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FLOWERING NEWSLETTER REVIEW

Interacting duplications, fluctuating selection, and convergence: the complex dynamics of flowering time evolution during sunflower domestication

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Abstract

Changes in flowering time and its regulation by environmental signals have played crucial roles in the evolutionary origin and spread of many cultivated plants. Recent investigations into the genetics of flowering time evolution in the common sunflower, *Helianthus annuus*, have provided insight into the historical and mechanistic dynamics of this process. Genetic mapping studies have confirmed phenotypic observations that selection on flowering time fluctuated in direction over sunflower's multistage history of early domestication and modern improvement. The *FLOWERING LOCUS T/TERMINAL FLOWER 1* (*FT/TFL1*) gene family appears to have been a major contributor in these adaptive shifts. Evolutionary and functional investigations of this family in sunflower provide some of the first empirical evidence that new competitive interactions between recent gene duplications can contribute to evolutionary innovation. Notably, similar results in additional systems that validate this hypothesis are now being discovered. With a sunflower genome sequence now on its way, further research into the evolution of flowering time and its regulation by environmental signals during sunflower domestication is poised to lead to additional, equally important contributions.

Key words: Domestication, flowering time, gene duplication, *Helianthus annuus*, photoperiod, sunflower.

Introduction

Evolutionary changes to the mechanisms regulating flowering time have been critical to the domestication process of many crop species. For instance, a substitution conferring reduced photoperiod sensitivity and an enhanced vernalization requirement rose from low frequency to fixation during the domestication of cultivated beet (Pin *et al*., 2012). Alterations in the response of flowering to vernalization and photoperiod appear to have played key roles in the expansion of barley and wheat agriculture into the temperate environments of northern Europe (Turner *et al*., 2005; Yan *et al*., 2006; Faure *et al*., 2012; Zakhrabekova *et al*., 2012). Similarly, evolutionary changes affecting photoperiod response probably fostered the spread of maize cultivation to high altitude and high latitude areas of North America (Meng *et al*., 2011; Hung *et al*., 2012). Recent work on the genetics of flowering time evolution has shown that the common sunflower, *Helianthus annuus*, is no exception to this trend among crop plants. Here, I review how these findings have informed our knowledge of the complex, dynamic process through which sunflower evolved from a wild plant into a modern oilseed crop. In addition, the broader implications of these investigations for our understanding of gene family evolution and the predictability of genetic evolution will be considered.

A brief history of sunflower cultivation

As is the case for many crop species, our understanding of where and when domesticated sunflower was first cultivated has been the source of much controversy and confusion. The problems date to the first known historical record of sunflower cultivation. Dodanaeus, a European herbalist

in the 16th century, described sunflower as a crop grown by the native peoples of Peru (Dodonaeus, 1578). By Peru, he was probably referring to the entire Spanish territory in the New World rather than the area of the modern nation. Nevertheless, and although the wild progenitor of cultivated sunflower is not native to Peru and native Peruvians did not cultivate sunflower during the historical period, this misconception persisted for several centuries.

Today, however, thanks to abundant and persuasive historical, linguistic, archaeological, and genetic evidence, it is clear that the major sunflower domestication centre was located in the eastern and central USA (Heiser, 1951; Smith, 1989, 2006; Harter *et al*., 2004; Wills and Burke, 2006; Blackman *et al*., 2011*c*). Approximately 5000 years ago, the breeding practices of Native Americans living in this region dramatically transformed sunflower. Starting from the wild progenitor *H. annuus*, a branched plant with many small heads and many small seeds of moderate oil content, early farmers derived the now familiar, unbranched crop plant that has one large head containing many large seeds of high oil content. Native Americans roasted and ground wild and cultivated sunflower seeds for food, ate seeds raw, used flowers ceremonially, anointed their hair with oil, dried stalks for building material, and, in some regions, extracted anthocyanins from achene coats for use as a dye (Heiser, 1951). The discovery of several archaeological specimens identified as sunflower at sites in Mexico recently raised the possibility that sunflower may have been independently domesticated there (Lentz *et al*., 2008, 2001). However, subsequent surveys of neutral markers and domestication alleles in extant Mexican landraces and wild populations determined that all cultivated sunflowers descend from a single eastern North American lineage (Harter *et al*., 2004; Wills and Burke, 2006; Blackman *et al*., 2011*c*). Thus, if an independent Mexican crop lineage existed previously, it has since become extinct.

