Mechanisms of Floral Induction in Grasses: Something Borrowed, Something New[1]

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Almost all that is known about the transition to flowering in grasses is based on studies of agronomic species. The grain produced by two tropically derived grasses, maize (*Zea mays*) and rice (*Oryza sativa*), and a temperate origin grass, wheat (*Triticum aestivum*), provides most of the world's food. Other grasses, such as barley (*Hordeum vulgare*), ryegrass species (*Lolium* spp.), sorghum (*Sorghum bicolor*), and oats (*Avena sativa*), are grown in lesser amounts, but also fill important food production niches. In grass species, such as sugarcane (*Saccharum* spp.), the vegetative portion of the plant is harvested for the Suc that accumulates in its stalks; in this crop, the inability to flower is desirable because sugar levels drop after plants make the transition to flowering as carbon assimilates are shunted to seed production. In all of these grasses, manipulation of the timing of the floral transition is a vitally important trait in maximizing yield potential. Extensive agronomic studies have been done on grass species, but studies of the small flowering dicot plant Arabidopsis (*Arabidopsis thaliana*) have provided an abundance of information on the genetic and molecular control of flowering. What has emerged is a complex network of genes and pathways, some parts of which are also found in the grasses. Conversely, recent discoveries show that grasses also have developed unique mechanisms to regulate flowering.

RIGHT TIME, RIGHT PLACE: FEATURES OF THE FLORAL TRANSITION

With regard to the floral transition, all higher plants share some common mechanisms that control this important switch from vegetative to reproductive growth (for review, see Baurle and Dean, 2006; Imaizumi and Kay, 2006; Turck et al., 2008). First, the shoot apical meristem (SAM), which gives rise to both vegetative and reproductive structures, is the part of the plant where the actual transition occurs. Second, the SAM must be competent to perceive inductive signals to make inflorescence and floral meristems. Third, although the SAM is the target of floral inductive signals, the signals themselves, in most cases, originate in vegetative tissues, usually the leaves. Determining the biochemical nature of this hypothetical floral inductive signal, once, and now again, called florigen, has been very difficult. However, as described below, recent studies in Arabidopsis have led to the identification of a mobile protein that fits the criteria of a long-distance florigenic signal. Finally, the floral transition can be affected by signals that feed into both environmental and endogenous (or autonomous) pathways (Fig. 1).

In considering the molecular chain of events that starts with the perception of signals that cause flowering and ends with the conversion of a vegetative meristem into a flower-generating reproductive meristem, it is clear that the genetic machinery that controls both ends of this chain is highly conserved in angiosperms. This is because perception of environmental signals, and floral meristem specification and flower development, are ancestral functions shared by all flowering plants. It is in the middle part of this chain—the integration of external stimuli into signals that can be interpreted as a developmental response—where plants exercise some flexibility in creating novel regulatory functions. Because the floral transition machinery is so intimately connected to the environment, a plant will use all the levers, springs, and mechanisms at its disposal or invent new ones to optimize flowering time. This is not surprising if one considers that the transition to flowering is the most critical event in the life cycle of most plants, especially monocarpic grass species that have one shot at flowering at the best time to produce seeds. Through comparison with the Arabidopsis flowering-time model, it is evident that grasses are dependent on some ancestral functions, but also have evolved their own unique mechanisms to integrate and transmit floral inductive signals.

PHOTOPERIOD, COINCIDENCE, AND THE CONSTANS/FLOWERING LOCUS T REGULATORY MODULE

First defined through genetic analysis of photoperiod mutants in Arabidopsis, the CONSTANS (CO)/FLOWERING LOCUS T (FT) regulatory system (for review, see Turck et al., 2008) appears to operate in

