

# All in good time: Understanding annual and perennial strategies in plants<sup>1</sup>

One of the most fundamental questions faced by all organisms is when is the best time to reproduce to maximize the survival and success of their offspring. In plants, there are two broad categories of reproductive strategies—annuals that reproduce once and die (monocarpic or semelparous) and perennials that reproduce repeatedly and cycle through vegetative and reproductive phases (used here synonymously with polycarpic or iteroparous) (Fig. 1). Not surprisingly, given the importance of reproduction to fitness, studies on flowering time and related life history decisions have been the subject of intense investigations from many angles. These include a rich body of life history theory, detailed molecular mechanisms and genetic architecture of flowering time in a few model species, studies of resource allocation, trade-offs, and ecological interactions between flowering plants and their biotic communities. However, these fields have largely developed in isolation from one another, and there are few attempts to integrate across disciplines to form a comprehensive understanding of the evolution of life history strategies and reproductive timing.

Evolutionary transitions between perenniality and annuality are among the most common transitions in angiosperms and encompass decisions on the allocation to vegetative growth versus flowering and also the timing of such decisions. Transitions in both directions can be quite frequent, suggesting considerable lability of life cycle, at least among herbaceous species (Barrett et al., 1996). However, compared with other common transitions, such as the evolution of selfing from outcrossing, we know very little about the selective mechanisms and genetic changes responsible for this transition. In this perspective piece, we discuss the potential to integrate current knowledge from research on geographical and ecological patterns, with studies of resource allocation and decisions about when to flower, with our knowledge of the molecular mechanism underlying the transition to flower. We suggest that by integrating studies across levels we can gain a general and synthetic understanding on the evolution of life history strategies.

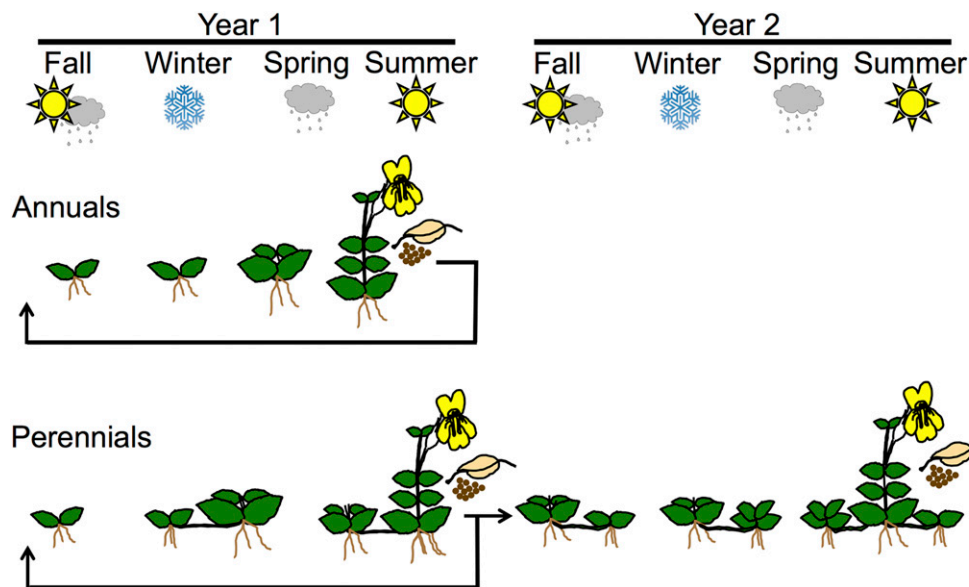
Ancestral state reconstructions using phylogenetic approaches generally have found that annuals are derived from perennial ancestors, including multiple origins of annuals within a genus (e.g., *Nemesia* [Datson et al., 2008], *Sidalcea* [Andreasen and Baldwin, 2001]). However, in some genera, a switch back to perennial behavior might have occurred (Bena et al., 1998; Tank and Olmstead, 2008). Theoretical models predict that the annual habit evolves as an adaptive response to unpredictable environments, including frequently disturbed habitats and aridity

(Stearns, 1992). Empirical data generally supports this idea, with a shift to annual life histories often occurring in hot and dry conditions that would adversely affect adult perennial plants (Barbier et al., 1991; Evans et al., 2005; Cruz-Mazo et al., 2009). Thus, macroevolutionary patterns suggest that selection has acted in consistent ways to favor the association of annual life history strategies with particular environments. However, whether there is any shared pattern in the traits that have been under selection or in the genetic architecture underlying the transition remains an open question.

Early theoretical models of the evolution of annual versus perennial life histories focused on the number of offspring produced per reproductive bout and differing survival between juvenile and adult stages (Cole, 1954; Charnov and Schaffer, 1973). In general, life history theory involves optimization of the timing of reproduction, the number of offspring, and trade-offs between survival and fecundity. Moving from these optimization models to a mechanistic understanding of selection on life history strategies requires understanding the underlying morphological, developmental, and physiological characters. Using a quantitative genetic framework that incorporates variances and covariances between traits (Lande, 1982) may reveal whether selection on life history characters follows predictable evolutionary trajectories (Schluter, 1996). Multiyear field experiments that examine quantitative genetic traits and their selection components provide an opportunity to reconcile theoretical expectations with the underlying evolutionary processes and genetic architecture.

