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Evolutionary genetics of plant adaptation: insights from new model systems

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Flowering time and mating system divergence are two of the most common adaptive transitions in plants. We review recent progress toward understanding the genetic basis of these adaptations in new model plant species. For flowering time, we find that individual crosses often reveal a simple genetic basis, but that the loci involved almost always vary within species and across environments, indicating a more complex genetic basis species-wide. Similarly, the transition to self-fertilization is often genetically complex, but this seems to depend on the amount of standing variation and time since species divergence. Recent population genomic studies also raise doubts about the long-term adaptive potential of self-fertilization, providing evidence that purifying selection is less effective in highly selfing species.

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Introduction

Heterogeneity across the natural landscape provides a rich substrate for adaptation among plant populations. Reciprocal transplant experiments in numerous taxa have shown that plants are strongly adapted to their local environments [1,2], and this may be particularly true with regards to traits that influence the timing [3,4] or system of reproduction. In recent years, studies of wild plant systems, many of which are highly tractable for field experiments, have made significant strides toward identifying the genetic architecture of ecologically important adaptive shifts. In addition to addressing the question of whether adaptive traits diverge by major or minor steps, these studies have begun to address fundamental questions about the repeatability of evolutionary transitions. In this review, we focus on progress from these new models on the genetics of two traits that are also important axes of adaptive divergence between plant populations and species: flowering time and mating system. For both of these key quantitative traits, we highlight the strong influence of complex environments on their evolution. For example, even when flowering time loci have major phenotypic effects, they are often polymorphic and only locally distributed within species. We also point to differences in the origin of mating system transitions that may affect genetic architecture. Lastly, we discuss new studies that indicate a shift in mating system (i.e., from outcrossing to self-fertilization) may limit the long-term adaptive potential of affected plant lineages. We conclude by underscoring the need for quantitative genetics field experiments across the native ranges of plant populations and species that differ in flowering behavior and mating system.

Genetic basis of divergence in flowering phenology, a key component of local adaptation

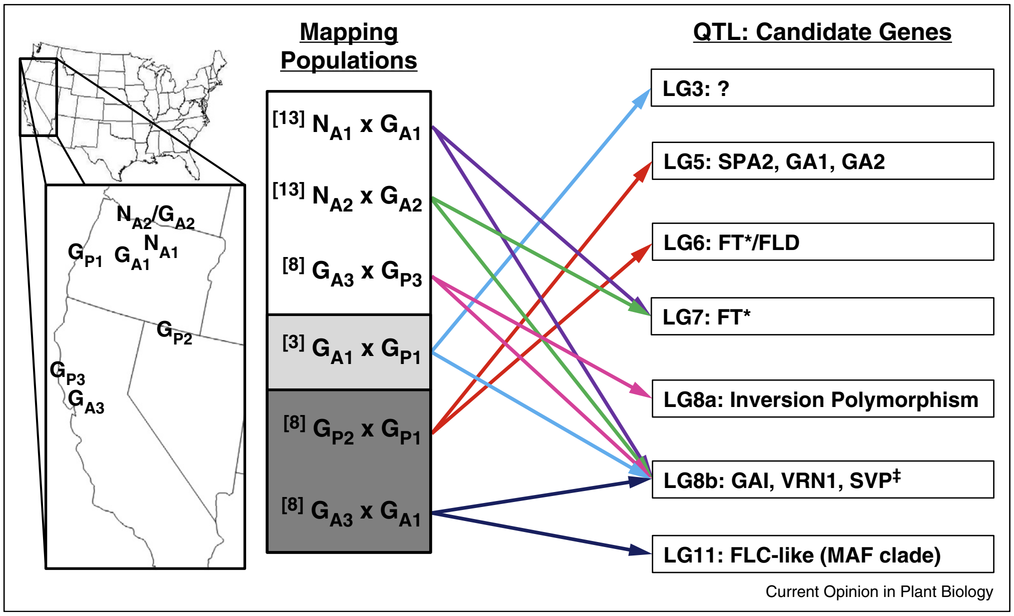
In angiosperms, the initiation of flowering is a complex trait that is highly dependent on edaphic and climatic conditions, with the decision to flower regulated by an integrated genetic network responding to both autonomous signals and environmental cues [5]. The timing of reproduction is critically important for plant fitness, and natural selection can optimize flowering phenology to coincide with locally favorable conditions. Over evolutionary time, this process leads to divergence among plant populations in how they respond to the length of winter (vernalization), temperature, photoperiod, and/or nutrient levels [6•,7,8••]. In *Arabidopsis thaliana*, studies of natural accessions have identified a number of genes that contribute to quantitative variation in flowering time [9,10], but until quite recently, little was known about the genetic basis of flowering phenotypes in other wild plant species.