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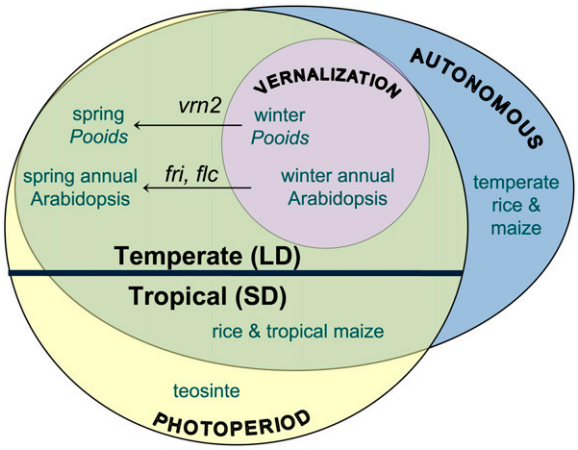

Figure 1. Representation of overlapping floral induction pathways in agronomically important grasses and the model plant Arabidopsis. The majority of species utilize daylength cues to accelerate flowering. In general, temperate plants are induced under lengthening photoperiods, while tropical plants respond to shortening days. Often, a plant becomes competent to respond to photoperiodic signals only after undergoing a period of vernalization, as is the case with winter annual Arabidopsis and the winter pooids (wheat, barley, rye, oats). Vernalization requirement is often controlled by a small number of loci. For, example, *fri* or *flc* mutations are found in Arabidopsis with a summer annual growth habit. Similarly, spring varieties of the pooids result from loss of *VRN2*. Of the tropical grasses, teosinte is an obligate short-day plant, whereas rice has been shown to coordinate photoperiod and endogenous cues to initiate flowering. Similar to Arabidopsis, pooid grass flowering time is determined by the interaction of a network of signals including daylength and vernalization, as well as cues endogenous to the plant. Temperate maize is a tropical origin grass that has adapted to temperate climates, thereby becoming less sensitive to shortening days and more reliant on endogenous cues indicative of the plant's physiological status and overall readiness to flower. LD, Long days; SD, short days.

several grasses examined so far, as described below. In Arabidopsis, the *CO* gene integrates inductive photoperiod information via the circadian clock and activates the *FT* gene. Regulation of CO stability, and therefore activity, provides a particularly elegant demonstration of the external coincidence model (for review, see Imaizumi and Kay, 2006). In brief, the output from the clock, via the GIGANTEA (GI) protein, activates expression of *CO*, a B-box-type zinc finger transcription factor-encoding gene expressed in leaves. Levels of *CO* transcript oscillate in a circadian pattern, and when they coincide with a light period, indicating long days of summer, the translated CO protein is stable and directly activates its prime target, the *FT* gene. FT protein then acts as a transcriptional cofactor that interacts with another flowering-time transcription factor encoded by the *FLOWERING LOCUS D* (*FD*) gene to activate expression of *APETALA1* (*AP1*) and promote floral meristem identity at the shoot apex (Abe et al., 2005; Wigge et al., 2005). Expression of *CO* in dark periods of a long night, however, results in degradation of CO protein and no *FT* activation.

Genes with similarity to *GI*, *CO*, and *FT* have been identified in many agronomically important grass species (Yano et al., 2000; Kojima et al., 2002; Griffiths et al., 2003; Hayama et al., 2003; Nemoto et al., 2003; Faure et al., 2007; Danilevskaya et al., 2008a). In rice, quantitative trait loci (QTL) associated with different flowering times, or *Heading dates* (*Hd*), were found to correspond to specific genes orthologous to versions of Arabidopsis flowering-time regulatory genes. Most notably, *Hd1* was found to encode an ortholog of the *CO* gene (Yano et al., 2000), and *Hd3a* corresponds to a gene with the same function as *FT* (Kojima et al., 2002). So far, the functional significance of these genes in flowering time has been shown in rice (Yano et al., 2000) and, to some extent, in wheat (Bonnin et al., 2008). The putative *CO* ortholog in perennial ryegrass (*Lolium perenne*), a long-day species, has also been shown to cause early flowering when overexpressed in Arabidopsis (Martin et al., 2004). Miller et al. (2008) reported a putative maize *CO* ortholog (*conz1*) that maps to a location that is syntenic with the rice *Hd1* and whose expression appears to vary in a circadian pattern. Similarly, a large maize *FT*-related gene family called *ZCN* (for *Zea CENTRORADIALIS*), after the first member of this protein discovered in *Antirrhinum* (Bradley et al., 1996), was described with some of the members exhibiting leaf-specific expression patterns that suggest a florigenic function (Danilevskaya et al., 2008a). Moreover, one member of this family, *ZCN8*, physically interacts with a shoot meristem-localized FD-like protein. The gene encoding this bZIP protein, *delayed flowering1*, corresponds to one of only three genes identified so far that, when mutated, cause a late-flowering phenotype in maize (Muszynski et al., 2006). Overexpression of a wheat version of *FT*, *TaFT*, in transgenic wheat caused earlier flowering in this temperate grass (Yan et al., 2006). More recently, Li and Dubcovsky (2008) showed that TaFT protein interacts with two bZIP putative orthologs of FD, called TaFDL2 and TaFDL6, and that this interaction mediates activation of the wheat *VERNALIZATION1* (*VRN1*), a MADS-box gene with high similarity to *AP1* (Yan et al., 2003).

