Hormonal Regulation of Branching in Grasses[1,2[C]]

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Axillary meristems, which form in the axils of leaves, play an essential role in plant architecture and reproduction. During vegetative development, axillary meristems give rise to branches, called tillers in grasses, while during reproductive development, axillary meristems give rise to flowering branches or to flowers. The control of branching by axillary meristems is under hormonal, environmental, developmental, and genetic control. In this *Update* I review the role of hormones in regulation of axillary meristem initiation and outgrowth during both vegetative and inflorescence branching.

Hormones play a critical role in regulating branching (McSteen and Leyser, 2005; Beveridge, 2006; Ongaro and Leyser, 2008). Auxin is required for axillary meristem initiation during both vegetative and inflorescence development. In addition, basipetal movement of auxin from the shoot apex suppresses axillary bud outgrowth in the phenomenon known as apical dominance. Cytokinin regulates meristem size and hence indirectly affects branching (Shani et al., 2006; Kyozuka, 2007). In addition, acropetal movement of cytokinin coming from the roots promotes axillary bud outgrowth. It has long been proposed that an additional hormone travels acropetally from the root to inhibit bud outgrowth. The highlight of last year was the identification of this new plant growth hormone, strigolactone (Gomez-Roldan et al., 2008; Umehara et al., 2008).

The environment also plays a significant role in regulating branch outgrowth. It is commonly known, especially in grasses, that increased planting density leads to reduced branching (Doust 2007a, 2007b; Kebrom and Brutnell, 2007). This could be due to shading, which is known to inhibit branching, or competition for resources, as fertilizer and nutrients are known to promote branching.

Developmental control of axillary meristems is evident from the different fates of axillary meristems during vegetative and reproductive development in different species (Steeves and Sussex, 1989; McSteen and Leyser, 2005). During vegetative development in Arabidopsis (*Arabidopsis thaliana*), axillary meristems appear late during leaf ontogeny, produce a few leaf primordia, and then arrest until signaled to grow. In maize (*Zea mays*), axillary buds remain suppressed during development (except for the ear shoot), leading to a single axis of growth (Fig. 1A; Kiesselbach, 1949). In rice (*Oryza sativa*), axillary meristems grow out to produce a highly tillered plant, though the buds are still under hormonal and environmental control (Fig. 1B; Shimamoto and Kyozuka, 2002).

During inflorescence development in Arabidopsis, floral meristems arise in the axils of reduced leaves called bract leaves (Long and Barton, 2000; Grbic, 2005). In grass inflorescence development, axillary meristems give rise to branches and spikelets before they give rise to flowers (McSteen et al., 2000; Bommert et al., 2005). The identity and determinacy of these different meristem types are controlled by transcription factors (Bortiri and Hake, 2007; *Update* by Thompson and Hake, this issue [Thompson and Hake, 2009]). Although hormones have been implicated in regulation of inflorescence branching, the exact mechanism is unknown (Barazesh and McSteen, 2008).

The differences in the activity of axillary meristems produced during development imply that all axillary meristems do not respond similarly to the same stimuli. For example, in Arabidopsis, there is acropetal outgrowth of buds during vegetative development and basipetal outgrowth of axillary buds during reproductive development (Hempel and Feldman, 1994; McSteen and Leyser, 2005). In grasses, the basal nodes are the ones from which tillers arise (Fig. 1B). Heterochronic mutations that extend the juvenile phase lead to increased tiller number (Poethig, 1988; Chuck et al., 2007). In foxtail millet (*Setaria italica*), branches are also produced from the upper nodes of the plant, in addition to tillers from basal nodes, and these are under separable genetic and environmental control (Doust et al., 2004; Doust, 2007a). These studies indicate that genetic, hormonal, and environmental signals intersect with developmental signals.

Many genes have been identified that regulate axillary meristem initiation and outgrowth during vegetative and reproductive development (Schmitz and Theres, 2005; Bennett and Leyser, 2006; Doust 2007b). Most of these genes have been identified as mutants

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[2] Note on genetic nomenclature: Arabidopsis and rice use the same nomenclature, but the nomenclature differs for maize. For consistency, the Arabidopsis/rice nomenclature was used throughout this article even for maize and other grasses.

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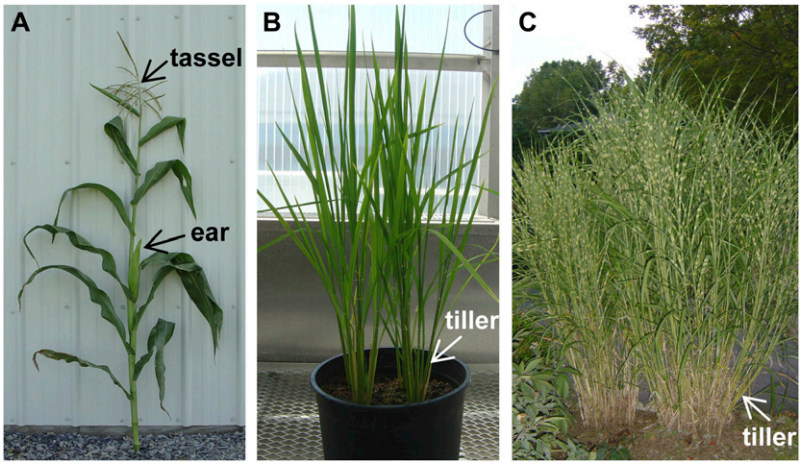