Although kept in kitchen gardens and cultivated as an ornamental in Europe since its introduction in the late 1500s, modern breeding of elite sunflower crop lines did not begin in earnest until the end of the 19th century (Putt, 1997). Fuelled in part by demand generated because sunflower oil was an oil not specifically forbidden by the Orthodox Church during Lent, breeding of sunflower as an oilseed crop initially took off in Russia (Heiser, 1976). The first high oil content lines as well as 'Mammoth Russian' varieties with enormous heads commonly sold for gardens were developed there. Several decades later, Canadian and American breeders established breeding programmes incorporating Russian material. Major sunflower agriculture centres also began taking root in the rest of Europe and Argentina at this time, and the crop is now grown worldwide (Putt, 1997).

The diversity of flowering time regulation in sunflower

Sunflowers are summer annuals that go from seed to seed without overwintering as vegetative rosettes. They germinate in the spring and flower in the mid-summer to mid-autumn depending on genotype. Thus, experience of winter, or vernalization, does not regulate flowering in *H. annuus*. Instead, photoperiod and temperature are the primary environmental influences regulating the transition to flowering (Schuster and Boye, 1971; Goyne and Schneiter, 1987, 1988; Goyne *et al*., 1989). Gibberellic acid (GA) signalling also regulates flowering in sunflower (Almeida and Pereira, 1996; Fambrini *et al*., 2011). However, the mechanisms by which GAs or other hormones are integrated with or act independently of photoperiod and temperature regulation have not been well studied in this species (but see Rueda *et al*., 2005; Dezar *et al*., 2011).

Sunflower was once erroneously reported to be solely day neutral (Allard and Garner, 1940; Habermann and Wallace, 1958; Marc and Palmer, 1981; Almeida and Pereira, 1996). Broader surveys of wild populations and cultivated accessions now clearly demonstrate that all three major classes of photoperiod response—day neutrality, short-day response, and long-day response—are observed in *H. annuus* (Dyer *et al*., 1959; Goyne and Schneiter, 1987; Yanez *et al*., 2005; Wien, 2008; Blackman *et al*., 2011*a*). These responses are facultative or quantitative, as plants will flower under any daylength, but particular genotypes flower earlier under inductive conditions.

The breadth of diversity in photoperiodic flowering found within *H. annuus* is rather unique. Although day-neutral variants are frequently observed in photoperiod-responsive species, observations of both long-day and short-day photoperiod responses within a single species have been rarely reported. In their comprehensive treatment of photoperiodism, Thomas and Vince-Prue (1997) only report two species, *H. annuus* and *Salvia splendens*, exhibiting such diversity. Short-day and long-day varieties have also been observed for the perennial wild strawberry, *Fragaria vesca* (Koskela *et al*., 2012). Besides these major response classes, several more complex responses have been described for particular sunflower cultivars (Goyne and Schneiter, 1987). For instance, ambiphotoperiodic accessions, which flower later under intermediate daylengths than under short or long days, and long–short-day accessions, which flower earlier if exposed to long days before short days, are known. Notably, different developmental phases may exhibit distinct responses to photoperiod in sunflower, but the consequences of this complexity for classifying accessions by photoperiod response type have not been broadly addressed (Schuster and Boye, 1971; Fonts *et al*., 2008).

To learn how flowering time and its regulation by environmental cues evolved during domestication, it is first necessary to understand the standing variation in these traits that probably pre-existed in the wild progenitor. Wild *H. annuus* populations exhibit a latitudinal cline in flowering time (Blackman *et al*., 2011*a*), a pattern commonly observed in geographically widespread species (Bohlenius *et al*., 2006; Zhang *et al*., 2008; Takahashi *et al*., 2009; Kawakami *et al*., 2011). Under common garden conditions, northern populations flower earlier than southern populations. Differentiation among populations in flowering time is greater than differentiation in most other quantitative traits and in neutral genetic marker diversity, observations consistent with natural selection as the major force driving this geographic pattern. Photoperiod

response also varies geographically (Blackman *et al*., 2011*a*). Most wild populations in the heart of the wild sunflower's range are facultative short-day plants, but populations at the northern and southern range limits have evolved day-neutral and long-day responses, respectively. Surveys of natural variation in the plasticity of flowering to temperature have yet to be completed for wild sunflower.

