With an increasing human population, we are facing the need to grow more food, potentially expanding the environmental tolerances of our staple crops (Godfray et al., 2010; Campbell et al., 2016). The barriers to this include temperature, rainfall, soil type, daylength, and seasonality. In this issue, Williams et al., in their study entitled ‘The genetic architecture of flowering time changes in pea from wild to crop’, advance our understanding of crop adaptation to photoperiod by revealing the genetic basis of photoperiod sensitivity in peas.

Plants are adapted to their local environment in terms of the environmental cues (temperature and daylength) that promote or repress flowering, ensuring that this key physiological transition occurs at a time when the conditions are best suited for producing flowers, fruits, and seeds. Maladaptation (e.g. translocating a temperate crop to a tropical environment) would result in no flowering, or poorly timed flowering, and a reduction in yield. Based on the environmental cues plants use to transition into flowering, they are typically separated into long-day (LD), short-day (SD), and day-neutral types.

Understanding the genetic basis of flowering time, especially in relation to different environmental conditions, is a vital goal if we wish to expand the environments in which we can grow our crops (Cockram et al., 2007; McClung, 2021). Mapping studies have indicated the quantitative genetic basis of this trait in many crops and, in a handful, we know the genes underlying the trait. Some patterns have emerged in the literature; for example, photoperiod evolution in different crops can be controlled by orthologous genes (e.g. maize ZmCCT and its rice orthologue Ghd7, and PHYA in common bean and soybean). Further, several photoperiod-related genes act in pathways that include florigen/FT genes, for example soybean E1 and barley ELF3. In others, mutations affecting FT directly confer adaptive photoperiod responses and flowering induction under specific conditions (Box 1).

Less well studied is the genetic basis of flowering time under SD and LD conditions in the same germplasm, and Williams et al. buck this trend, doing exactly this for field pea (Pisum sativum). Because some photoperiod-related genes are induced only under certain daylength environments, mapping quantitative trait loci (QTLs) for flowering in one environment probably identifies only a subset of the adaptive variation and does not allow for photoperiod sensitivity to be examined. Another advantage of the approach taken by Williams et al. is generating and examining a mapping population derived from crossing the wild progenitor (P. sativum ssp. humile, an LD plant incapable of flowering under SDs) to a cultivated accession (P. sativum ssp. sativum), thus identifying more about the domestication pathway and not simply the genetic basis of flowering in the domesticate. Variation found in wild progenitors (potentially bred out of cultivated accessions) may well be adaptive in a changing climate (McCouch et al., 2013).

Pea is an important crop worldwide—approximately 9.7 Mt ha were grown in 2020 (FAO, 2020)—and a valuable model for studying adaptation to photoperiod which has clearly occurred post-domestication, allowing the latitudinal expansion of pea cultivation. Pea was one of the earliest plants domesticated in the Neolithic (Lev-Yadun et al., 2000). In addition, the extensive study of inheritance patterns in peas by Mendel has led to several important genes being cloned (reviewed in Reid and Ross, 2011).

In the study by Williams et al., the recombinant inbred line (RIL) mapping population was grown under LD (16 h light) and SD (8 h light) conditions. The population was genotyped with >4500 markers, providing a good degree of coverage and
short intermarker distances which aids in identifying candidate genes underlying QTL peaks. The genetic basis of photoperiod sensitivity has been examined in other germplasm, and three genes have been cloned that underlie this trait.

The first major finding was that five QTLs were identified with significant effects on days to flower (DTF) and were named DTF1, 3, 5a, 5b, and 6 based on the chromosome they reside on (with two on chromosome 5). Three of these (DTF1, 5a, and 6) were previously identified in pea. Two of these QTLs (DTF5a, and 6) have been cloned and the causative gene identified.

Some of the QTLs were followed up to identify candidate genes underlying each QTL. Firstly, DTF5b was shown to map close to the LE locus initially identified by Mendel, and, because of the similar phenotype observed (shorter stature, fewer nodes), it was assumed that DTF5b was equivalent to LE, a gibberellin 3β-hydroxylase (Lester et al., 1997). DTF1 and 3 were mapped in further populations wherein the target QTL was segregating but all other DTF QTLs were fixed for the wild allele; hence the role of the single QTL could be observed.

DTF1, although previously identified, had not been characterized at the molecular level. Williams et al. demonstrated that the domesticated allele in a wild background induced a domesticate-like phenotype (early flowering), and the wild allele induced a wild-like phenotype (late flowering) under both SD and LD conditions. Similar to the loci mapped above, after fixing other QTLs in the population, the marker at the peak of the QTL co-segregated with an FT paralogue, Fl1a. Expression analysis of this gene revealed higher expression in plants with the domesticated allele than with the wild allele in both LD and SD conditions.

For DTF3, similarly the domesticated allele induced early flowering, but plants with this allele flowered at an intermediate time to the parental types. At the genomic location of the QTL peak was a cluster of FT genes. Again, examining expression, the authors were able to narrow down to one of these, FT1a, probably being causative because of its differential expression between plants carrying the domesticated and wild alleles.

The action of TFL1c which underlies DTF6 was also followed up. Again, differential expression appeared to be causative in regulating the flowering response.