Figure 1. Divergent mechanisms of tillering in the grasses. A, Maize with a single axis of growth. One or two axillary shoots containing the female inflorescence (the ear) grow out. Tillers are generally suppressed. B, Several young rice plants showing that tillers grow out early in vegetative development. C, Ornamental *Miscanthus*. Tillers grow out from rhizomes beneath the soil surface. A triploid variety, *Miscanthus* × *giganteus*, is being investigated as a potential biofuel crop. [See online article for color version of this figure.]

that have fewer branches, because axillary meristems fail to initiate, or that are bushier than normal due to constitutive outgrowth of axillary buds. Some of these genes encode integral components of hormone biosynthesis, perception or signaling pathways providing a direct link to hormone control. Here, I highlight the conservation and diversification of the mechanisms that control branching within grasses and between grasses and eudicots.

AXILLARY MERISTEM INITIATION

Many of the genes regulating axillary meristem initiation affect both vegetative and reproductive development (Table I). In some cases, genes have been reported to affect only one stage of development, but often additional roles in either vegetative or reproductive development have been discovered by constructing double mutants. Thus, how much this distinction is due to redundancy with related genes remains to be seen.

Role of Auxin in Axillary Meristem Initiation during Vegetative and Inflorescence Development

Auxin plays a fundamentally important role in polar growth of all organ primordia, including floral meristems (Cheng and Zhao, 2007; Benjamins and Scheres, 2008; Delker et al., 2008). Multiple mutants have been identified that fail to make flowers in Arabidopsis, resulting in a pin-shaped inflorescence phenotype (Bennett et al., 1995; Fig. 2, A and B). *PINFORMED1* (*PIN1*) encodes one of the auxin efflux carriers (Galweiler et al., 1998), while *PINOID* (*PID*) encodes a Ser/Thr protein kinase that phosphorylates and regulates the localization of PIN1 (Christensen et al., 2000; Benjamins et al., 2001; Friml et al., 2004; Michniewicz et al., 2007). Knockout of multiple genes in the *YUCCA* (*YUC*) family of flavin monooxygenases also causes a pin phenotype (Cheng et al., 2006). *YUC* genes are involved in localized auxin biosynthesis, indicating that auxin biosynthesis is also required for floral meristem initiation (Zhao, 2008). Recent work in maize and rice suggests that the role of auxin transport and auxin biosynthesis in axillary meristem initiation is conserved in monocots.

Three *PIN1* loci have been identified in maize and rice (Xu et al., 2005; Carraro et al., 2006; Gallavotti et al., 2008b). The maize *ZmPIN1a* gene complements the Arabidopsis *pin1* mutant, restoring its ability to make flowers, indicating that *ZmPIN1a* likely functions in auxin transport in maize (Gallavotti et al., 2008b). ZmPIN1a is localized in all axillary meristems and lateral organ primordia in maize similar to Arabidopsis (Carraro et al., 2006; Gallavotti et al., 2008b). Therefore, even though maize makes multiple types of axillary meristems in the inflorescence, all are characterized by expression of PIN1. Antisense knockdown

Table I. *Genes regulating axillary meristem initiation in monocots and eudicots*

Protein	Rice	Maize	Arabidopsis	Pea	Tomato
Auxin efflux carrier	*OsPIN1*	*ZmPIN1*	*PIN1*	*PsPIN1*	
Ser/Thr kinase	*OsPID/OsBIF2*	*BIF2*	*PID*	*PsPID*	
Flavin mono-oxygenase	*OsYUC1*	*SPI1*	*YUC1,2,4,6*		*ToFZY*
Basic helix-loop-helix transcription factor	*LAX*	*BA1*			
GRAS transcription factor	*MOC1/SPA*		*LAS*		*LS*
NAC transcription factor	*OsTIL1/OsNAC2*	*ZmCUC3* *ZmNAC*	*CUC1,2,3*		
HD ZIP transcription factor	*OsHB3*		*REV/IFL*		
MYB transcription factor			*RAX1,2,3*		*BLIND*