Phenotypic observations have been reported for a limited number of extant landraces. These early domesticates that have been maintained as distinct lineages to the present day exhibit a similar latitudinal trend in flowering, and the majority are late or very late flowering in common garden conditions (Heiser, 1951). These observations suggest that later flowering may have been favoured during early domestication, at least in some regions. In contrast, modern breeding has generally selected for early flowering to shorten the growing period and thus expand the region suitable for cultivation (Putt, 1997). This trend has locally shifted with the expansion of sunflower agriculture in Argentina, where later flowering varieties may produce higher yields by completing reproductive development during late-season periods of higher rainfall (Gonzalez *et al*., 2011).

Although an abundant diversity of photoperiod responses has been observed in modern elite cultivars (Goyne and Schneiter, 1987), to our knowledge, no studies have examined the diversity of photoperiod response types in the landraces. However, several lines of evidence—(i) many landraces are late flowering; (ii) population genetic evidence indicates that sunflower was domesticated in the mid-latitudes of eastern North America (Harter *et al*., 2004); and (iii) many Russian and ornamental cultivars are short-day plants (Dyer *et al*., 1959; Yanez *et al*., 2005; Wien, 2008)—support the inference that the landraces were solely derived from a short-day ancestor. Thus, the diversity of photoperiod response observed among elite lines probably arose independently of the diversity observed in wild lines.

The combination of multiple evolutionary transitions during the domestication process with the abundant variation in flowering time and its response to environmental cues makes *H. annuus* a very promising system for addressing diverse research questions. Close examination of the remarkable variety of photoperiod responses is an exciting avenue for evolutionary and developmental investigations of the gene regulatory networks governing seasonal timing, as this rich complexity probably involves both the repurposing of known conserved regulators (e.g. Hayama *et al*., 2003) and intercalation of novel signalling pathways (e.g. Itoh *et al*., 2010). Genetic dissection of the molecular changes through which flowering time evolved during domestication and improvement will clarify the proposed history of temporal and spatial variability in selection and reveal the means by which organisms cope with such evolutionary dynamics. In addition, characterizing the pleiotropic effects of flowering time domestication loci may reveal whether flowering time was a direct or indirect target of selection by early farmers. Finally, the likely convergent evolution of long-day and day-neutral flowering in wild and cultivated sunflower provides an opportunity to ask whether similar phenotypes predictably evolve by convergent mechanisms or whether multiple genetic paths can lead to the same end. The subsequent sections will evaluate how our current knowledge of the genetic basis of flowering time variation in *H. annuus* illuminates these questions.

Genetic architecture is consistent with dynamic selection patterns

The first foray into determining the genetic architecture of sunflower domestication traits was conducted by quantitative trait locus (QTL) mapping in a cross between a Nebraskan wild plant and an elite crop line (Burke *et al*., 2002). Flowering time divergence was found to have an oligogenic genetic architecture, with a major locus explaining ~30% of the observed variation, in addition to several minor loci. Notably, the effect of the major locus was in the opposite direction from expectation: plants carrying alleles from the earlier flowering elite parent flowered later than plants carrying alleles from the later flowering wild parent. Because an elite line served as one parent, the genetic differences accumulated between the two parents represented the combined heritage of both early domestication and modern improvement. Consequently, this counterintuitive pattern of genotypic effects may be explained if the initial stages of domestication favoured and fixed alleles for late flowering.

