et al. 1997, Vollbrecht et al. 2000). *KNOX* genes positively regulate meristem identity in both monocots and dicots as the Arabidopsis ortholog of *KN1*, *SHOOTMERISTEMLESS*, and the rice ortholog, *OSH1*, display conserved meristem termination phenotypes (Long et al. 1996, Tsuda et al. 2011).

There has been considerable interest in the mechanism by which *KNOX* genes promote meristematic activity. In several different model species, KNOX proteins have been shown to bind directly and either activate or repress gibberellic acid biosynthesis genes, modifying levels of active gibberellic acid in meristems and boundary regions (Sakamoto et al. 2001, Chen et al. 2004, Bolduc and Hake 2009). KNOX proteins also regulate cytokinin biosynthesis in Arabidopsis by activating isopentenyl transferase genes (Jasinski et al. 2005, Yanai et al. 2005). In addition, inducible overexpression of the KNOX gene *OSH15* up-regulates expression of several cytokinin biosynthesis genes in rice (Sakamoto et al. 2006). Tsuda et al. (2011) also showed that *OSH1* and *OSH15* activate their own expression, and are positively regulated by cytokinin. Taken together, the data suggest that *KNOX* genes and cytokinin mutually reinforce SAM identity.

A genome-wide binding profile for KN1 was recently identified by chromatin immunoprecipitation-sequencing (ChIP-seq), and targeted genes were compared with a list of genes differentially expressed in the *kn1* loss-of-function mutant (Bolduc et al. 2012). This analysis revealed that KN1 targets genes involved in four major hormone pathways (auxin, cytokinin, gibberellic acid and brassinosteroids), orchestrating a careful balance that promotes meristem maintenance. Direct targets also included many other transcription factors, placing KN1 at the summit of a regulatory cascade controlling shoot meristem function (Bolduc et al. 2012).

Additional pathways required for meristem maintenance

The *FLATTENED SHOOT MERISTEM* (*FSM*) gene is another factor required for meristem maintenance in rice, as mutants have a flatter and smaller SAM than wild-type plants (Abe et al. 2008). *FSM* encodes a Chromatin Assembly Factor-1 (CAF1) subunit, and is the ortholog of the Arabidopsis gene *FASCIATA1* (*FAS1*). Interestingly, *FAS1* displays an enlarged meristem, suggesting that this layer of meristem maintenance may function quite differently in the monocot and dicot lineages (Abe et al. 2008).

Several classes of small RNAs and associated biosynthetic machinery have been implicated in meristem maintenance in rice. Mutants in *trans*-acting small interfering RNA (ta-siRNA) biogenesis components, such as *SHOOTLESS4* (*SHL4*)/*ARGONAUTE7* (*AGO7*) and *SHOOT ORGANIZATION1* (*SHO1*)/*DICER-LIKE4* (*DCL4*), fail to maintain a SAM through embryogenesis (Nagasaki et al. 2007). The meristem defect in these plants is partially explained by a strong down-regulation of class III HD-ZIP genes, caused by an accumulation of miR166 (Nagasaki et al. 2007). In addition, mutants in *WAVY LEAF1* (*WAF1*), which encodes the ortholog of the Arabidopsis RNA methyltransferase *HUA ENHANCER1* (*HUA1*), have reduced levels of ta-siRNAs and microRNAs, due to decreased RNA stability (Abe et al. 2010). *waf1* mutants enhance the meristem maintenance defects of hypomorphic *sho* mutants, further demonstrating the importance of the ta-siRNA population for meristem function.

Phyllotaxy and Plastochron Regulation

Most members of the grass family display an alternate phyllotaxy, or pattern of leaf initiation, with one organ initiated at the

flank of the meristem at a time, resulting in one leaf per node (Jackson and Hake 1999). The pattern of leaf arrangement is important for plant traits such as stalk strength and optimal light capture. Maize *aberrant phyllotaxy1* (*abph1*) was the first mutant cloned that has a specifically altered phyllotaxy program (Giulini et al. 2004), although other *aberrant phyllotaxy* mutants await molecular identification (D. Jackson, unpublished). *ABPH1* is expressed in the SAM during embryonic development, and in the incipient leaf primordium (P0) post-germination (Guilini et al. 2004). Mechanistic studies showed that *ABPH1* expression is dependent on polar auxin transport, and that *ABPH1* activates expression of the auxin transporter PIN1, suggesting that a complex interplay between auxin and cytokinin signaling regulates phyllotaxy and leaf initiation (Lee et al. 2009).