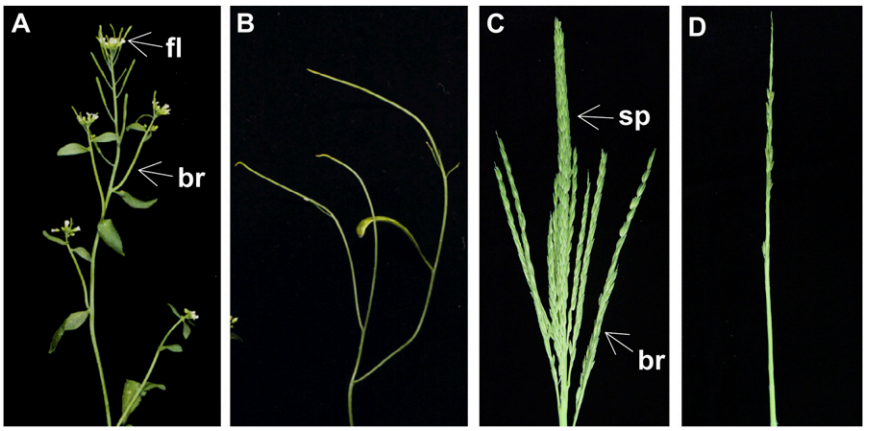

Figure 2. Auxin plays a role in axillary meristem initiation in the inflorescence. A, Arabidopsis inflorescence with secondary branches (br) and flowers (fl). B, *pid* mutant in Arabidopsis showing the pin-shaped inflorescence due to lack of flower production. C, Normal maize tassel with long branches (br) at the base of the main spike. Short branches called spikelet pairs (sp) cover the branches and the central spike. D, *bif2* mutant of maize with very few branches and spikelets. [See online article for color version of this figure.]

of the rice *OsPIN1* gene supports the conserved function of PIN1 genes in auxin transport in monocots (Xu et al., 2005).

barren inflorescence2 (*bif2*) mutants in maize have a phenotype analogous to the pin phenotype in Arabidopsis (Fig. 2, C and D). In *bif2* mutants, fewer branches and spikelets form; however, these arise from the first axillary meristems produced by the inflorescence (McSteen and Hake, 2001). The maize *BIF2* gene encodes a Ser/Thr protein kinase co-orthologous to *PID* (McSteen et al., 2007). BIF2 phosphorylates ZmPIN1a and affects ZmPIN1a localization, indicating that BIF2 regulates PIN1 in maize, similar to the function of PID in Arabidopsis (A. Skirpan and P. McSteen, unpublished data; Friml et al., 2004; Michniewicz et al., 2007). Overexpression of rice *OsPID* has effects on seedling development similar to the effects of treatment with an auxin transport inhibitor, providing further evidence for a function in auxin transport (Morita and Kyozuka, 2007). Therefore, it is likely that PID-like proteins have conserved roles in regulating auxin transport in monocots and eudicots.

On the other hand, BIF2 is localized in the nucleus as well as at the cell periphery, indicating that it plays additional roles in development (Skirpan et al., 2008). Yeast two-hybrid screening with PID identified calcium-binding proteins that act upstream of PID (Benjamins et al., 2003). In contrast, a yeast two-hybrid screen with BIF2 identified BARREN STALK1 (BA1), a nuclear localized basic helix-loop-helix putative transcription factor as an interacting partner with BIF2 (Gallavotti et al., 2004; Skirpan et al., 2008). In vitro kinase assays showed that BIF2 phosphorylates BA1 (Skirpan et al., 2008). *bif2* and *ba1* mutants both have defects in axillary meristem initiation, indicating that the in vitro interaction may have in vivo relevance (McSteen and Hake, 2001; Ritter et al., 2002; Skirpan et al., 2008). Therefore, in maize, *BIF2* also functions in the nucleus. Whether the same is true for *PID* in Arabidopsis or *OsPID/OsBIF2* in rice is not yet known. Although PID has not been reported to be nuclear localized, other PID-like proteins in Arabidopsis have been reported to be localized in the nucleus (Zegzouti et al., 2006). There is an ortholog of *BA1* in rice, *LAX PANICLE* (*LAX*; Komatsu et al., 2003), but an ortholog of *BA1* has not been reported in Arabidopsis.

While the exact molecular mechanism of the interaction of *BA1/LAX* with auxin is not clear, there does appear to be a connection with auxin (Gallavotti et al., 2008b; Skirpan et al., 2008). As already mentioned, BA1 has been shown to physically interact with BIF2 (Skirpan et al., 2008). *BA1* may be auxin induced, as it is not expressed following treatment with an auxin transport inhibitor (Wu and McSteen, 2007). In addition, the auxin reporter DR5 indicates that auxin maxima do not form in the *ba1* mutant (Gallavotti et al., 2008b). Overexpression of *LAX* in rice leads to defects in development, indicating that *LAX* functions in auxin-mediated development (Komatsu et al., 2003). Therefore, it is likely that *BA1/LAX* plays a role in auxin-mediated axillary meristem initiation.