Three flowering QTLs detected in a subsequent cross between the late-flowering Hopi landrace and a Nebraskan wild plant supported this hypothesis (Wills and Burke, 2007). Two minor QTLs co-localized with previously detected QTLs, including the former major QTL, and QTL effects were now in the expected direction: Hopi alleles conferred later flowering than wild alleles. The effect size of these QTLs was diminished relative to the previous cross however, because a major QTL residing in a new genomic region and explaining ~47% of the observed variation was detected. Since regional adaptation to the dry areas inhabited by the Hopi in the southwestern USA probably imposed strong selection for even later flowering, this genomic region probably contributed to post-domestication divergence as this tribe adopted sunflower agriculture. A number of additional traits—including seed shape, dye content, and oil content—show similar patterns of enhanced divergence in phenotype and genetic architecture in the southwestern landraces (Wills *et al*., 2010).

A substantial number of QTL mapping studies have also been conducted in crosses between elite lines of sunflower (Leon *et al*., 2000., 2001; Mokrani *et al*., 2002; Bert *et al*., 2003; Al-Chaarani *et al*., 2004; Haddadi *et al*., 2011). Generally, all these studies have reported oligogenic sets of moderate to large QTLs contributing to variation in flowering, and QTL regions detected in different studies frequently overlap. In an elite cross between a short-day parent and a long-day parent, two moderate QTLs for photoperiod response were detected. Subsequent evaluation of near isogenic lines for these two regions confirmed these findings (Leon *et al*., 2001; Fonts *et al*., 2008).

Evolving interactions between *FT*/*TFL1* gene family members during domestication and improvement

Several recent studies have made critical progress in identifying compelling candidates for genes contributing to the complicated history of flowering time evolution during sunflower domestication and improvement (Chapman *et al*., 2008; Blackman *et al*., 2010, 2011*b*). In the absence of a sequenced genome, students of sunflower evolution have relied on candidate gene and population genetic screens to identify putative domestication genes. For instance, candidate domestication and improvement genes were identified by screening a random set of several hundred microsatellite loci for signatures of selective sweeps (Chapman *et al*., 2008). Some outlier loci were located in genes homologous to flowering time regulators in other plants (e.g. homologues in the CONSTANS-LIKE/B-BOX ZINC FINGER and CYCLING DOF FACTOR gene families; Fornara *et al*., 2009; Khanna *et al*., 2009), and a subset of these genes co-localized with known flowering QTLs. Transcriptional and functional analyses confirming that these candidates—rather than linked genes—causally contribute to divergence in flowering time remain to be reported.

The search for candidate domestication and improvement genes in sunflower has also taken a focused approach leveraging the exceptional knowledge we have gained about the flowering time gene regulatory network in the past several decades. In-depth genetic and biochemical studies conducted in *Arabidopsis* and rice have revealed the identities of many genes involved as well as the detailed mechanisms by which they interact and regulate each other. As comprehensively reviewed elsewhere (e.g. Farrona *et al*., 2008; Amasino, 2010; Tsuji *et al*., 2011; Andres *et al*., 2012; Ietswaart *et al*., 2012), information from environmental cues such as photoperiod, temperature, and vernalization is integrated at multiple hierarchal levels with endogenous regulators including hormonal pathways and the circadian clock. These interactions are realized through diverse mechanisms such as chromatin modification (He *et al*., 2003; Adrian *et al*., 2010; Yun *et al*., 2012), regulation by short and long RNA molecules (Swiezewski *et al*., 2007, 2009; Mathieu *et al*., 2009; Wu *et al*., 2009; Liu *et al*., 2010), and light- and hormone-dependent protein degradation (Valverde *et al*., 2004; Imaizumi *et al*., 2005; Ueguchi-Tanaka *et al*., 2005; Sawa *et al*., 2007).

When considered in combination with parallel insights drawn from an ever-greater diversity of non-model taxa however (Reeves *et al*., 2007; Zhang *et al*., 2008; Albani and Coupland, 2010; Pin *et al*., 2010; Ballerini and Kramer, 2011; Hsu *et al*., 2012; Koskela *et al*., 2012), it is now clear that the gene regulatory network governing flowering time is not only mechanistically beguiling but also evolutionarily capricious. Although involvement of homologous genes is often conserved for many pathways, the relationships between these genes and mechanisms of biochemical regulation may be radically different across taxa. For instance, the degradation of *CONSTANS* (*CO*) protein in the absence of light found in *Arabidopsis* is not observed for the rice orthologue *Heading date 1* (*Hd1*), and *Hd1* represses rather than promotes expression of the *FT*-homologue *Heading date 3a* (*Hd3a*) under long-day conditions (Hayama *et al*., 2003; Ishikawa *et al*., 2011). In some instances, entire pathways present in one taxonomic group have no homologue in another, as observed for certain pathways regulating photoperiod response in monocots relative to dicots (Itoh *et al*., 2010).

