

Shedding light on the role of seasonal flowering in plant niche transitions

Siri Fjellheim^{ac} and Jill C. Preston^b

^aDepartment of Plant Sciences, Faculty of Biosciences, Norwegian University of Life Sciences, 1432 Ås, Norway

^bDepartment of Plant Biology, The University of Vermont, Burlington, Vermont 05405

^cCorresponding author

At the beginning of the 20th century, Garner and Allard (1920) described photoperiodic responses in plants in detail for the first time. Whereas short-day (or more accurately, long-night) plants only flowered when day length dropped below a critical threshold, long-day (short-night) plants only flowered if day length exceeded such a threshold. Some years later, Garner (1933) put the significance of photoperiodic flowering into an ecological context to explain how environmental conditions favor different photoperiodic types. In temperate regions, the critical day length of a short-day species would have passed before temperatures are favorable for flowering in the spring. In contrast, critical day lengths of temperate long-day taxa coincide with increasingly favorable temperatures, favoring the presence of these species at higher latitudes.

Given the importance of flowering time for plant fitness, there has been surprisingly little focus on how flowering responses have evolved. It is suggested that the drastic fall in temperatures at the turn of the Eocene-Oligocene 34 million years ago induced the formation of temperate clades (Kerkhoff et al., 2014). Concomitantly, seasonality increased toward the poles (Eldrett et al., 2009), increasing the importance for correct timing of seasonal responses at higher latitudes. In this essay, we hypothesize that repeated transitions between tropical and temperate regions were constrained by the ability of plants to correctly use seasonal cues – specifically photoperiod – for timely reproduction.

As we know from comparisons between distantly related species like the mustard *Arabidopsis thaliana*, and the grasses (Poaceae) rice (*Oryza sativa*) and barley (*Hordeum vulgare*), flowering is controlled by complex molecular pathways that are partly conserved across land plants. Central to sensing and responding to photoperiod is the *CONSTANS-FLOWERING LOCUS T (CO-FT)* regulon. FT and related proteins function as universal signals to promote flowering and are

facilitated by photoperiod in both long- and short-day taxa. CO is a transcriptional activator of *FT* expressed diurnally under control of the circadian clock (reviewed in Song et al., 2010). In long-day *A. thaliana* and barley, CO and CO1, respectively, induce flowering through activation of *FT* and the *FT*-like gene *VRN3*. Remarkably, in short-day subtropical rice, the CO homolog *Hd1* also interacts with *Hd3a*, the rice homolog of *FT*. However, in contrast to *A. thaliana* and barley, rice Hd1 represses *Hd3a* and prevents flowering under unfavorable long-day conditions. For an extended overview of seasonal flowering responses in grasses see Fjellheim et al. (2014).

What modulates the conserved *CO-FT* regulon to give different outputs under different conditions is largely unknown. Both transcription factors are members of gene families. The role of other family members in flowering time and related traits is little understood, but they may have profound implications for promoting or constraining trait evolution through natural selection. For instance, in barley, two copies of CO (CO1 and CO2) exist. Both are involved in *FT/VRN3* induction (Mulki and von Korff, 2016), but their evolutionary history and role in photoperiodic shifts since the divergence from rice is unknown. Another member of the CO gene family that has been extensively studied in grasses is *VRN2* (*Ghd7* in rice, Woods et al., 2016). *VRN2* represses flowering under long-days both in short-day rice and long-day barley, in the latter case to suppress flowering prior to impending winter. In the most speciose group of temperate grasses – the so-called core group of subfamily Pooideae (e.g. barley) – *VRN2* is negatively regulated by proteins of the vernalization pathway (Woods et al., 2016). However, in non-core Pooideae, *VRN2* transcription is not repressed by cold (Woods et al., 2016). Together, these data paint a picture of successive modifications to an ancestral flowering time pathway, the rewiring of which can reinforce precision timing in the most extreme environments where precocious or delayed flowering comes with heightened fitness costs.