Localized auxin biosynthesis is also required for axillary meristem initiation in maize as in Arabidopsis, but, interestingly, there is a higher level of redundancy in Arabidopsis than in maize. The *sparse inflorescence1* (*spi1*) mutant of maize has fewer branches and spikelets due to the absence of axillary meristems (Gallavotti et al., 2008a). *SPI1* encodes a monocot-specific *YUC* gene family member required for localized auxin biosynthesis (Gallavotti et al., 2008a). Knockout of four *YUC* genes is required in Arabidopsis to generate a phenotype as severe as the *spi1* mutant in maize (Cheng et al., 2006). Phylogenetic analysis shows that this is due to massive expansion of the gene family in both monocots and eudicots. Interestingly, the expression of *SPI1* differs from the expression of *OsYUC1*, the ortholog of *SPI1* in rice (Yamamoto et al., 2007). Furthermore, antisense knockdown of *OsYUC1* in rice has severe defects in root and stem elongation, but a defect in the inflorescence was not reported (Yamamoto et al., 2007). Therefore, there has been functional diversification of the *YUC* gene family even within the grasses.

BIF2, *BA1/LAX*, and *SPI1* also play a role in axillary meristem initiation during vegetative development (Ritter et al., 2002; Komatsu et al., 2003; McSteen

et al., 2007; Gallavotti et al., 2008a). As maize does not normally tiller, these studies took advantage of the *teosinte branched1* (*tb1*) mutant of maize (discussed further in the outgrowth section). *tb1* mutants are highly tillered, because all axillary buds that are normally suppressed grow out producing a bushy plant (Doebley et al., 1997). Double mutant combinations between *ba1* and *tb1* produced no tillers, indicating that *BA1* is required for axillary meristem initiation during vegetative development (Ritter et al., 2002). *bif2;tb1* and *spi1;tb1* double mutants also produced fewer tillers than *tb1* single mutants, indicating that they too function in axillary meristem initiation (McSteen et al., 2007; Gallavotti et al., 2008a). In rice, double mutants between *lax* and *small panicle* (*spa*) lead to an absence of tillers, indicating that *LAX* and *SPA* play overlapping roles in tiller development (Komatsu et al., 2003).

In contrast, *pid1*, *pin1*, and *yuc* mutants in Arabidopsis do not apparently produce fewer side branches (Bennett et al., 1995; Cheng et al., 2006). In fact, plants containing a knockout of multiple *YUC* genes have a bushy appearance due to reduced apical dominance. These differences could be due to genetic redundancy, but it is interesting that the initiation of vegetative axillary meristems in Arabidopsis does not appear to be as sensitive to reductions in auxin biosynthesis or transport as in maize.

Other transcription factors that regulate axillary meristem initiation in monocots and eudicots include the GRAS-type transcription factor *LAS1/LS/MOC1* (Schumacher et al., 1999; Greb et al., 2003; Li et al., 2003) and the HD ZIP class III transcription factor *REV/OsHB3* (Otsuga et al., 2001; Itoh et al., 2008; Table I). The NAC domain transcription factors *CUC1,2,3* play a role in axillary meristem initiation in Arabidopsis, but in rice, overexpression of *OsTIL1* enhances axillary meristem outgrowth rather than initiation (Vroemen et al., 2003; Hibara et al., 2006; Mao et al., 2007; Raman et al., 2008). R2 R3 Myb transcription factors *RAX1,2,3/BLIND* (Schmitz et al., 2002; Keller et al., 2006; Muller et al., 2006) play a role in eudicots, but a homolog in monocots has not yet been identified. Therefore, the roles of these transcription factors still need to be clarified in monocots. Furthermore, the relationship of these transcription factors with hormonal regulation is not clear.

Role of Cytokinin in Regulating Apical Meristem Size

Cytokinin also regulates branch and spikelet number in grasses, but in this case, the effect on branching is a secondary effect due to a defect in the shoot apical meristem. Cytokinin plays a fundamental role in regulation of apical meristem size (Shani et al., 2006; Kyozuka, 2007; Zhao, 2008). In Arabidopsis, increased cytokinin levels lead to increased meristem size and reduced cytokinin levels lead to reduced meristem size (Nogue et al., 2000; Werner et al., 2003).

Two recent articles have demonstrated the fundamental importance of cytokinin in branching and, hence, yield in rice. CYTOKININ OXIDASE (CKX) is an enzyme that degrades cytokinin (Sakakibara, 2006). Mutations in the rice *CKX* gene led to increased panicle branch and spikelet number in the inflorescence and increased yield (Ashikari et al., 2005). Conversely, mutations in the rice *LONELY GUY* gene, which encodes an enzyme that catalyzes the last step in cytokinin biosynthesis, led to the production of fewer branches and spikelets and decreased yield (Kurakawa et al., 2007). Therefore, the role of cytokinin in controlling meristem size appears to be conserved in monocots and eudicots.

AXILLARY MERISTEM OUTGROWTH

Role of Auxin and Cytokinin in Control of Bud Outgrowth

Once axillary buds have initiated, the outgrowth of axillary buds is under hormonal as well as environmental control (Ongaro and Leyser, 2008). Apical dominance is a well-known phenomenon in which auxin traveling basipetally from the shoot apex suppresses the outgrowth of axillary buds (Thimann and Skoog, 1933; Leyser, 2003; Fig. 3). If a shoot is decapitated, the axillary buds are activated. If auxin is applied to the cut end of the shoot, suppression of buds reoccurs. Apical dominance occurs in many plants, leading horticulturists to prune plants to promote branching. Arabidopsis exhibits some apical dominance, as decapitation causes one additional branch to grow out (Aguilar-Martinez et al., 2007). Even though rice is quite bushy, it was recently demonstrated to exhibit apical dominance. Removal of the panicle (inflorescence) caused an increase in tiller elongation, which was suppressed by the addition of auxin (Arite et al., 2007).