Despite these emerging caveats, the many conserved network participants—light receptors, circadian clock components, hormone biosynthetic genes, and downstream floral inducer or identity genes—nonetheless provide a sizeable gateway for comparative investigation. Consequently, by bringing genetic map position data, sequence and expression divergence, and population genetic signatures of selective sweeps to bear on a large set of sunflower flowering time gene homologues, several putative domestication and improvement genes have been successfully identified (Blackman *et al*., 2011*b*). Remarkably, all of these candidates are members of the same gene family: the *FT*/*TFL1* gene family.

FT and *TFL1* have opposing functions (Kardailsky *et al*., 1999; Kobayashi *et al*., 1999). *FT* is a critical and conserved inducer of flowering in response to photoperiod cues. Its expression in leaf tissue is the main output of upstream pathways that integrate light and circadian signals such that sufficient active FT protein is only produced under inductive photoperiods (Suárez-López *et al*., 2001; Yanovsky and Kay, 2002; Hayama *et al*., 2003; An *et al*., 2004; Valverde *et al*., 2004; Imaizumi *et al*., 2005; Sawa *et al*., 2007). FT protein is then transported through the phloem to the shoot apical meristem (SAM) where, through interactions with additional partners, it enters nuclei and activates transcription of floral identity genes to promote flowering (Abe *et al*., 2005; Wigge *et al*., 2005; Jaeger and Wigge, 2007; Lin *et al*., 2007; Mathieu *et al*., 2007; Tamaki *et al*., 2007; Shalit *et al*., 2009; Taoka *et al*., 2011; Liu *et al*., 2012). Vernalization and temperature also regulate *FT* expression in several systems (Searle *et al*., 2006; Yan *et al*., 2006; Kumar *et al*., 2012). In contrast, *TFL1* is expressed in the SAM and represses floral identity genes and flowering (Bradley *et al*., 1997; Pnueli *et al*., 1998). Lineage-specific duplications in these genes are common throughout angiosperms (Ballerini and Kramer, 2011), and several examples of how duplicates were recruited to newly regulate diverse seasonal and developmental traits have recently been reported (Komiya *et al*., 2009; Danilevskaya *et al*., 2010; Hecht *et al*., 2011; Hsu *et al*., 2011; Navarro *et al*., 2011; Wang *et al*., 2011).

One *H. annuus* homologue of *TFL1* (*HaTFL1*) and four homologues of *FT* (*HaFT1–HaFT4*) have been identified (Fig. 1; Blackman *et al*., 2010). *HaFT3* is probably a pseudogene. Its expression was undetectable in a broad tissue survey, and multiple putative loss-of-function variants segregate in cultivars and wild populations. The remaining three *HaFT* paralogues all partially rescue the *Arabidopsis thaliana ft* mutant when overexpressed, indicating substantial functional equivalence. *HaFT2* and *HaFT4* are expressed in leaf tissue only under inductive photoperiods, consistent with *FT* function. *HaFT1* is divergent in several ways. It is not expressed in leaves, has a novel expression domain in the shoot apex, and also has a novel splice form. Yet, the sequences of *HaFT1*,