Both annuals and perennials must undergo a developmental switch from vegetative growth to flowering. In annuals, this transition occurs once and is followed by senescence and death of the plant, while perennial plants cycle repeatedly through vegetative and reproductive modes. Because perennial plants maintain vegetative growth after flowering, the perennial strategy requires differential behavior of meristems on a single plant so that either some meristems remain vegetative while others undergo floral transition or meristems revert back to vegetative development (Amasino, 2009). We have a limited understanding of the ecological and evolutionary significance of meristem usage, and future research should consider meristem fate as a target of selection. For example, in perennials, there may be a decision between immediate use of meristems for flowers or for vegetative growth that may enable more flowers in the future (e.g., Geber, 1990). In addition, trade-offs may exist between a less-risky strategy of immediate meristem allocation to reproduction and a strategy of vegetative growth where later meristems will experience different, and possibly less favorable, conditions (see Fig. 1 illustrating different routes toward fitness for perennials).

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**FIGURE 1.** Annuals and perennials differ in patterns of reproductive and vegetative allocation as a result of differences in flowering time and meristem usage. Annuals complete their life cycle within a single year, and seed produced in year 1 then complete the same life cycle in a following year. Perennials can produce both vegetative and reproductive structures in year 1. In year 2, seed produced in year 1 can repeat the year 1 life cycle but, unlike annuals, the vegetative structures from year 1 survive into year 2 to grow and reproduce.

The genetic control of flowering is exceptionally well characterized in the model plant *Arabidopsis thaliana* (reviewed in detail elsewhere, e.g., Simpson and Dean, 2002; Andrés and Coupland, 2012), and this knowledge should facilitate studies of the relations between seasonal cues, flowering time, and life history strategies. Understanding the genes involved in the transition to flowering in *A. thaliana* has assisted in finding many flowering time gene homologs and orthologs in related species (e.g., *Brassica rapa* [Irwin et al., 2012], *Capsella rubella* [Guo et al., 2012]) and distantly related crop species (Buckler et al., 2009; Blümel et al., 2015). While research is suggesting that the genetic mechanisms discovered in *Arabidopsis* can be extended to other species (e.g., Wang et al., 2009; Albani and Coupland, 2010; Anderson et al., 2011), there is limited scope to ask questions about evolutionary transitions between strategies or the processes that generated differences in the both the timing and number of reproductive bouts between annuals and perennials.

We suggest that to understand the evolution of life history transitions, researchers take advantage of natural intraspecific variation in life history strategies. Given the strong ecological correlates of life history, many herbaceous plants show variation in strategies among closely related taxa in different parts of their range. This type of variation can facilitate a multi-pronged approach that combines forward genetics, field experiments, and population genomic studies. Phylogenomic analyses and studies of genotype by environment associations can reveal the patterns of differentiation and the molecular mechanisms underlying divergence (e.g., Roda et al., 2013). Furthermore, by performing crosses between annual and perennial relatives, and testing the effects of segregating alleles in a species' native environment (e.g., Ågren and Schemske, 2012), one can understand the genetic basis of changes in life history strategy, as well as explore ecological differences that may be associated with these strategies (e.g., Hall and Willis, 2006; Friedman and Willis, 2013). By combining mapping

experiments with reciprocal transplant experiments, one can assess the adaptive role of different strategies and genes in different environments.

If we are to understand evolutionary transitions between strategies and selection in perennial plants, multiyear field experiments are necessary. While we recognize the challenge such studies impose, extended field experiments allow tests of fitness consequences and selection within a single season and across interannual heterogeneous environments. A shortcoming of approaches that use controlled experiments in greenhouses and growth chambers is the removal of seasonal variation within a year and variation across years, which may impose different selection on annuals and perennials. Annuals may cope with heterogeneity by being short-lived and producing genetically variable offspring each generation (to the extent that they outcross), whereas perennials may allocate meristems to vegetative or clonal growth that must survive to flower in a later season. The consequences of these different strategies on population dynamics and patterns of genetic variation are not clear. Finally, incorporating environmental heterogeneity into studies of evolutionary processes may facilitate an understanding of the kinds of environments that select for different strategies.

To move the field forward, we suggest using study systems with rich natural variation and combining mapping and selection experiments in the field with extensive genotyping to explore the genetic mechanisms underlying different strategies and their association with ecological conditions. By examining various components of fitness within and across years, one can test key predictions from life history theory about the consequences of different decisions regarding meristem fate and trade-offs between flowering and growth. Since life history divergence often involves suites of traits, identifying the primary targets of selection can illustrate whether traits evolve in correlated ways, and examining divergence across variable groups can identify whether there is convergent evolution at the genomic level. We are hopeful

that future studies will address how ecological and genetic factors interact over evolutionary time to generate the diversity of life history strategies that exist in nature.

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