THE MEDIUM AS THE MESSAGE: DO GRASS FT ORTHOLOGS ACT AS FLORIGENIC SIGNALS?

An interesting feature of the Arabidopsis CO/FT system is that FD protein functions at the shoot meristem, yet CO activates FT only in mature leaf tissue (An et al., 2004). Thus, the implications of the recent finding that FT protein is translated in leaf vasculature cells, enters the phloem stream, and migrates to the shoot apex to interact with FD, suggests that FT protein has properties of the long-sought florigen (Corbesier et al., 2007). Biochemical studies have shown that phloem sap is chock full of all sorts of

macromolecules, including proteins, but the identification of FT as the signal provides a nice finishing touch to the chain of events that start with photoperiod induction.

One of the original criteria of florigen is that it is a universal signal that is common to all flowering plants. Do grass FT orthologs act as mobile flowering signals? Preliminary evidence suggests that, similar to FT, the protein encoded by *Hd3a* is synthesized in leaves and migrates through the phloem to the shoot apex (Tamaki et al., 2007), although direct evidence that mobile Hd3a causes flowering has yet to be shown. More recently, the report that *RFT1*, another *FT*-like homolog in rice closely related to *Hd3a*, has a similar or supportive role in causing flowering suggests that the story may be more complicated, and that there may be a multitude of florigenic proteins (Komiya et al., 2008). Of course, there is no a priori reason why *FT* and its orthologs are long-distance proteins that act the same way in all species. However, the finding that *Hd3a*, and *FT* orthologs in dicots such as tomato (*Solanum lycopersicum*), melon (*Cucumis melo*), and trees, also encode mobile long-distance signals gives credence to the original florigen criterion of universality (Bohlenius et al., 2006; Lifschitz et al., 2006; Lin et al., 2007). So far, only the role of rice Hd3a protein as a putative mobile, flower-inducing signal has been shown for any grass species. Future research will determine whether the photoperiod − circadian clock − CO-FT (leaf) → FT (apex) − FD − AP1 regulatory circuit, where → represents long-distance movement, is conserved among diverse species, including the grasses.

GRASSES SEE THE LIGHT AND TELL TIME TOO

One of the first investigations of the effects of daylength on grass flowering was done by Emerson (1924), who was trying to cross the wild progenitor of maize, teosinte (*Zea mays* subsp. *parviglumis*), into northern latitude maize. Working with various accessions of teosinte, and inspired by the recent discovery of photoperiodism by Garner and Allard (1920), Emerson found that teosinte had an absolute requirement for short-day conditions to flower. As little as 2 weeks of 10-h days could induce these plants to flower months earlier than uninduced plants, which would otherwise flower in October in response to shortening days. Teosinte plants kept under long-day conditions do not flower (J. Colasanti, unpublished data).