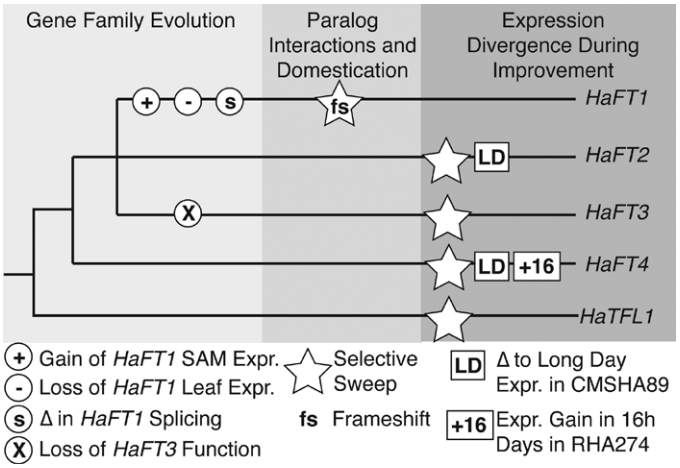

Fig. 1. Functional changes and adaptive events in the evolution of the *HaFT/HaTFL1* gene family.

HaFT2, and *HaFT3* are more closely related to each other than to *HaFT4*. Few synonymous substitutions have evolved among these three paralogues, and they all map to the same genomic region, suggestive of origins by very recent segmental duplications, though gene conversion has not been ruled out as a cause of the high sequence similarity.

Notably, this genomic region also falls within the major flowering time QTL detected in the elite×wild cross (Blackman *et al*., 2010). In near isogenic lines segregating for this QTL on a cultivated background, homozygous domesticated individuals flowered ~7 d later than homozygous wild individuals; however, this effect was only observed under long days. Of the three co-localizing paralogues, *HaFT1* was shown to be the strongest candidate for the causal locus. The domesticated allele (*HaFT1-D*) is altered by a frameshift mutation that leads to expression of a divergent, extended protein, and population genetic surveys of sequence diversity in wild and domesticated sunflower found that this substitution experienced a selective sweep during early domestication.

Surprisingly, the frameshift allele appears to confer its photoperiod-specific effect on flowering by dominant-negative interference with another paralogue, *HaFT4* (Blackman *et al*., 2010). Overexpression of *HaFT4* in *ft* mutant *Arabidopsis* plants rescued the late flowering mutant phenotype. However, plants overexpressing both *HaFT1-D* and *HaFT4* were late flowering, indicating that the domesticated allele of *HaFT1* exerts a dominant-negative effect on *HaFT4* function. Curiously, no interaction was observed between *HaFT1-D* and *HaFT2*, suggesting that the proteins of the two leaf-expressed paralogues have functionally diverged.

Together, these results represented some of the first empirical evidence for a longstanding hypothesis that lineage-specific duplications can lead to phenotypic evolution through the emergence of new competitive interactions between paralogues (Pereira-Leal *et al*., 2007; Lynch, 2011). The molecular interactions of young paralogues are frequently wholly or partially redundant, and, until this redundancy is resolved, pairs of duplications are consequently well positioned for the evolution of novel interactions. Though biochemical studies detailing the mechanism by which *HaFT* paralogues interact are still needed, similar findings have recently been reported in beet and tobacco, suggesting that the broad implication of the sunflower findings is generalizable (Pin *et al*., 2010; Harig *et al*., 2012). In each case, one or multiple *FT* paralogues have evolved into floral repressors. The *FT*/*TFL1* family may be uniquely poised for the repeated evolution of functional reversals since paralogous family members interact with a largely overlapping set of protein partners (Pnueli *et al*., 2001; Taoka *et al*., 2011). Indeed, substituting a single amino acid residue between *FT* and *TFL1* can entirely reverse their activities in *A. thaliana* (Hanzawa *et al*., 2005; Ahn *et al*., 2006). A more interesting possibility, though, is that the evolution of new interactions between paralogues is a general phenomenon observable for any network where functional redundancy in protein–protein interactions, DNA-binding sites, or enzymatic activity persists.