In rice, *decussate* (*dec*) mutants also display a transformation to opposite phyllotaxy, as well as a larger SAM characterized by an increased rate of cell division (Itoh et al. 2012). Conversely, the mutants have a smaller RAM, and the mutants die before reaching the reproductive phase. It is well established that cytokinin exerts an opposite effect on cell division in the SAM compared with the RAM (Werner et al. 2003). Consistent with this, *dec* mutants have decreased expression of several type A-RRs, as well as decreased sensitivity to applied cytokinin (Itoh et al. 2012). *DEC* encodes a glutamine-rich protein with domains of unknown function shared with fungi and animals (Itoh et al. 2012), thus it will be interesting to explore further connections with cytokinin and auxin signaling.

Another property of organ initiation from the meristem is plastochron, the elapsed time between the initiation of two leaves. Three rice mutants, *plastochron1*, *2* and *3*, display greatly reduced plastochron length, with a large increase in the number of leaves originating from the SAM (Miyoshi et al. 2004, Kawakatsu et al. 2006, Kawakatsu et al. 2009). The plastochron phenotype is associated with larger meristems, with much higher rates of cell division than wild-type plants (Miyoshi et al. 2004). Similarly, the *shoot organization* (*sho1*, *2* and *3*) mutants generate an abnormally high number of leaves in a random phyllotaxy (Itoh et al. 2000). Loss-of-function *aberrant panicle organization1* (*apo1*) mutants also have decreased plastochron length, while dominant gain-of-function alleles display a corresponding increase in plastochron time (Ikeda-Kawakatsu et al. 2009).

An outstanding question is to what degree changes in meristem size and structure are correlated with, or causative of, changes in phyllotaxy and plastochron. Larger meristems are present in the *abph1* and *dec* mutants described above, but a larger vegetative meristem does not always produce a change in phyllotaxy in other mutants. Changes in plastochron length are also usually accompanied by changes in meristem size (Wang et al. 2008, Kawakatsu et al. 2009). An analysis using various mutants with defects in the rate of leaf initiation found a correlation between meristem shape parameters (i.e. height/width ratios) and phyllotaxy and plastochron parameters; however, no such relationship existed with meristem size per se (Itoh et al. 2000).

Axillary Meristem Dormancy and Tillering

Tillering, the production of secondary shoots by AMs, is a widespread property of grasses. Maize domestication selected very strongly for untillered maize plants, with dormant AMs, with the exception of one to two ear shoots per plant. This architecture is extremely important for achieving high planting density while maintaining ease of harvest. In contrast, an appropriate degree of tillering is essential to high yield production in rice. Secondary shoot production is determined first by the initiation of AMs, and then by factors controlling dormancy of the axillary shoots.

Several key regulators of AM initiation have been identified based on loss-of-function mutant phenotypes. The maize mutant *barren stalk1* (*ba1*) encodes a basic helix–loop–helix (bHLH) transcription factor that is required to establish AMs in vegetative and reproductive stages (Gallavotti et al. 2004). The orthologous rice gene *LAX PANICLE1* (*LAX1*) is required only to initiate AMs in the inflorescence (Komatsu et al. 2003). Both of these grass-specific transcription factors are expressed in boundary domains associated with all AMs, but not in the meristems, and act non-cell autonomously (Komatsu et al. 2003, Gallavotti et al. 2004). The LAX1 protein moves directionally into the developing AM in a stage-specific manner, and this trafficking is required for its function (**Fig. 2A**) (Oikawa and Kyozuka 2009). The role of *LAX1* in vegetative AMs is more clearly revealed when *lax1* is combined with the *monoculm1* (*moc1*) or *lax panicle2* (*lax2*) mutants (Li et al. 2003, Tabuchi et al. 2011). Vegetative AMs are completely abolished in the *lax1 moc1* double mutant, and tillers are very strongly reduced in the *lax1 lax2* double mutant (Tabuchi et al. 2011). *moc1* encodes the rice ortholog of the GRAS family transcription factor *LATERAL SUPPRESSOR* (*LAS*) of Arabidopsis (Li et al. 2003), and recent work has implicated a role for proteasome-mediated degradation of MOC1 in regulating AM dormancy (Lin et al. 2012, Xu et al. 2012). *LAX2* encodes a plant-specific nuclear protein that physically interacts with LAX1 to regulate AM formation cooperatively (Tabuchi et al. 2011).