Migration of crop grasses into different latitudes required that they adopt other signals to induce flowering so that they could adapt to different growing seasons. Because the underlying principle of flowering time is the synchronization of the plant's internal rhythms with environmental conditions, alterations in daylength associated with seasonal changes are among the most accurate cues to determine the right time to flower. In grasses, it is clear that the core photoperiod response pathway is largely conserved with Arabidopsis, albeit less well understood (Laurie et al., 2004; Turck et al., 2008). It is interesting to note that, although major components of photoperiod sensitivity are conserved among distantly related species, optimal flowering conditions are distinctly different among the grasses. While tropical grasses, such as rice and tropical maize, respond to short days to initiate flowering, temperate cereals like wheat and barley are sensitive to lengthening days, and maize adapted to high latitude growth is largely daylength insensitive. Examples have emerged that may shed light on how these differing demands are addressed within the framework of the conserved CO/FT pathway. In rice, for example, reduced *Hd1* activity results in early flowering in long days (Yano et al., 2000), an observation that led to the discovery that conserved *OsGI*/*Hd1* genes cooperate to inhibit flowering under noninductive conditions (Hayama et al., 2003). This dual function of *Hd1* as both repressor and activator of *Hd3a* is likely dependent on levels of active photoreceptor phytochrome B (*phyB*), Pfr, which accumulates during long days (Izawa et al., 2002). An observation that further supports this model of *Pfr*/*Hd1* repressor action is the extremely early-flowering phenotype of *photoperiodic sensitivity5* (*se5*) mutants in long days. These rice mutants also lack typical phytochrome responses, substantiating the role of *SE5* in phytochrome biosynthesis (Izawa et al., 2000).

Further evidence for grass-specific modulation of CO/FT activity comes from studies with spring wheat, in which the wheat *CO* ortholog, *TaHd1*, was able to complement a rice line with a nonfunctional *Hd1* allele, and resulted in early flowering under long days, which are inductive for wheat but not rice (Nemoto et al., 2003). So it seems that, although CO protein is conserved between these grasses, alterations to the mode of CO action confer grass-specific differences in flowering-time control.

Two novel regulatory genes that appear to be absent in Arabidopsis have been shown to act in the daylength control of flowering time in rice, supporting the likelihood that unique flowering-time mechanisms have evolved in grasses. First, *Early heading date1* (*Ehd1*), which encodes a B-type response regulator, is able to activate *Hd3a* expression independently of *Hd1* in short days (Doi et al., 2004). The expression of *Ehd1* was shown recently to be kept in check by a novel CCT (for CO, CO-like, TOC1) domain protein encoded by the *Ghd7* gene, which suppresses *Ehd1* expression in long-day conditions (Xue et al., 2008).

The new-found variants of orthologous gene functions and the discovery of novel flowering-time genes support the notion of species-specific adaptation due to rapid migration of grasses outside their native range. Temperate accessions of maize are considered largely unresponsive to photoperiod in terms of flowering time, yet maize responds to variation in daylength. In addition to the distinct rhythms of *conz1* described above, photoreceptor mutants have a minor

effect on maize flowering (i.e. *phyB* mutants as well as *elongated mesocotyl1* mutants that are deficient in functional phytochromes, flower early under long-day growth conditions; Sawers et al., 2002; Sheehan et al., 2007), a situation similar to phytochrome mutants in rice. These observations point to the possibility that, while photoperiodic input likely contributes to flowering-time variation in modern maize, endogenous signaling pathways have overridden daylength cues to optimize flowering time (Fig. 1).

Dissection of flowering-time pathways in the temperate grasses wheat and barley have identified a daylength response based on what seems to be a *Triticeae* lineage-specific group of pseudo response regulator *Photoperiod* (*Ppd*) genes. In barley, a two-gene system is in place. *Ppd-H1* is a CCT domain-encoding gene under circadian control, which is the major determinant of barley photoperiod response and promotes flowering in inductive long days (Turner et al., 2005). *Ppd-H2* expressed in winter varieties is inhibitory to flowering in noninductive photoperiods (Turner et al., 2005). In contrast to barley, dominant wheat *Ppd-1* alleles are constitutively expressed, thus reducing photoperiod sensitivity and causing early flowering in short days (Worland et al., 1998). Interestingly, reduced expression of barley *CO*-like genes, *HvCO1* and *HvCO2* in the *ppd-H1* mutant, combined with significantly lower levels of *HvFT* and a late-flowering phenotype in long days, provides a possible link between photoperiod perception by the *Ppd* genes and the downstream CO/FT floral induction module (Turner et al., 2005).