The tug-of-war between *HaFT* paralogues also appears to have provided raw material for modern breeders. The remaining members of the sunflower *FT*/*TFL1* family—*HaFT2*, *HaFT3*, *HaFT4*, and *HaTFL1*—all experienced selection during improvement (Fig. 1; Blackman *et al*., 2011*b*). The signature of a selective sweep on non-functionalized *HaFT3* is probably a consequence of hitchhiking. However, the remaining paralogues may have responded to selection for early flowering. Notably, they co-localize with flowering QTLs in wild×cultivated crosses (Blackman *et al*., 2011*b*). Genetic variation associated with elevated *HaFT2* expression in domesticated sunflower maps in *cis* to this locus as well (Blackman *et al*., 2010). As members of the same gene family, these duplicates may have been in the best position mechanistically to respond to selection by modern breeders given the changes in *HaFT1* function that occurred during early domestication. It is noteworthy that the *HaFT1* frameshift was not eliminated during modern improvement. This may be trivially explained if no alternative alleles were present in the germplasm from which the elite crop lines were derived. However, it is more interesting to consider that the *HaFT1-D* allele may have advantageous pleiotropic effects that allowed it to be maintained. Since this genomic region is also associated with potentially favourable variation in disc diameter, seed size, and leaf size (Burke *et al*., 2002; Wills and Burke, 2007; Baack *et al*., 2008; Blackman *et al*., 2010), future additional fine mapping of the region may provide evidence supporting this alternative hypothesis. Indeed, such work would shed light on whether the effect of the *HaFT1* frameshift on flowering was the primary or indirect target of selection during early domestication as well.

The genetics of convergent evolution in the photoperiod response

As discussed above, both day-neutral and long-day responses have evolved from a short-day progenitor among elite-bred cultivars during improvement (Goyne and Schneiter, 1987; Yanez *et al*., 2005; Fonts *et al*., 2008; Wien, 2008) and as wild *H. annuus* extended its range northward and southward into

new climate regimes (Blackman *et al*., 2011*a*). These similar but independent transitions provide a suitable comparison for asking whether convergent or distinct mechanistic changes underlie the evolution of similar phenotypes. In other words, genetic scrutiny of these similar transitions allows assessment of whether genetic evolution is predictable (Stern and Orgogozo, 2008, 2009).

There does appear to be some level of predictability in the evolution of day neutrality. In contrast to *HaFT2* and to its typical short-day expression pattern in other lines/populations, *HaFT4* is expressed under both long-day and short-day conditions in two day-neutral accessions: a northern wild population (Manitoba; Blackman *et al*., 2011*a*) and the cultivated line RHA274 (Fig. 1; Blackman *et al*., 2012). Thus, substitutions affecting *cis*-regulatory regions in the *HaFT4* promoter and/or changes affecting genes regulating *HaFT4* in *trans* are likely to be involved in the shift to day neutrality in both cases. *HaFT4* expression is just an intermediate stage of the genotype to phenotype map, though. Further genetic dissection is necessary to determine whether the causative changes are indeed in the same loci and also to test whether introgression of alleles from wild germplasm into the improved cultivar could have fostered genetic convergence.

In contrast to the evolution of day neutrality, the independent evolution of long-day response in wild and cultivated sunflower appears to have involved rather distinct mechanisms. *HaFT2* and *HaFT4* expression in leaves is induced by long days instead of short days in the long-day cultivar CMSHA89 (Fig. 1), indicating that the causative changes act in *cis* and/or in *trans* to these paralogues (Blackman *et al*., 2010). However, in wild *H. annuus* from Texas, neither paralogue is expressed in leaves under either long or short days (Blackman *et al*., 2011*a*). Instead, variation in *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* homologue transcript abundance in the shoot apex is associated with the transition to long-day response. Thus, the causative changes leading to these two independent transitions from short-day to long-day response act in different tissues and influence distinct portions of the flowering time gene regulatory network. Differences in standing allelic variation, initial genetic constraints (CMSHA89 flowers much earlier than the Texas population), or the optimal phenotype under natural and artificial selection may explain why these distinct mechanistic paths were taken. Alternatively, the achievement of similar transitions in photoperiod response by different mechanisms may have been purely stochastic.

A broader taxonomic perspective

While investigations of the wild progenitor have provided an essential context for interpreting flowering time evolution in domesticated sunflower, additional insights may be gained from taking a taxonomic step back and considering the diversity in flowering and its regulation across the genus. Most *Helianthus* species are perennials. Annuality appears to have evolved twice independently in *Helianthus* (Timme *et al*., 2007). Although these shifts are relatively ancient, crosses between *H. annuus* and perennials are achievable (e.g. Kantar *et al*., 2012). Consequently, mapping and expression studies of candidate genes, such as the *FT*/*TFL1* family (Hsu *et al*., 2011; Wang *et al*., 2011), may reveal the evolutionary mechanisms leading to these convergent transitions.