Maize underwent strong selection for AM dormancy during domestication from its highly branched ancestor, teosinte. Five classical QTLs differentiate the architecture of modern maize from its wild progenitor (Doebley, 2004). One of these QTLs maps to *teosinte branched1* (*tb1*), a mutant with a teosinte-like morphology due to elaboration of axillary shoots (Doebley et al. 1997). *TB1* is a founding member of the TCP [*TB1-CYCLOIDEA* (*CYC*)-*PROLIFERATING CELL FACTOR* (*PCF*)] family of transcription factors, which modulate rates of cell division (Martin-Trillo and Cubas 2010). *TB1* orthologs in rice and Arabidopsis play conserved roles in regulating plant branching architecture (Takeda et al. 2003, Aguilar-Martinez et al. 2007). Population genetic studies have identified a selective sweep signature upstream of the *TB1* gene in maize, and a region approximately 70 kb upstream was shown to act as a transcriptional enhancer (Clark et al. 2006). Recent work has narrowed down the

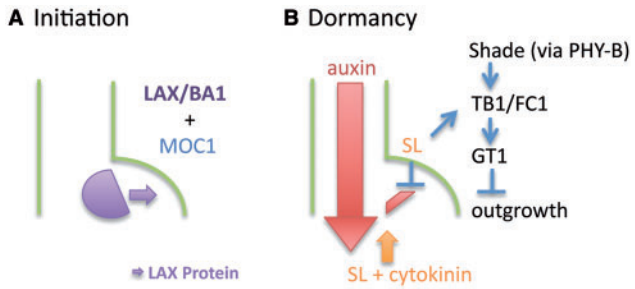

Fig. 2 Tillering is controlled by a two-step process of axillary meristem (AM) initiation and dormancy. (A) Initiation of AMs is controlled by the cooperative action of *LAX PANICLE1* (*LAX1*)/*BARREN STALK1* (*BA1*) and *MONOCULM1* (*MOC1*). Initiation depends on the stage-specific trafficking of the LAX1 protein into the meristem. (B) AM dormancy is controlled by the antagonistic interactions of three phytohormones and two genes that are responsive to shade signals (*TEOSINTE BRANCHED1* and *GRASSY TILLERS1*). Auxin (red arrow), which is transported basipetally through the polar auxin transport stream, inhibits the outgrowth of axillary buds. Cytokinin is transported in the opposite direction, and directly promotes growth. Strigolactones (SLs) are hypothesized to limit outgrowth by mitigating polar auxin transport out of AMs, and may also act by activating *FINE CULM1* (*FC1*).

enhancer activity to a *HOPSCOTCH* retrotransposon insertion in this upstream region. The *HOPSCOTCH* insertion pre-dates the domestication of maize by approximately 10,000 years, indicating that selection during domestication acted on standing variation in the teosinte gene pool (Studer et al. 2011).

Another likely target of selection for reduced tillering is the *GRASSY TILLERS1* (*GT1*) gene, encoding a HD-ZIP I protein (Whipple et al. 2011). *GT1* appears to be under the transcriptional control of TB1, as its expression is greatly reduced in the *tb1* mutant. Furthermore, in teosinte and *Sorghum bicolor*, *TB1* and *GT1* appear to inhibit axillary bud outgrowth in response to shade signals perceived by phytochrome B (**Fig. 2B**). The shade avoidance pathway represses axillary bud outgrowth in many grasses, but axillary buds are constitutively dormant in domesticated maize (Whipple et al. 2011).

AM dormancy is also influenced by the antagonistic action of several classes of plant hormones (**Fig. 2B**). The phenomenon of apical dominance plays an important role in regulating axillary shoots. Auxin, synthesized at the growing tip of the plant, is transported basipetally through the polar auxin transport (PAT) stream, and indirectly suppresses bud outgrowth (McSteen and Leyser 2005). In contrast, cytokinin is transported acropetally through the xylem system, into the AMs, where it promotes growth. The mechanisms by which these two hormones influence AM determinacy are well established, and are reviewed by McSteen and Leyser (2005).