Flowering is not the only trait under photoperiodic control and other traits include cold acclimation, tuberization, bud set, and growth cessation. Thus, molecular crosstalk has the potential to constrain the direction of flowering time evolution through either antagonistic or adaptive pleiotropy. For example, it has been shown that *FT*-like genes function in growth regulation in tomato (*Solanum lycopersicum*) (Lifschitz et al., 2006; Soyk et al., 2017), that different *FT* genes are involved in regulation of tuberization and flowering time in potato (*S. tuberosum*) (Navarro et al., 2011) and that the *CO-FT* regulon is involved in bud set and growth

cessation in aspen trees (Böhlenius et al., 2006). This exemplifies that molecular adaptation of one trait is not independent of others, and hence evolution of the photoperiodic sensory machinery is contingent on phylogenetic history and genetic architecture.

The time is perhaps right to test Garner's (1933) predictions about species distributions along latitudinal gradients in a phylogenetic context to learn to what extent the evolution of photoperiodic flowering responses is constrained by the integrated control of adaptive (or indeed maladaptive) syndromes. This will require a detailed knowledge of the phylogenetic history of transitions between long- and short-day flowering in relation to niche shifts, and clade-specific insights into individual gene function within the context of higher order network operation.

Photoperiodic control of flowering is one of the traits most intensively studied in agricultural crops. This knowledge can be used for evolutionary studies in a phylogenetically widespread sample of model crop relatives. The growing number of fully sequenced genomes, as well as high throughput sequencing accessible for non-model species, provide an excellent starting point for exploring flowering time evolution and its molecular basis. The challenge will be to test a large number of non-model species for photoperiodic flowering responses using time-demanding experimental approaches, and to carefully dissect the underlying molecular mechanisms of these responses. Model system choice is key. A good system would be one that includes both tropical and temperate clades, several model crop species, and plentiful genomic resources, such as the grass family. Grasses are distributed across all Earth's major biomes and have two major (Pooideae and Danthonioideae), and several minor, temperate clades. Moreover, the grass family contains phylogenetically diverse tropical and temperate crop species, a substantial body of genomic resources, and several known examples of both long- and short-day flowering taxa.

Increasing our knowledge about evolution and genetic control of flowering responses is timely in a period where climate is changing rapidly. The delicate fine-tuning of flowering time is the result not only of photoperiodic cues but also of other signals, e.g. temperature. Although seasonal shifts in photoperiod will remain constant on a global scale, warming trends and increasingly frequent extreme weather events have already created mismatches between previously synchronized phenological cues and favorable time-windows for flowering. Understanding if and how plants keep pace with such changing conditions will provide insights into the potential constraints on

rapid evolution, and inform efforts for agricultural improvement as our demand for food production increases.

Acknowledgements

The authors thank Marian Schubert and two anonymous reviewers for comments on the manuscript. This work was funded by the Research Council of Norway (Grant 231009 to Siri Fjellheim)