The role of auxin in apical dominance is also illustrated by mutants with defects in auxin signaling, biosynthesis, and transport. For example, auxin-resistant mutants in Arabidopsis, such as *auxin resistant1* (*axr1*), are bushy (Lincoln et al., 1990). Reduction of auxin biosynthesis by multiple *yuc* mutants causes reduced apical dominance (Cheng et al., 2006). Similarly, reductions in auxin transport led to increased tillering in monocots. *OsPIN1* knockdown mutants almost doubled the number of tillers, indicating that reduced auxin transport results in outgrowth of tillers even in rice, which has a large number of tillers (Xu et al., 2005). *OsPIN1* knockdown mutants also affected tiller angle such that tillers were at a wider angle than normal. This phenotype is also seen in other mutants that affect auxin transport in rice and indicates that auxin transport is required for tiller gravitropism as well as tiller outgrowth (Li et al., 2007).

As auxin does not enter the bud to inhibit bud outgrowth, a second messenger was proposed (Booker

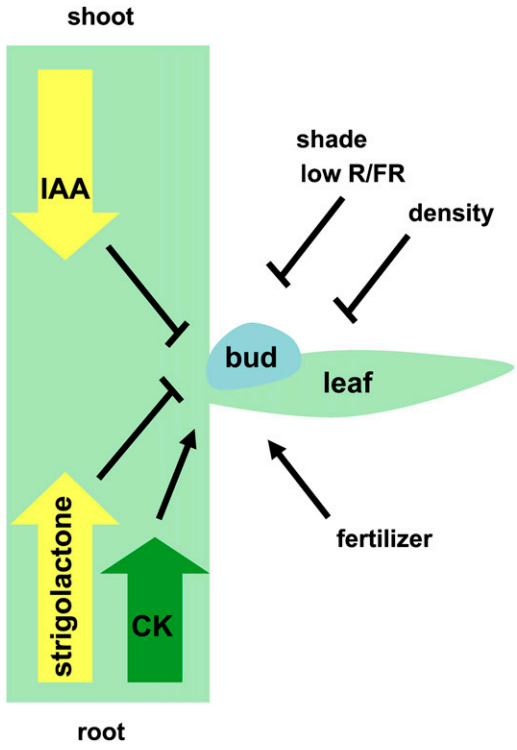

Figure 3. Model for endogenous and exogenous factors controlling bud outgrowth. The blue ball represents an axillary bud in the axil of a leaf. Both endogenous and exogenous factors determine whether or not the axillary bud grows out. Endogenous hormones regulate branching. Auxin (IAA) traveling basipetally inhibits bud outgrowth, cytokinin (CK) moving acropetally promotes outgrowth, while acropetal movement of strigolactone inhibits bud outgrowth. Exogenous factors such as shading and density inhibit bud outgrowth, while fertilizer and nutrients promote bud outgrowth.

et al., 2003). Cytokinin was a good candidate for the second messenger, as cytokinin travels from the root to the shoot and enters the bud where it promotes outgrowth (Fig. 3; Ongaro and Leyser, 2008), and auxin has been shown to inhibit cytokinin biosynthesis (Nordstrom et al., 2004; Tanaka et al., 2006). However, there is also evidence that cytokinin acts independently of auxin (Chatfield et al., 2000). Mutants that overproduce cytokinin are bushy (Helliwell et al., 2001; Tantikanjana et al., 2001). The identification of another class of bushy mutants led to the discovery of the new branching hormone, strigolactone (Fig. 3).

Role of Strigolactones in Suppressing Axillary Bud Outgrowth

A novel compound required for regulation of branching was proposed based on the identification of the *more axillary meristem* (*max*) mutants in Arabidopsis, *ramosus* (*rms*) mutants in pea (*Pisum sativum*), and *decreased apical dominance* (*dad*) mutants in petunia (*Petunia hybrida*; Beveridge, 2006; Ongaro and Leyser, 2008; Table II). Grafting experiments demonstrated the existence of a long-distance signal traveling from the root, that instead of promoting outgrowth like cytokinin, suppressed outgrowth like auxin (Fig. 3). Cloning the *MAX/RMS* genes indicated that the compound was likely derived from the carotenoid biosynthetic pathway.