VERNALIZATION IN TEMPERATE GRASSES AND ARABIDOPSIS

Like many of the temperate grasses, some Arabidopsis ecotypes flower earlier in response to prolonged cold (i.e. vernalization). This is an adaptive trait that prevents seeds sown in late summer or early fall from flowering until the next spring, thereby delaying flowering until the spring rather than just before a possibly harsh winter. Analyses of mutants that interfere with this vernalization response have defined a separate pathway in the flowering model (for review, see Sung and Amasino, 2005). Vernalization does not create an inductive signal; rather, it results in the removal of a block to flowering that must be overcome so that inductive signals can cause flowering in plants that are suitably competent to undergo the floral transition. The Arabidopsis *FLOWERING LOCUS C* (*FLC*) gene has been identified as a central flowering repressor whose activity is reduced by vernalization. *FLC* encodes a MADS-box transcription factor that represses flowering by directly interfering with *FT* expression in leaves and *FD* expression at the SAM (Searle et al., 2006). Most Arabidopsis ecotypes that flower early without vernalization have nonfunctional versions of *FLC*, or its positive regulator, *FRIGIDA* (*FRI*; Fig. 1).

Vernalization in temperate cereals with a winter growth habit, such as winter wheat and barley, similarly removes a block to flowering so that the plant can perceive inductive signals, such as long-day photoperiods. However, neither *FLC* nor *FRI* orthologs have been found in grasses so the underlying molecular machinery controlling vernalization in winter cereals is different from that of Arabidopsis. Three genes that act together to maintain a winter growth habit in cold-tolerant pooid grasses have been identified: *VRN1*, *VRN2*, and *VRN3* (for review, see Trevaskis et al., 2007a). *VRN1* encodes an *AP1*-related MADS-box protein that falls into the *FRUITFULL1* (*FUL1*) gene lineage (Preston and Kellogg, 2006). *VRN1* expression is low in the absence of vernalization, but transcript levels increase in direct proportion to time of exposure to cold temperatures (Yan et al., 2003; Trevaskis et al., 2003). Modulation of *VRN1* levels thus provides a quantitative measure of the length of time a plant is exposed to cold, with longer exposure resulting in earlier flowering. The finding that *VRN1* expression is detected first in leaves and later at the shoot apex suggests that it has a bifunctional role; first, it accelerates flowering by mediating a systemic response to vernalization and, second, *VRN1* specifies inflorescence meristem identity at the shoot apex (Trevaskis et al., 2007b; Preston and Kellogg, 2008). In maize, which does not respond to vernalization, a potential ortholog of *VRN1*, *ZMM4*, was identified in a differential expression screen comparing vegetative and reproductive shoot apices and shown to cause earlier flowering when ectopically expressed in transgenic maize (Danilevskaya et al., 2008b). Therefore, the floral meristem promotion function of this MADS-box transcription factor, along with *FUL2* (Preston and Kellogg, 2008), appears to be conserved in tropical and temperate grasses.

The vernalization function of *VRN1* acts through the repression of *VRN2* (Hemming et al., 2008). In this respect, there is a superficial similarity between grass and Arabidopsis vernalization in that *FLC* and *VRN2* both encode floral repressors whose activities must be overcome to allow inductive signals to act on a competent apex. However, apart from encoding different types of transcription factor proteins (FLC = MADS-box; VRN2 = CCT zinc finger), other differences exist. For example, the main role of *FLC* is repression of *FT*; during vernalization, prolonged cold exposure reduces *FLC* levels and allows inductive signals to activate *FT*. In temperate cereals, *VRN2* acts as a repressor of flowering under long-day conditions, which suggests that *VRN2* is not strictly a vernalization gene, but that its job is to repress flowering under long days of summer so that plants do not initiate flowering prior to winter (Trevaskis et al., 2007a). More evidence of mechanistic similarities between vernalization and photoperiod components comes from the report of rice *Ghd1*, which encodes a CCT-like zinc finger that is closely related to *VRN2* (Xue et al., 2008). Rice does not respond to vernalization, but, similar to

pooid *VRN2*, *Ghd1* represses flowering in noninductive long days. So, in this case, similar mechanisms are used to integrate different environmental stimuli.

