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Measuring Daylength: Pharbitis Takes a Different Approach

In many plants species, the initiation of flowering is determined by seasonal changes in daylength. Long-day (LD) plants, such as *Arabidopsis*, initiate flowering when daylength grows longer, whereas short-day (SD) plants, such as rice, initiate flowering under shorter days. Other cues that affect flowering, such as vernalization (requirement for lengthy cold period) and developmental timing, may be superimposed on daylength responses. The last common ancestor of dicots and monocots existed ~150 to 300 million years ago (Sanderson et al., 2004), so *Arabidopsis* (a dicot) and rice (a monocot) are distantly related, and a comparison of the components involved in the photoperiodic response to flowering in these two species might provide a starting point for understanding the mechanistic basis of these opposing responses. However, photoperiodic responses to flowering have evolved independently several times throughout evolutionary history, underscoring a need to examine a wider range of species to fully understand this phenomenon. For example, the monocot grasses include both LD and SD species, so it is important to ask how LD grasses differ from (or are similar to) the SD grass rice and the LD dicot *Arabidopsis*.

In this issue of *The Plant Cell*, **Hayama et al. (pages 2988–3000)** investigate the photoperiodic response to flowering in the SD dicot Pharbitis (*Ipomoea nil*; also called Japanese morning glory; see figure), a member of the Convolvulaceae in the order Solanales. The Solanales are more closely related to *Arabidopsis* than are the monocot grasses but still are distant relatives to *Arabidopsis*, which belongs to the Brassicales. The Solanales and Brassicales belong to two distinct major clades within the eudicots, the asterids and rosids, respectively, which are believed to have diverged by the early to mid Cretaceous period (>100 million years ago; Sanderson et al., 2004).

A number of investigations have revealed that homologs of *Arabidopsis* FLOWERING LOCUS T (*FT*) are central players regulating flowering in numerous diverse species, including SD and LD plants, such as *Arabidopsis*, rice, and poplar as well as in day-neutral plants, such as some varieties of tobacco, tomato, and squash (cucurbits). *Arabidopsis* *FT* encodes a RAF kinase inhibitor-like protein that interacts with other proteins, including FD, to activate the floral initiation genes *SOC1* and *AP1* in the shoot apical meristem. In *Arabidopsis*, rice, and a number of other species that have been investigated, *FT* induces flowering, and differences in photoperiodic re-

sponses between LD and SD plants, as well as other factors affecting flowering, such as vernalization and developmental stage, may in large part reflect differences in the regulation and activity of *FT*.

In *Arabidopsis*, the transcription factor CONSTANS (*CO*) activates transcription of *FT*, and flowering is promoted when *CO* accumulates to a threshold level in the nucleus (reviewed in Hayama and Coupland, 2004; Kobayashi and Weigel, 2007). *CO* induces the expression of *FT*, and the *FT* protein (possibly also *FT* mRNA) is transported through the phloem to the shoot apical meristem, where it plays a principal role in the induction of flowering. *CO*



Pharbitis Grown under Noninductive LD (Left) and Inductive SD (Right) Conditions.

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expression in *Arabidopsis* is regulated by the circadian clock. Under SDs, there is a diurnal peak in expression during the night, whereas under LDs, the expression pattern is broadened and begins to rise in the light. The circadian rhythm of expression, together with degradation of a repressor of CO in the light, stabilization of CO protein in the light, and degradation in the dark, ensure that CO protein only accumulates in the nucleus under LDs and therefore that *FT* transcription, and subsequent promotion of flowering, occurs under LDs but not SDs (Valverde et al., 2004). Other signaling pathways that affect flowering, such as the autonomous pathway and vernalization, also appear to converge on *FT*; thus, it represents a major control point for intergrating multiple environmental and developmental signals that influence flowering.

Interestingly, the main differences in the photoperiodic flowering response between *Arabidopsis*, an LD plant, and rice, an SD plant, appears to be that the rice homolog of CO, called Hd1, acts as a repressor of FT (which in rice is called Hd3a) rather than an activator (Hayama et al., 2003). This suggests that the various mechanisms regulating CO in *Arabidopsis* and Hd1 in rice (the circadian clock and factors affecting repression of gene expression as well as stabilization and degradation of CO/Hd1 protein) are at least somewhat similar in these two species.