MAX3/RMS5 encodes carotenoid cleavage dioxygenase CCD7 (Booker et al., 2004; Johnson et al., 2006), and *MAX4/RMS1/DAD1* encode carotenoid cleavage dioxygenase CCD8 (Sorefan et al., 2003; Snowden et al., 2005). These enzymes are proposed to act in tandem to cleave β-carotene into an unknown product (Schwartz et al., 2004). *MAX1* encodes a Cyt P450 enzyme that acts downstream of *MAX3* and *MAX4* in the synthesis of this unknown carotenoid-derived compound (Booker et al., 2005). Cloning of a number of highly tillered mutants from rice showed that this pathway is conserved in grasses. *HIGH TILLERING DWARF1* (*HTD1*) encodes an ortholog of *MAX3/RMS5* (Zou et al., 2006) and *DWARF10* (*D10*) encodes an ortholog of *MAX4/RMS1* (Arite et al., 2007). The dwarfing in the rice mutants is a secondary effect of the formation of tillers, as removal of tillers restores plant height (Zou et al., 2006).

The search was on for the elusive compound. The answer, strigolactone, was completely unexpected. To understand how the breakthrough was made, I will first explain what strigolactones are. Strigolactones were discovered as a group of compounds released from plant roots that promote the germination of seeds of parasitic plants (Bouwmeester et al., 2007). Parasitic *Striga* species infect monocots and are a major cause of crop loss in Africa. Similarly, *Orobanche* species infect eudicots. Recently, strigolactones were also discovered to be involved in colonization of roots by symbiotic arbuscular mycorrhyzal (AM) fungi (Akiyama et al., 2005). In this case, the interaction is beneficial to the plant, leading to increased uptake of nutrients. Another clue to the breakthrough was the publication of an article showing that strigolactones are synthesized from the carotenoid pathway (Matusova et al., 2005).

Table II. *Genes regulating axillary bud outgrowth in monocots and eudicots*

Protein	Rice	Maize	Arabidopsis	Pea	Petunia
Carotenoid cleavage dioxygenase 7	*HTD1/D17*		*MAX3*	*RMS5*	
Carotenoid cleavage dioxygenase 8	*D10*		*MAX4*	*RMS1*	*DAD1*
Cyt P450			*MAX1*		
F box	*D3*		*MAX2*	*RMS4*	
TCP transcription factor	*FC1*	*TB1*	*BRC1*		

The discovery that strigolactones are involved in shoot branching came from two directions. Researchers working on the colonization of roots by AM fungi wanted to identify the genes regulating the biosynthesis of strigolactone. As the *rms* mutants are defective in carotenoid cleavage enzymes, they contacted the researchers working on the pea *rms* mutants. The first clue that the *rms* genes may be involved in synthesis of a strigolactone came when it was discovered that the *rms* mutants failed to interact with AM fungi (Gomez-Roldan et al., 2008). Coming from a biochemical direction, the rice researchers determined that the rice *dwarf* mutants were deficient in strigolactones (Umehara et al., 2008).

In both pea and rice, it was shown that root exudates of the *rms/dwarf* mutants are deficient in strigolactones (Gomez-Roldan et al., 2008; Umehara et al., 2008). Importantly, the rice group also showed that *dwarf* mutants have lower endogenous levels of strigolactone (Umehara et al., 2008). In the case of pea, orbanchyl acetate is one of the strigolactones that are missing (Gomez-Roldan et al., 2008), while in rice, 2′-epi-5-deoxystrigol and another compound are absent (Umehara et al., 2008). The availability of GR24, a synthetic analog of strigolactone, facilitated the research. The direct addition of GR24 to the buds of pea *rms* or Arabidopsis *max* mutants inhibited branching (Gomez-Roldan et al., 2008). The rice group used hydroponics to show that feeding of GR24 to rice *dwarf* or Arabidopsis *max* mutants caused complete suppression of branching (Umehara et al., 2008). To complete the story, it was shown that root exudates from the pea mutants were unable to promote germination of *Orbanche* seed (Gomez-Roldan et al., 2008), while the rice mutants were unable to be parasitized by *Striga* (Umehara et al., 2008). Hence, a strigolactone may be the elusive second messenger for auxin in the control of apical dominance.

How are strigolatones perceived? Some of the *max/rms* mutants did not respond to grafting and were proposed to be involved in perception of the *max* hormone. *MAX2/RMS4* encode an F box Leu-rich repeat protein that is a component of the SCF complex (Stirnberg et al., 2002; Johnson et al., 2006). The rice ortholog is *D3* (Ishikawa et al., 2005). The F box provides substrate specificity to the SCF complex, which promotes the ubiquitination and subsequent degradation of target proteins. SCF complexes are involved in multiple hormone signaling pathways, where they usually degrade a transcription factor required for signaling (McSteen and Zhao, 2008). A major question that remains is: What is the target of *MAX2/RMS4/D3*? It must be a protein, perhaps a transcription factor, that is involved in promoting bud outgrowth so that its degradation by the $SCF^{MAX2/RMS4/D3}$ complex inhibits bud outgrowth. Another question that remains unresolved is: How does the $SCF^{MAX2/RMS4/D3}$ complex perceive strigolactones? Do strigolactones bind the F box protein MAX2/RMS4/D3 in the same way that auxin binds the auxin receptor F box protein TIR1 (Tan et al., 2007)? An interesting evolutionary question is: How is the strigolactone signal perceived by AM fungi and *Striga* seed? Is there an F box protein expressed in *Striga* seed or in AM fungal hyphae?