The discovery that *VRN3* corresponds to an ortholog of Arabidopsis *FT* reinforces the intimate link between the vernalization response and photoperiod induction. (Note, pooid versions of *VRN3* are now known as *TaFT* in wheat and *HvFT1* in barley.) Further, experiments conducted with doubled haploid barley have led to speculation that *HvFT1* acts as a possible point of integration between the requirement for low temperature and inductive long days to cause flowering. In the absence of *VRN2*, flowering time becomes dependent strictly on daylength cues mediated through *Ppd-H1* (Fig. 1). Thus, flowering is early if *Ppd-H1* is present, whereas plants lacking both *VRN2* and *Ppd-H1* flower late (Hemming et al., 2008). Therefore, it seems that, in the long days of summer, *VRN2* counteracts *Ppd-H1* to prevent flowering prior to vernalization, and that once vernalized, a plant is competent to respond to long days through the action of *Ppd-H1*, which, ultimately, acts to up-regulate *HvFT1*.

THE SIGNAL WITHIN: ENDOGENOUS CUES THAT CAUSE FLOWERING

Arabidopsis mutants that affect flowering under both inductive and noninductive conditions are placed in the autonomous pathway. Autonomous flowering is inherently more difficult to understand compared to other pathways because the signals are linked to developmental processes rather than environmental stimuli that can be switched on and off. For example, most of what we know about flowering in temperate grasses was revealed from examining the underlying causes of vernalization, and in rice most of the genes identified have a role in photoperiod-induced flowering. This may explain why relatively little is known about flowering time in maize compared to other grasses because most studies are done with nearly day-neutral maize that relies almost exclusively on autonomous signals to control flowering. Most plants have a functioning autonomous flowering pathway because flowering usually occurs even in the absence of inductive environmental signals. Nevertheless, a few reports of autonomous flowering genes are emerging from the grasses. The difficulty in identifying autonomous pathway genes may explain why, in the long history of maize genetics, only a handful of mutants with a dramatic effect on flowering time have been identified (for review, see Colasanti and Muszynski, 2008). Although QTL analysis has identified over 300 loci associated with flowering-time differences, most of these effects are minor (Chardon et al., 2004). The *indeterminate1* (*id1*) mutation has the most severe effect on flowering time of any maize gene, yet *id1* does not seem to lie within a QTL with a large effect on flowering time. More incisive genome analyses are under way to determine whether a nearby medium effect QTL is in fact associated with *id1* function (E. Buckler, personal communication). Maize *id1* encodes a novel zinc finger transcriptional regulator that appears to act in the autonomous pathway (Colasanti et al., 1998; Kozaki et al., 2004). The invariability of *id1* transcript and ID1 protein levels in response to diurnal light changes further suggests a role in autonomous control (Wong and Colasanti, 2007). The finding that *id1* acts only in developing leaves suggests that *id1* regulates either the production or transmission of a leaf-derived, florigenic signal. At present, there appears to be no connection between *id1* function and putative *FT*-like orthologs in maize that may encode florigenic proteins.