Whilst a mixture of expression and coding sequence changes are evident under previously identified domestication genes (Meyer and Purugganan, 2013), the genetic basis of domestication for altered flowering time in pea appears largely based upon the combination of expression and coding sequence changes.
on expression divergence. In the study of Williams et al., expression divergence between wild and domesticated pea was evident for the three genes examined which underlie DTF1 (FTa3), DTF3 (FTa1), and DTF6 (TFL1). The FT gene family is of clear importance in pea as well as in many other and diverse crops (Box 1). Mutations affecting gene expression are clearly more common than those affecting the coding region in the evolution of photoperiod response here and are apparent in many, but not all, other studies (Box 1).

A final and exciting observation is made by Williams et al. regarding a second, independent domestication of peas, recently characterized by Trněný et al. (2018). This domesticated subspecies, *Pisum sativum* ssp. *abyssinicum*, known as the Abyssinian pea or *dekoke*, is restricted to low latitudes in Ethiopia and Yemen, where days do not exceed 12.5 h in length and the ability to flower under SDs is therefore essential (Weller et al., 2012). This ability must represent either an ancient expansion of a now-extinct lineage domesticated at higher latitudes, or an in situ domestication from a now-extinct wild population already adapted to lower latitude. In either case, it opens the door in peas for investigations into the parallel evolution of adaptation to novel photoperiods and other agronomically favourable phenotypes. Such studies would provide a complement to those in common bean which was also domesticated to food security from climate change. Global Food Security 2016.

Reducing risks of parallel evolution under domestication in legumes more generally.

Keywords: Domestication, flowering time, peas, photoperiod, quantitative trait loci.

References

Bitocchi E, Bellucci E, Giardini A, et al. 2013. Molecular analysis of the parallel domestication of the common bean (*Phaseolus vulgaris*) in Mesoamerica and the Andes. New Phytologist 197, 300–313.

Blackman BK, Strasburg JL, Raduski AR, Michaels SD, Rieseberg LH. 2010. The role of recently derived FT paralogs in sunflower domestication. Current Biology 20, 629–635.

Campbell BM, Vermeulen SJ, Aggarwal PK, et al. 2016. Reducing risks to food security from climate change. Global Food Security 11, 34–43.

Cockram J, Jones H, Leigh FJ, O’Sullivan D, Powell W, Laurie DA, Greenland AJ. 2007. Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. Journal of Experimental Botany 58, 1231–44.

Cuevas HE, Zhou C, Tang H, et al. 2016. The evolution of photoperiod-insensitive flowering in Sorghum, a genomic model for panicoid grasses. Molecular Biology and Evolution 33, 2417–28.

FAO. 2020. FAOSTAT database collections. Rome, Italy: Food and Agriculture Organization of the United Nations.

Godfray HJC, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C. 2010. Food security: the challenge of feeding 9 billion people. Science 327, 812–8.

Guo L, Wang X, Zhao M, et al. 2018. Stepwise cis-regulatory changes in ZCN8 contribute to maize flowering-time adaptation. Current Biology 28, 3005–3015.e4.

Lester DR, Ross JJ, Davies PJ, Reid JB. 1997. Mendel’s stem length gene (*Le*) encodes a gibberellin 3 beta-hydroxylase. The Plant Cell 9, 1435–43.

Lev-Yadun S, Gopher A, Abbo S. 2000. The cradle of agriculture. Science 288, 1602–3.

McClung CR. 2021. Circadian clock components offer targets for crop domestication and improvement. Genes 12, 374.

McCouch SR, Baute GJ, Braden J, et al. 2013. Agriculture: feeding the future. Nature 499, 23–24.

Meyer RS, Purugganan MD. 2013. Evolution of crop species: genetics of domestication and diversification. Nature Reviews Genetics 14, 840–52.

Reid JB, Ross JJ. 2011. Mendel’s genes: toward a full molecular characterization. Genetics 189, 3–10.

Soyk S, Müller NA, Park SJ, Schmaalbach I, Jiang K, Hayama R, Zhang L, Van Eck J, Jiménez-Gómez JM, Lippman ZB. 2017. Variation in the flowering gene SELF PRUNING 5G promotes day-neutrality and early yield in tomato. Nature Genetics 49, 162–168.

Trněný O, Brus J, Hradilová I, Rathore A, Das RR, Kopecký P, Coyne CJ, Reeves P, Richards C, Smykal P. 2018. Molecular evidence for two domestication events in the pea crop. Genes (Basel) 9, 535.

Turner A, Beales J, Faure S, Dunford RP, Laurie DA. 2005. The pseudo-response regulator Ppd-H1 provides adaptation to photoperiod in barley. Science 310, 1031–4.

Wang S, Li H, Li Y, Li Z, Qi J, Lin T, Yang X, Zhang Z, Huang S. 2020. FLOWERING LOCUS T improves cucumber adaptation to higher latitudes. Plant Physiology 182, 908–918.

Weller JL, Liew LC, Hecht VF, et al. 2012. A conserved molecular basis for photoperiod adaptation in two temperate legumes. Proceedings of the National Academy of Sciences, USA 109, 21158–21163.

Williams O, Vander Schoor JK, Butler JB, Ridge S, Sussmilch FC, Hecht VFG, Weller JL. 2022. The genetic architecture of flowering time changes in pea from wild to crop. Journal of Experimental Botany 73, 3978–3990.

Wu F, Sedivy EJ, Price WB, Haider W, Hanzawa Y. 2017. Evolutionary trajectories of duplicated FT homologues and their roles in soybean domestication. The Plant Journal 90, 941–953.