References

- Bohlenius, H., T. Huang, L. Charbonnel-Campaa, A. M. Brunner, S. Jansson, S. H. Strauss, and D O. Nilsson. 2006. *CO/FT* regulatory module controls timing of flowering and seasonal growth cessation in trees. *Science* 312: 1040-1043.
- Eldrett, J. S., D. R. Greenwood, I. C. Harding, and M. Huber. 2009. Increased seasonality through the Eocene to Oligocene transition in northern high latitudes. *Nature* 459: 969-991.
- Fjellheim, S., S. Boden, and B. Trevaskis. 2014. The role of seasonal flowering responses in adaptation of grasses to temperate climates. *Frontiers in Plant Science* 5.
- Garner, W. W., and H. A. Allard. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Journal of Agricultural Research* 18: 553–606.
- Garner, W. W. 1933. Comparative responses of long-day and short-day plants to relative length of day and night. *Plant Physiology* 8: 347-356.
- GBIF Secretariat: GBIF Backbone Taxonomy. doi:10.15468/39omei Accessed via <http://www.gbif.org/species/3073> and <http://www.gbif.org/species/2704913> on 26th January 2018
- Kerckhoff, A. J., P. E. Moriarty, and M. D. Weiser. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* 111: 8125-8130.
- Lifschitz, E., T. Eviatar, A. Rozman, A. Shalit, A. Goldshmidt, Z. Amsellem, J. P. Alvarez, and Y. Eshed. 2006. The tomato *FT* ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. *Proceedings of the National Academy of Sciences of the United States of America* 103: 6398-6403.
- Mulki, M. A., and M. Von Korff. 2016. *CONSTANS* controls floral repression by up-regulating *VERNALIZATION2 (VRN-H2)* in barley. *Plant Physiology* 170: 325-337.
- Navarro, C., J. A. Abelenda, E. Cruz-Oró, C. A. Cuéllar, S. Tamaki, J. Silva, K. Shimamoto, and S. Prat. 2011. Control of flowering and storage organ formation in potato by *FLOWERING LOCUS T*. *Nature* 478, 119.
- Song, Y. H., S. Ito, and T. Imaizumi. 2010. Similarities in the circadian clock and photoperiodism in plants. *Current Opinion in Plant Biology* 13: 594-603.
- Soyk, S., N. A. Müller, S. J. Park, I. Schmalenbach, K. Jiang, R. Hayama, L. Zhang, J. Van Eck, J. M. Jiménez-Gómez, and Z. B. Lippman. 2016. Variation in the flowering gene *SELF PRUNING 5G* promotes day-neutrality and early yield in tomato. *Nature Genetics* 49, 162.

Woods, D. P., M. A. McKeown, Y. X. Dong, J. C. Preston, and R. M. Amasino. 2016. Evolution of *VRN2/Ghd7*-like genes in vernalization-mediated repression of grass flowering. *Plant Physiology* 170: 2124-2135.

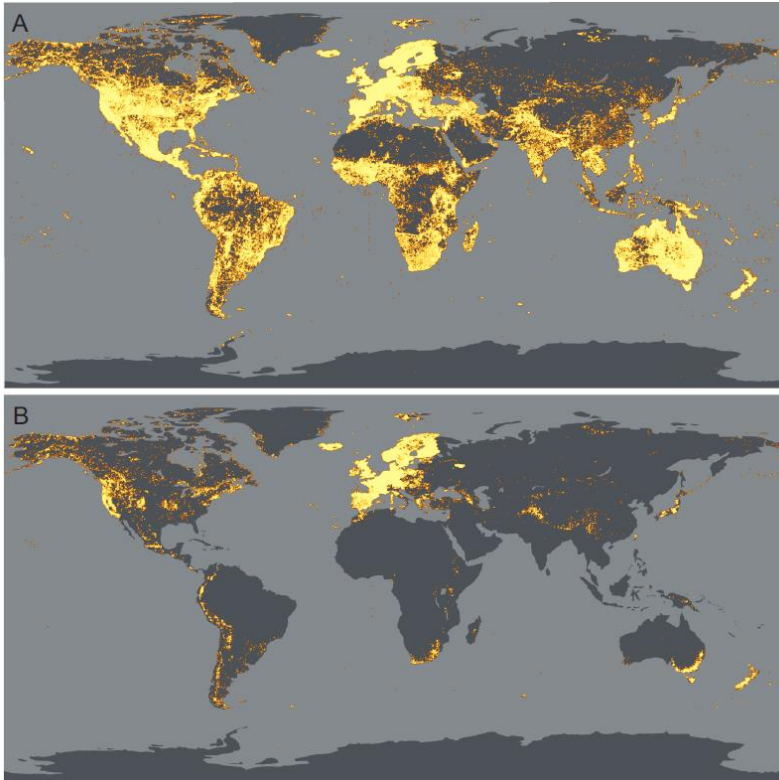


Figure 1. A. The grass family (Poaceae) is distributed on all continents. B. However, not all grass species are distributed everywhere. The subfamily Pooideae is mainly distributed in temperate regions, here represented by the genus *Festuca*, one of the largest genera in Pooideae. Data downloaded from the Global Biodiversity Information Facility (GBIF Secretariat, 2018)