A third hormone plays a central role in regulating AM dormancy. The existence of this signal was postulated based on a collection of Arabidopsis, rice and pea mutants with increased branching, which encoded biosynthetic machinery for an unknown carotenoid-based hormone (for a review, see Ongaro and Leyser 2008). Reciprocal grafting experiments provided evidence that this hormone moved acropetally from the roots into the shoot. Levels of root-synthesized terpenoid hormones called strigolactones (SLs) were reduced in these biosynthetic mutants, and exogenous application of SLs rescued the shoot branching phenotypes (Gomez-Roldan et al. 2008, Umehara et al. 2008). Thus, SLs are a novel and specific inhibitor of AM outgrowth.

An important unanswered question in the field has been the nature of the SL receptor. Several candidate genes were identified in rice based on insensitivity to exogenous SLs, including *DWARF14* (*D14*) (Arite et al. 2009). Homology modeling showed that this α-β fold hydrolase could potentially interact with a natural SL ligand (Gaiji et al. 2012). Recently, the pea ortholog of *D14*, *DAD2*, was shown to encode a catalytically active candidate SL receptor, which physically associates with *PhMAX2A*, a key signal transduction component (Hamiaux et al. 2012). Therefore, it is likely that D14 and related proteins represent authentic SL receptors in grasses and dicot species.

One putative downstream effector of SL signaling in rice is *FINE CULM1* (*FC1*), as mutants in this *TB1* ortholog are insensitive to exogenously applied SL (Minakuchi et al. 2010). Interestingly, treatment with cytokinin reduces expression of *FC1*, suggesting that this gene may be important in integrating multiple hormonal signaling pathways in axillary buds (Minakuchi et al. 2010). Further work is needed to elucidate the downstream consequences of SL signaling in the AM. For example, the relationship between SLs and auxin is still not fully understood. It has been suggested that SLs prevent axillary shoot branching by limiting auxin polar transport, such that auxin export cannot be established from axillary buds, a process that is essential for outgrowth (**Fig. 2B**) (Crawford et al. 2010).

The Floral Transition

Grasses have evolved a spectrum of different pathways that coordinate the floral transition in response to environmental and endogenous cues. Some features of grass flowering pathways are conserved between all flowering plants, while others represent innovations specific to various grass lineages. For example, different species of grasses have different sensitivities and thresholds for daylength-dependent flowering. Rice is considered a photoperiod-sensitive species, with a facultative short-day requirement. On the other hand, floral induction in maize reflects its domestication from a tropical grass, but subsequent breeding and improvement over a wide range of temperate environments. Most temperate maize inbred lines are essentially day-neutral, whereas tropical lines respond to short-day inductive cues (Colasanti and Coneva 2009). Other temperate grasses, such as wheat and barley, have a long-day requirement with a vernalization switch (for a review, see Cockram et al. 2007); this section will focus on flowering pathways in maize and rice.

Much of what we know about the floral transition comes from studies in Arabidopsis. The *CONSTANS* (*CO*) gene integrates the main outputs of the circadian clock, and serves to synchronize flowering time with long-day photoperiods (for a review, see Turck et al. 2008). Under long-day conditions, CO, a zinc finger transcription factor, is stable and activates the expression of *FLOWERING LOCUS T* (*FT*) in leaves. Subsequently, the FT protein product is translocated through the phloem to the SAM, where it interacts with the bZIP transcription factor FLOWERING LOCUS D (FD) and targets floral regulators. FT is regarded to fulfill the criteria for the universal leaf-derived flowering signal, 'florigen' (Corbesier et al. 2007, Turck et al. 2008).