Hayama et al. examined the function and regulation of FT homologs in the SD dicot *Pharbitis* and compared the photoperiodic mechanisms of *Pharbitis* with those of *Arabidopsis* and rice. The authors isolated two homologs of *FT* in *Pharbitis*, called Pn *FT1* and Pn *FT2*. (Although the scientific name of *Pharbitis* is now *I. nil*, the authors retained the two-letter taxonomic designation Pn, as the species was formerly known as *Pharbitis nil* and the Pn designation has been widely used in the past). Overexpression of Pn *FT1* accelerated flowering in *Arabidopsis* and *Pharbitis*, and the accumulation of Pn *FT1* and Pn *FT2* mRNA occurred only under conditions that promote flowering (SD), suggesting that Pn *FT1* functions like At *FT* and Os *Hd3a* to promote flowering.

In *Arabidopsis*, *FT* expression is strongly dependent on exposure of plants to light and on the circadian rhythm of CO expression, such that *FT* transcription shows a circadian rhythm under constant light (Harmer et al., 2000; Imaizumi et al., 2005). The prevailing model of the photoperiodic response in *Arabidopsis* involves light activation of CO protein, which, as noted above, is orchestrated by a number of factors that affect (negatively and positively) CO expression and CO protein stability such that *FT* expression sufficient to promote flowering only occurs under LDs.

Hayama et al. found that, by contrast, Pn *FT1* and *FT2* mRNA levels show robust cycling under constant darkness but do not show a circadian rhythm under constant light. The authors concluded that activation of Pn *FT* in darkness is an important component of the photoperiodic flowering response in *Pharbitis*, unlike the situation in *Arabidopsis*. Also, the rhythm determining the timing of Pn *FT* expression was started at dusk by the light–dark transition, and Pn *FT* expression was activated only if the night was sufficiently long enough. Furthermore, the pattern of expression of Pn CO, the closest described homolog of At CO in *Pharbitis*, was not highly correlated with the expression of Pn *FT1* and *FT2* under darkness, leading the authors to conclude that CO is not a principal regulator of *FT* expression in *Pharbitis*. They postulate the existence of another clock-controlled gene, whose phase is set specifically by the light–dark transition, as being a principal factor regulating Pn *FT* expression.

Identification of such genes will be important to arrive at a complete picture of the regulation of FT activity and the photoperiodic control of flowering in this species. It will also be important to determine the function of CO in *Pharbitis*. Does it act either to activate or repress *FT* under any conditions, or does it have another function altogether?

As noted by Hayama and Coupland (2004), there are at least several plant genera, including *Nicotiana* and *Lemna*, that include both SD and LD plants, suggesting that a daylength response can diverge rapidly during evolution. The work of Hayama et al. suggests that widely

different mechanisms may have evolved to control the photoperiodic response of flowering in plants and that there may be other mechanisms for measuring daylength in addition to those described in *Arabidopsis*. In addition, the work illustrates the importance of comparative approaches in gaining new insights to this fundamental problem in plant biology.

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REFERENCES

- Harmer, S.L., Hogenesch, J.B., Straume, M., Chang, H.S., Han, B., Zhu, T., Wang, X., Kreps, J.A., and Kay, S.A. (2000). Orchestrated transcription of key pathways in *Arabidopsis* by the circadian clock. *Science* **290**: 2110–2113.
- Hayama, R., Agashe, B., Luley, E., King, R., and Coupland, G. (2007). A circadian rhythm set by dusk determines the expression of *FT* homologs and the short-day photoperiodic flowering response in *Pharbitis*. *Plant Cell* **19**: 2988–3000.
- Hayama, R., and Coupland, G. (2004). The molecular basis of diversity in the photoperiodic flowering responses of *Arabidopsis* and rice. *Plant Physiol.* **135**: 677–684.
- Hayama, R., Yokoi, S., Tamaki, S., Yano, M., and Shimamoto, K. (2003). Adaptation of photoperiodic control pathways produces short-day flowering in rice. *Nature* **422**: 719–722.
- Imaizumi, T., Schultz, T.F., Harmon, F.G., Ho, L.A., and Kay, S.A. (2005). FKF1 F-box protein mediates cyclic degradation of a repressor of CONSTANS in *Arabidopsis*. *Science* **309**: 293–297.
- Kobayashi, Y., and Weigel, D. (2007). Move on up, it's time for change mobile signals controlling photoperiod-dependent flowering. *Genes Dev.* **21**: 2371–2384.
- Sanderson, M.J., Thorne, J.L., Wikström, N., and Bremer, K. (2004). Molecular evidence on plant divergence times. *Am. J. Bot.* **91**: 1656–1665.
- Valverde, F., Mouradov, A., Soppe, W., Ravenscroft, D., Samach, A., and Coupland, G. (2004). Photoreceptor regulation of CONSTANS protein in photoperiodic flowering. *Science* **303**: 1003–1006.

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