The absence of a clear *id1* ortholog in Arabidopsis suggests that *id1* represents yet another regulatory gene that does not have a counterpart in all higher plants (Colasanti et al., 2006). However, recent reports reveal that *id1* function may be prevalent in grasses. Ten years after the isolation of maize *id1*, three papers have appeared almost simultaneously describing a rice *id1* ortholog. These papers confirm that a rice equivalent of *id1*, called *RID1* (Wu et al., 2008), *Ehd2* (Matsubara et al., 2008), or *OsId1* (Park et al., 2008), exists in rice and functions as a key regulator of the flowering transition. (For the sake of clarity, we will call it *OsID1*.) Moreover, similar to maize, the highest levels of *OsID1* are detected in developing leaves and its expression is unperturbed by diurnal day/night cycles. All three papers report that *OsID1* acts upstream of *FT* ortholog *Hd3a*, as well as the unique *Ehd1* gene. *OsID1* may act independently of the *CO* ortholog *Hd1*; however, an interesting observation by Wu et al. (2008) is that loss of *OsID1* function results in plants that never flower, even under inductive SD conditions. This has prompted the authors to designate *OsID1* as a master regulator of flowering that stands astride both photoperiod and autonomous pathways. Nevertheless, the discovery of an *id1* ortholog in rice suggests that species even closer to maize, such as sorghum and sugarcane, may have *id1* equivalents as well, and this may shed some light on autonomous flowering in grasses.

In other grass species, as recently summarized by Cockram et al. (2007), other cereal loci, termed *earliness per se* (*eps*), have been shown to affect flowering time independently of environmental signals. Although many *eps* QTL have been mapped in wheat and barley, these sources of flowering-time variation remain poorly characterized to date, whereas the debate over whether they are truly unaffected by environmental cues remains unresolved. However, the existence of *eps* loci underlines the fact that many plants utilize endogenous cues to coordinate flowering time with their developmental or physiological status (Fig. 1).

HORMONES AND FLOWERING: IMPORTANT FOR SOME SPECIES, NOT OTHERS

Arabidopsis mutants with reduced GA synthesis are late flowering and therefore a separate GA pathway

has been included in the floral regulatory model. In ryegrass, GA appears to play a major role in the floral transition, and it has been suggested that it acts as a leaf-derived, long-distance signaling molecule (King et al., 2006). Whether GA has a similar important role in other grasses has not been reported, although there could be minor effects on flowering due to reduced GA levels.

In some crop plants, hormones, or chemicals that mimic their activity, are used to alter flowering time. One example is the commercial use of ethephon (2-chloroethylphosphonic acid), which is converted to ethylene, to prevent flowering in sugarcane and increase sugar yields (Moore and Osgood, 1989). However, it is not clear whether ethylene acts by inhibiting the shoot apex from initiating further growth or by allowing vegetative growth to resume at the expense of reproductive organ formation.

PERSPECTIVES: WHAT'S NEXT?

Great progress has been made in deciphering the molecular mechanisms that regulate flowering in both Arabidopsis and agronomically significant grass species, but fundamental aspects of this important developmental transition remain unanswered. In particular, the underlying physiological changes that cause or are associated with the transition to flowering have yet to be extensively characterized. For example, vernalization pathways have been deciphered at the molecular level, but how cold-induced biochemical changes are perceived and transmitted to the regulatory network through physiological response is still unknown. Similarly, day-neutral plants, such as temperate maize and rice, flower when a developmental or physiological threshold is reached, yet the nature of these endogenous physicochemical changes is unknown. The next obvious step is to link the regulatory networks, which are controlled largely by pivotal transcription factors, with the downstream metabolic alterations that mediate the activity of these regulators.

An emerging precedent from studies of flowering, especially from research into Arabidopsis vernalization, is that epigenetic mechanisms are at work to establish a cellular memory that maintains a florally competent SAM once the stimulus (cold) is no longer present (Dennis and Peacock, 2007). In this model, the memory of winter is imprinted in SAM cells such that repression of floral inhibitors is maintained once spring returns. Future research may show that epigenetic mechanisms are more widespread, perhaps operating in the grass SAMs to maintain competency to flower.

Can knowledge gleaned from studies of monocot cereals inform us about how flowering is controlled in other grasses? Given that many diverse and unique grass-specific mechanisms are turning up, a complete understanding of flowering may require consideration on a case-by-case basis. One intriguing phenomenon concerns certain bamboos that flower synchronously decades after planting, even when offshoots derived from the original plant are separated by many degrees of latitude (Isagi et al., 2004). In this case, an autonomous signal of unknown origin must indicate when flowering will occur. Clearly a deeper understanding of flowering time mechanisms is required to answer these questions.

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