This extensively characterized photoperiod-responsive flowering module is conserved in grasses; however, there are obvious differences in the daylength perception (**Fig. 3**). A major rice QTL for photoperiod responsiveness, *HEADING DATE1* (*HD1*), was cloned and revealed to encode an ortholog of *CO* (Yano et al. 2000). HD1 is an activator of the rice *FT* ortholog *HEADING DATE 3a* (*HD3a*) under short-day conditions, but is a repressor of *HD3a* expression under long-day condition (Tamaki et al. 2007). Another factor, *EARLY HEADING DATE1* (*EHD1*), which encodes a B-type cytokinin response regulator, also activates the expression of *HD3a* under short-day conditions, independently of *HD1*. The exquisitely sensitive daylength response of rice flowering is conferred by *EHD1* regulation via the opposing action of blue light-mediated floral promotion and phytochrome-mediated floral repression pathways (Itoh et al. 2010). *GRAIN NUMBER, PLANT HEIGHT AND HEADING DATE7* (*GHD7*), a CCT-domain protein, which is induced through phytochrome signaling, represses the expression of *HD3a* under long days by suppressing blue light induction of *EHD1* in the morning. This results in a highly sensitized system where an increase in daylength of only 30 min is sufficient to delay floral induction (Itoh et al. 2010). A paralog of *HD3a*, *RICE FLOWERING LOCUS T1* (*RFT1*), is induced under long-day conditions by *EHD1* and *OsMADS50*, and also acts as a transmissible florigen signal (Komiya et al. 2009). Thus, in contrast to Arabidopsis, two separate photoperiod-sensing pathways converge on two FT/florigen genes in rice (**Fig. 3**).

Recent work has identified an intracellular receptor for the rice FT protein HD3a (Taoka et al. 2011). HD3a and OsFD1 do not directly interact at the apex, but rather are bridged together by the 14-3-3 protein GF14c, to form the florigen activation complex (FAC). Once assembled in the nucleus, the FAC is responsible for activating the expression of *OsMADS15*, the rice ortholog of *APETALA1* (*AP1*), a key floral regulator (Taoka et al. 2011).

Different cultivars of rice display natural variation in flowering time under short-day conditions (Tsuji et al. 2011). These differences are explained by variation in sequence and