The discovery of strigolactones may also explain some of the environmental effects of branching. As strigolactone biosynthesis is induced by low phosphorous and low nitrogen, it is proposed that this induces AM fungi to help scavenge these important nutrients (Bouwmeester et al., 2007). The rice group speculates that strigolactone would provide a mechanism for the plant to communicate nutrition status underground to the shoot, to increase branching when nutrients are not limited, or to decrease branching when nutrients are limited (Umehara et al., 2008). Furthermore, *MAX2* is also involved in perception of red/far-red light signals providing a mechanism to integrate light signals with branching (Shen et al., 2007).

Although strigolactone appears to be a conserved regulator of branching in monocots and eudicots, some differences in wiring between components have been identified (Bainbridge et al., 2005; Dun et al., 2006). For example, *RMS1* is induced by auxin in the shoot in pea and *D10* is induced by auxin in the shoot in rice (Foo et al., 2005; Arite et al., 2007), but *max4* is induced by auxin in the root in Arabidopsis (Bainbridge et al., 2005). Furthermore, *RMS1* in pea and *D10* in rice are up-regulated in other *rms/d* mutants (Foo et al., 2005; Arite et al., 2007), while *MAX4* is not appreciably up-regulated in the *max* mutants (Bainbridge et al., 2005). As pea, rice, and Arabidopsis have different morphology with respect to branch outgrowth, it is not surprising that there should be differences in the strength of the interaction between components. Gene regulatory network analysis in these species may determine which nodes are conserved and which differ. Analysis of more species is required to determine if differences in the strength of interactions between auxin, cytokinin, and strigolactone could explain differences in plant architecture.

Role of *tb1* in Integration of Responses to Hormones and the Environment

One of the best understood examples of domestication in plants is the discovery that selection on the expression of the *TB1* locus was involved in the domestication of maize from its wild ancestor teosinte (*Zea mays* ssp. *parviglumis*; Doebley, 2004). Teosinte plants are highly branched. Vegetative branches grow out at every node (except the last few), resulting in a very bushy plant. Maize, on the other hand, has a single axis of growth (Fig. 1A). *TB1* encodes a putative transcription factor expressed in axillary buds (Doebley et al., 1997; Hubbard et al., 2002). *TB1* is expressed in organs that are suppressed in both maize and teosinte (Hubbard et al., 2002). In maize, there is an increase in the expression of *TB1* relative to teosinte, causing buds to be suppressed, perhaps by affecting the cell cycle

(Kosugi and Ohashi, 1997; Hubbard et al., 2002; Li et al., 2005). The increase in expression is proposed to be due to selection at a distant enhancer upstream of the *TB1* locus (Clark et al., 2004, 2006).

Isolation of the *TB1* locus from rice (*OsTB1*) has shown that *TB1* also controls tillering in rice even though rice is already tillered (Takeda et al., 2003). Loss of function of *OsTB1* causes the *fine culm1* (*fc1*) mutant, which has more tillers and a thinner stem than normal (Takeda et al., 2003). Whether the thin stem is a secondary effect of increased tillering is not known, but overexpression of *OsTB1* also leads to reduced tiller number and increased culm thickness. Overexpression of maize *TB1* also leads to a reduction in tiller number in wheat (Lewis et al., 2008).

Tillering is regulated by many environmental components, including planting density, shading, and fertilizer treatment (Doust, 2007b; Kebrom and Brutnell, 2007). *fc1* mutants in rice are still affected by planting density, indicating that *OsTB1/FC1* is not entirely responsible for this response (Takeda et al., 2003). In sorghum (*Sorghum bicolor*), it has been shown that *SbTB1* responds to red/far-red light signaling (Kebrom et al., 2006). Red light is absorbed by plants and far-red light is reflected, so when plants are grown at high density, there is a decreased red to far-red ratio. This leads to the shade avoidance syndrome, one aspect of which is decreased branching (Kebrom and Brutnell, 2007). The red to far-red ratio is sensed by the PHYTOCHROMEs (PHYs). In sorghum, *phyB* mutants have reduced branching and increased *SbTB1* expression (Kebrom et al., 2006). Therefore, *TB1* integrates light signals as part of the shade avoidance pathway.