Photoperiod response and flowering time also vary greatly within and among other *Helianthus* species (Allard and Garner, 1940). As in *H. annuus*, natural selection maintains a latitudinal cline in flowering in the perennial *H. maximiliani* (Kawakami *et al*., 2011). A broad range of flowering times is also observed among wild and domesticated accessions of the Jerusalem artichoke, *H. tuberosus*, and short-day and day-neutral varieties have been described (Hackbarth, 1937; Kays and Kultur, 2005).

Tuberization is also short-day responsive in *H. tuberosus* (Kays and Nottingham, 2008). Notably, grafting leaves from flowering *H. annuus* onto *H. tuberosus* plants kept in long days promotes induction of both flowering and tuberization, suggesting that one or multiple *FT* paralogues are involved (Nitsch, 1965). The potential functions of *FT*/*TFL1* homologues in perenniality and tuberization raises the intriguing possibility that the *HaFT* duplicates initially arose during the evolution of these ancestral functions. Detecting a putatively functional *HaFT3* transcript in perennial *Helianthus* would corroborate this hypothesis and parallel the recent finding that an *FT* copy regulating tuberization in potato is a pseudogene in tomato, which lacks tubers (Navarro *et al*., 2011).

Conclusions and future prospects

The studies reviewed above have established that the common sunflower, in both wild and cultivated forms, exhibits a surfeit of diversity in flowering time and its regulation by environmental cues. How this variation evolved over sunflower's complex history of early domestication and very recent improvement efforts is a complicated story in terms of both selection and mechanism. Initial QTL studies revealed the genetic signature of a reversal in selection on flowering time. Subsequent characterization of the *FT*/*TFL1* gene family suggests that ongoing evolution of paralogue–paralogue interactions could be a major engine driving phenotypic innovation in response to these types of temporal dynamics. Finally, the independent origins of multiple forms of photoperiod response in wild and cultivated sunflower provide examples of both predictability and stochasticity in the genetic mechanisms underlying developmental evolution.

For all the noteworthy findings made so far, the pace of progress has been limited in part by the tools available and the power of particular methods. Positional cloning efforts have been hindered by lack of a sequenced genome to aid in marker and candidate gene identification, and the loci discovered are always contingent on the genetic variation captured by any given cross. In addition, signatures of selection are difficult to detect for traits where variation may be maintained by spatial variation in selection or by breeders' attempts to retain different forms of diversity in different lines. For instance, *HaDELLA1*, a homologue of major developmental

repressors acting in the GA pathway, does not fall within a QTL for flowering in wild×cultivated crosses. However, a radical non-synonymous mutation in the DELLA domain of this gene is strongly associated with divergence in plant height and flowering time between standard and dwarf lineages of improved sunflower (Ramos *et al*., 2012).

A bevy of new genomic tools is on the horizon for sunflower, thanks to the efforts of the Compositae Genome Project (compgenomics.ucdavis.edu) and the Sunflower Genome Resources Consortium (www.sunflowergenome.org). These exciting developments promise to deliver a deeper understanding of flowering time diversity and its evolution in sunflower across space and through time. Advanced association and QTL mapping populations now available will substantially improve the precision and power for detecting genetic variation affecting flowering and its regulation by environmental cues (Baack *et al*., 2008; Mandel *et al*., 2011; Bowers *et al*., 2012). A high density single nucleotide polymorphism (SNP) map (Bachlava *et al*., 2012; Bowers *et al*., 2012), the forthcoming sunflower genome sequence (Kane *et al*., 2011, 2012), and ongoing re-sequencing of diverse cultivated and wild lines will provide tremendous resources of positional and polymorphism information that will greatly accelerate discovery of causal substitutions. Finally, advances in population genomics methods for examining geographic- or lineage-specific selection patterns hold great promise for expanding the capacity to identify regionally and locally adaptive alleles of great utility to breeders (Coop *et al*., 2010; Hancock *et al*., 2011).

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