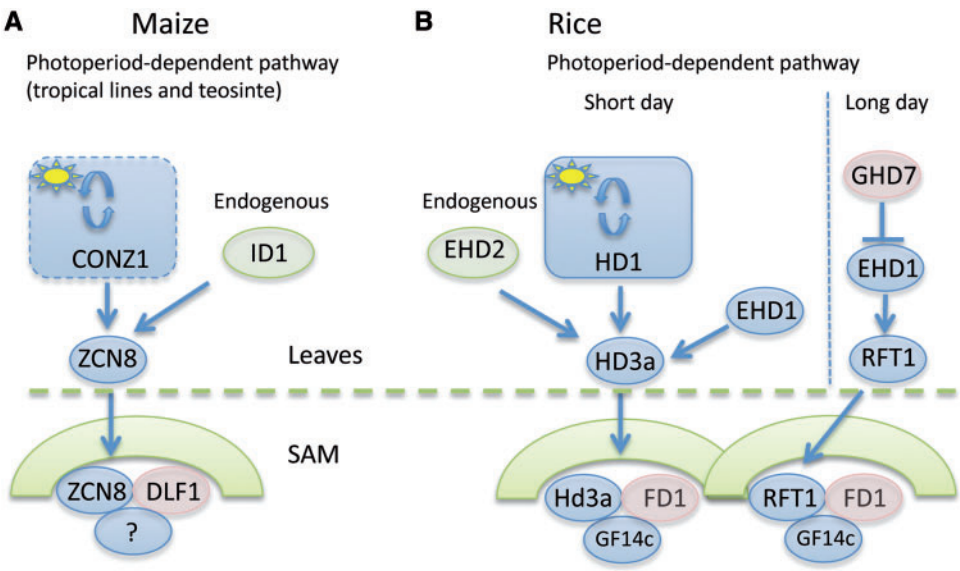

Fig. 3 Regulation of the floral transition in maize and rice. (A) Flowering in maize is controlled by an endogenous pathway regulated by *INDETERMINATE1* (*ID1*), and a short-day-inducible pathway specific to tropical inbred lines. The output of the circadian clock is integrated by *CONZ1* (Miller et al. 2008). *ZCN8* is a putative maize FT (florigen) ortholog, which is induced in the leaves and predicted to translocate to the SAM where it interacts with DLF1, an FD homolog (Muszynski et al. 2006). (B) The floral transition in rice is sensitive to changes in photoperiod. The output of the circadian clock is integrated by *HD1*. Short-day conditions induce flowering via *EHD1*-c and *EHD2*-dependent up-regulation of *HD3a* (florigen). A parallel pathway involving *GHD7* represses the expression of EHD1 under long days to prevent flowering, but the transition may proceed under long days via a second florigen protein, RFT1. Activation of floral regulators is achieved by the florigen activation complex (FAC) comprised of HD3a, FD1 and GF14c. *CONZ1*, *CONSTANS OF ZEA MAYS1*; *ZCN8*, ZEA CENTRORADIALIS8; *FT*, *FLOWERING LOCUS T*; *DLF1*, *DELAYED FLOWERING1*; *FD*, *FLOWERING LOCUS D*; *EHD1*, *EARLY HEADING DATE 1*; *EHD2*, *EARLY HEADING DATE2*; *HD3a*, *HEADING DATE 3a*; *GHD7*, *GRAIN NUMBER PLANT HEIGHT HEADING DATE7*; *RFT1*, *RICE FLOWERING LOCUS T1*.

expression levels of members of the photoperiodic flowering pathway, namely *HD3a*, *HD1* and *EHD1* (Takahashi et al. 2009). Natural variation in the floral repressor *GHD7* is correlated with different geographical areas of cultivation, and hypomorphic alleles have allowed the expansion of rice cultivation into more temperate northern latitudes (Xue et al. 2008).

An endogenous pathway regulating the floral transition operates in parallel with the photoperiod pathway in grasses, and takes on an increased importance in day-neutral temperate maize. A central player in this pathway, *INDETERMINATE1* (*ID1*), was identified as a mutant that failed to transition to the reproductive phase (Colasanti et al. 1998) (**Fig. 3**). This zinc finger transcription factor is localized to developing leaves, and acts non cell-autonomously to induce flowering at the apex. ID1 may also serve to connect the endogenous and photoperiod-dependent pathways, as expression of the *FT* homolog *ZEA CENTRORADIALIS 8* (*ZCN8*) is greatly reduced in the *id1* mutant (Lazakis et al. 2011). *ZCN8* displays circadian fluctuations in photoperiod-sensitive tropical lines, and is up-regulated in the leaves of teosinte under inductive short-day conditions (Lazakis et al. 2011, Meng et al. 2011). Similarly, the rice ortholog of *ID1*, *OsID1/EHD2*, is required to activate expression of *EHD1* (Matsubara et al. 2008, Park et al. 2008), indicating a conserved connection between the endogenous and photoperiod-dependent pathways in grasses.

Inflorescence Meristem Identity

Following the vegetative to reproductive transition, the IM functions much like the vegetative SAM, initiating lateral leaf (bract) primordia in a regular phyllotaxy, which are accompanied by AMs. Grasses have a program of bract suppression to limit leaf outgrowth, and thus the dominant features of the inflorescence are all derived from the AMs (e.g. spikelet and floral meristems) (Whipple et al. 2010). Not much is known about genes that regulate the identity and determinacy of the IM. A recent study revealed that *PANICLE PHYTOMER2* (*PAP2*) and three other AP1-like MADS-box genes are required to specify the identity of the rice IM downstream of the florigen signal (Kobayashi et al. 2012). Properties such as the determinacy, or persistence, of the IM have the ability to influence panicle size and ear length, and thus grain yield, greatly.

Perspective

Great progress has been made towards understanding the genetic factors that control meristem regulation in maize and rice; however, several fundamental questions remain unanswered. An important area of focus is identification of genes required for positive regulation of stem cell identity in grasses. Little is known about positive regulators of stem cell maintenance, such as *WUS*, in grasses, although understanding of negative regulators has accumulated, as described above. Where are the genes responsible for the positive regulation expressed in the meristem? Does the grass meristem have a domain corresponding to the OC, where *WUS* is expressed? How do the positive and negative regulators interact with each other to regulate stem cell homeostasis? These questions are especially interesting in light of the fact that the structure of the meristem in grasses differs from that of eudicots, since grass meristems generally lack a clonal L2 cell layer. Another salient question is which CLE peptides encoded in the maize genome function to regulate meristem size negatively. It is likely that many outstanding questions in grass meristem biology will be answered in the next few years through a combination of forward and reverse genetics, QTL mapping and functional genomics experiments, such as mRNA-seq, proteomics and ChIP-seq.

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