There are several genes related to *TB1* in Arabidopsis, but *TCP18/BRC1/TBL1* appears to play a similar role in Arabidopsis as *TB1* in grasses (Aguilar-Martinez et al., 2007; Finlayson, 2007). Similar to maize, *BRC1* is expressed in axillary buds, and loss-of-function mutants have more branches in particular from rosette leaves. Furthermore, extensive analysis of *BRC1* interactions showed that *BRC1* acts as an integrator of hormonal and environmental signals to regulate whether or not a branch grows out (Aguilar-Martinez et al., 2007; Finlayson, 2007). *BRC1* acts downstream of the *MAX* pathway as the levels of *BRC1* are significantly reduced in *max* mutants (Aguilar-Martinez et al., 2007; Finlayson, 2007). Furthermore, double mutants between *max* and *brc1* mutants are as bushy as either single mutant, indicating that *BRC1* acts in the same pathway as the *MAX* genes. It was proposed that the *MAX* pathway positively regulates *BRC1* at the transcriptional level to suppress branching. *BRC1* also interacts with auxin. *yuc1D* mutants that overexpress *YUC* have fewer branches, and *yuc1D;brc1* double mutants have many branches, indicating that *BRC1* is required for auxin-mediated apical dominance. The effect of auxin on *BRC1* levels was not as clear. One research group did not detect a statistically significant change in *BRC1* levels in the *yuc1D* or *axr1* mutants using real-time reverse transcription-PCR (Aguilar-Martinez et al., 2007), but another lab did find that *BRC1* is auxin regulated using semiquantitative reverse transcription-PCR on isolated buds (Finlayson, 2007). *BRC1* levels were also affected by decapitation and planting density. Hence, in eudicots, *BRC1* is proposed to act downstream of auxin and the *MAX* genes.

However, the interaction of *OsTB1/FC1* with auxin and the strigolactone pathway differs in rice. Unlike Arabidopsis, the expression of *FC1* was not downregulated in the first node of *dwarf* mutants even though tillers grow out (Arite et al., 2007). Therefore, *FC1* is proposed to act independently of the *max* pathway in rice (Arite et al., 2007). However, double mutants between the *dwarf* mutants and *fc1* have not yet been reported. Furthermore, *FC1* is not induced by auxin, although the mutant was found to be hypersensitive to auxin (Arite et al., 2007).

It is apparent that *TB1/FC1/BRC1* is an integrator of hormonal and environmental signals in both monocots and eudicots. However, the wiring between components appears to be different, perhaps reflecting the different growth habits of maize, rice, and Arabidopsis. As selection on the *TB1* promoter has occurred in maize, it would be interesting to compare the regulatory regions of *TB1/FC1/BRC1* in different plant species to determine if these differences in wiring are due to changes in the regulatory region of *TB1/FC1/BRC1*.

The Role of Hormones in the Regulation of Rhizomes in Perennial Grasses

There is great interest at the moment in the development of perennial grasses as biofuels (Heaton et al., 2004; Bouton, 2007). There are multiple mechanisms for perennialism, but the one used by many perennial grasses is the production of an over-wintering, underground stem called the rhizome. The rhizome arises from an axillary meristem from the basal part of the stem. Axillary meristems on the rhizome give rise to tillers (Fig. 1C). At the end of the growing season, nutrients from the plant are relocated to the rhizome, which has the capacity to overwinter. The following spring, tillers sprout anew from the rhizome. An understanding of the regulation of axillary meristem initiation and outgrowth from rhizomes will be critical for efforts to manipulate bioenergy grasses such as switchgrass (*Panicum virgatum*) and *Miscanthus* for use in biofuel production.

Interestingly, it appears that many of the mechanisms controlling rhizome function are similar to those already known to regulate axillary meristems. Auxin is involved in rhizome initiation as auxin is required to produce rhizomes in culture, and treatment of plants with auxin transport inhibitors prevents the initiation of rhizomes (Kapoor and Rao, 2006). The levels of various hormones, including auxin and cytokinin, vary in the rhizome during the life cycle of the plant (Maslova et al., 2007). For example, during summer when rhizomes are active, there are high auxin and

low cytokinin levels, while during the autumn when rhizomes are dormant, there are high cytokinin and low auxin levels. Therefore, hormones play a fundamental role in the control of tillering by rhizomes.

Furthermore, even though tillers in perennial grasses arise from rhizomes, they are still under the control of the same environmental conditions that regulate tillering in annual grasses (Ma et al., 2001; Heaton et al., 2004). For example, increased planting density reduces tiller number and increased fertilizer treatment increases tiller number. Genetic studies show that perennialism is controlled by relatively few genes (Hu et al., 2003; Westerbergh and Doebley, 2004). The identification of these genes will be essential for understanding the regulation of branching in perennial grasses.

FUTURE PERSPECTIVE

Different plants have different architecture regulated by the extent of branching from axillary meristems. Research on monocots and eudicots has shown that similar mechanisms control branching in these divergent species. As axillary meristems arose at the base of the seed plants, it is not surprising to see so many similarities in monocots and eudicots. Much research remains to be done to understand the function of additional components and how the components are integrated with each other. In particular, an understanding of how axillary meristems at different stages of development respond to genetic, environmental, and hormonal factors is lacking. A challenge for the future will be to understand how changes in the wiring or strength of interaction between components have led to the diversity of plant morphology seen today. An exciting area of research will be to determine how axillary meristems arose by understanding the function of these genes in emerging non-seed plant model systems.

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