One of the more striking results to emerge from studies of new plant model systems is the degree to which genes for flowering behavior are influenced by complex natural environments. In *Boechera stricta*, a perennial relative of *A. thaliana* found along a broad elevational gradient in the Rocky Mountains, recombinant inbred lines grown under field and controlled laboratory conditions display dramatically different flowering times and utilize distinct sets of quantitative trait loci (QTL) to initiate reproduction [11]. Similarly, in crosses between diverged populations of the perennial *Arabidopsis lyrata* [12], flowering time QTL identified in greenhouse and field environments are not identical (a disconnect between laboratory and field QTL has also been seen in *A. thaliana* [13]). These studies have led to awareness that, going forward, field experiments in species' native habitats will be critical for determining the genetic basis of adaptation in ecologically relevant contexts.

A number of recent studies in diverse plant taxa have detected loci with major effects on flowering time divergence among natural populations. Many of these same loci also co-localize with genes from the flowering time network. In *B. stricta*, variation in flowering time is partly explained by a major-effect QTL centered on the genomic region containing an ortholog of the *Arabidopsis* floral integrator gene *FLOWERING LOCUS T* (*FT*) [14]. Similarly, an ortholog of another key flowering time gene, FLOWERING LOCUS C (FLC) underlies the vernalization requirement for flowering *Arabis alpina*, an arctic-alpine perennial crucifer [6•,12]. QTL mapping in the yellow monkeyflowers of the *Mimulus guttatus* species complex has also detected loci with major effects on flowering responses to both critical photoperiod and vernalization (Figure 1, [8••,15••]). Members of the *M. guttatus* group vary widely in life history (small, selfing, and facultatively annual to large and perennial), and occupy diverse habitats across a range of elevations and latitudes. For the highly selfing *M. nasutus*, which is often found in drier microhabitats where it co-occurs with *M. guttatus* [16], early flowering is likely an adaptive strategy to avoid drought [17,18]. Flowering time variation between these two *Mimulus* species is almost entirely explained by only two QTL, suggesting that this evolutionary transition to short-day flowering may have occurred rapidly [15••]. Interestingly, a simple genetic architecture for flowering time divergence also appears to be the rule in *A. thaliana*: only a handful of loci explain much of the variation in flowering behavior across a diverse collection of accessions [10].

At the same time that major effect mutations have been found in individual crosses, it has become clear that flowering behavior at a species-wide scale might often be genetically heterogeneous. In *Mimulus*, unique sets of QTL for short-day flowering have been mapped in each of six distinct crosses between ecotypes [8••,19] and species [15••], suggesting that this parallel transition does not always share a common genetic basis (Figure 1). Of the few QTL that have been identified in multiple *Mimulus* crosses, one spans a genomic region with several flowering time candidates [8••,15••], including three copies of *SHORT VEGETATIVE PHASE* (*SVP*) family genes; in *A.*

Figure 1



Variation in the genetic basis of flowering time behavior within and between *Mimulus* species. Major effect QTL for flowering time in *Mimulus* were identified in three QTL mapping studies performed in the greenhouse [15,19] or growth chambers [8••]. The map shows collection sites for parental lines used in mapping experiments (N_{A2}/G_{A2} is a sympatric site). Crosses indicate annual *M. guttatus* (G_A), perennial *M. guttatus* (G_P), or annual *M. nasutus* (N_A), with numbers corresponding to distinct parental lines. Shading indicates flowering cue being tested: no shading = critical photoperiod, light grey = long-day flowering, and dark-grey = vernalization requirement under long days. Only two major effect QTL were identified in each population (colored arrows), indicating a simple genetic basis. QTL (linkage group: candidate genes) are listed on right. Notice that some QTL (LG7 and LG8b) are observed in multiple crosses, whereas all others vary with genotype and/or environment. Candidate genes: *SUPPRESSOR OF PHYA 2* (*SPA2*), *GIBBERELIC ACID REQUIRING 1* (*GA1*), *GIBBERELLIC ACID REQUIRING 2* (*GA2*), *FLOWERING LOCUS T* (*FT*), *GIBBERELLIC ACID INSENSITIVE* (*GAI*), *VERNALIZATION1* (*VRN1*), *SHORT VEGETATIVE PHASE* (SVP), *FLOWERING LOCUS D* (*FLD*), *FLOWERINC LOCUS C* (*FLC*), *MADS-BOX AFFECTING* (*MAF*). *The *M. guttatus* reference genome contains 8 full/partial copies of *FT*. ‡Three paralogous copies of *SVP* underlie this QTL.