ON THE NATURE OF THINGS: ESSAYS

New Ideas and Directions in Botany

The unique and multifaceted importance of the timing of flowering[1]

Steven J. Franks[2]

"The early bird gets the worm, but the second mouse gets the cheese" —Anonymous

Timing is critically important in many things in life. Sometimes it is best to be first, and sometimes it is decidedly not. A trait that illustrates this idea particularly well is the timing of flowering in plants (Primack, 1985; Rathcke and Lacey, 1985). A plant that flowers too early or too late can miss out on reproduction entirely and be quickly weeded from the gene pool. But while many traits influence fitness, flowering time is perhaps unique in influencing a multitude of ecological and evolutionary processes, including mating patterns, gene flow, and interactions between plant and animal pollinators (Elzinga et al., 2007). In addition to influencing ecological and evolutionary processes, phenology is also acutely shaped by them, with flowering time clearly responding (Parmesan and Yohe, 2003) and, in some cases rapidly adapting (Franks et al., 2007), to changing environmental conditions. Furthermore, the timing of flowering often has profound influences on connections between different levels of organization, with effects that ripple up the ecological hierarchy from individuals to populations, communities, and ecosystems. Flowering time can also directly interconnect ecological and evolutionary processes and play a key role in eco-evolutionary dynamics, which is the way that contemporary evolutionary changes influence ecological interactions (Pelletier et al., 2009). The profoundly important way in which flowering time influences these interconnections is an exciting, active area of research.

We are currently witnessing shifts to earlier flowering, caused by changes in climate, in a wide variety of plant species across the globe (Parmesan and Yohe, 2003). What are the consequences of such shifts in flowering time? If a shift to earlier flowering means an acceleration of development, as has been previously shown (Franks and Weis, 2008), rather than just a change in the timing of the growing season, then flowering earlier means that the shift from allocation to growth to allocation to reproduction comes sooner. Although the general trend is toward earlier flowering, this pattern can be complicated by such factors as differences in responses between spring-flowering compared with summer/fall-flowering species, with responses likely weaker in summer/fall-flowering species that are more cued to photoperiod (Aldridge et al., 2011), as well as differences in annuals and perennials, with some perennials actually flowering later because of a lack of a sufficient number of cold days in winter (Yu et al., 2010). While flowering early can have advantages, it can also have costs, particularly because plants will not have invested as much resources into such functions as growth and defense. Shifts to earlier flowering time could involve trade-offs, with plants ultimately producing fewer flowers or seeds or becoming more susceptible to herbivory or disease or frost (Inouye, 2008). These trade-offs can potentially lead to eco-evolutionary feedbacks, with evolutionary shifts in flowering time altering interactions among plants and other organisms such as pollinators, herbivores, or pathogens. The costs of shifts to earlier flowering and the extent to which these shifts will influence interactions with other species is currently not well known and is an important area of investigation, particularly with ongoing climate change.

Shifts in flowering time can have widespread ecological consequences. Earlier flowering may lead to more synchronous flowering within and among populations if plants all tend to flower earlier together. Shifts to earlier and more synchronous flowering within a population could decrease the amount of phenological assortative mating (earlier-flowering plants mating with other early-flowering plants and late with late) (Fox, 2003), because if all plants overlap in the timing of flower production, there is less assortative mating than if some plants have finished flowering before others have started. This decrease in assortative mating would decrease the amount of additive genetic variation in flowering time within populations, leaving less variation for selection to act upon. In addition to effects on mating patterns within populations, changes in phenology can also influence gene flow among populations, with potentially important consequences for evolution. For example, earlier and more synchronous flowering among different populations could increase gene flow, which could reduce local adaptation (Franks and Weis, 2009). Increased gene flow could be beneficial if it involves transfer of adaptive alleles, or if it increases genetic variation, making the populations more adaptable. But it could also be detrimental if it

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Department of Biology, Fordham University, New York
[2] Author for correspondence (franks@fordham.edu)
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involves the transfer of maladaptive alleles and reduces adaptation of populations to their local conditions. Shifts in flowering time could also put plants out of synchrony with their pollinators, seed dispersers, and other mutualists, greatly altering community dynamics. This asynchrony may be especially problematic given recent declines in populations of pollinators, especially bees. Changes in flowering time could alter ecosystem properties such as productivity and rates of nutrient cycling as well. For example, the acceleration of development and flowering might increase productivity and nutrient cycling rates early in the growing season. For such ecological consequences to be understood, it will take collaborative research projects that span traditional ecological disciplines and include measurements or manipulations of phenological traits along with experiments at the population, community, and ecosystem levels.

Flowering time is shifting, and some of the ecological and evolutionary consequences are currently under investigation, as described. But what causes the underlying variation in flowering time to begin with? New tools in genetics and genomics are beginning to open up this area of investigation. Studies of *Arabidopsis thaliana* have shown that flowering time is controlled by a large and complex genetic regulatory network (Michaels, 2009). This network integrates signals that indicate conditions relevant to appropriate flowering timing, such as photoperiod and temperature, as well as plant age and size, and involves genetic and epigenetic regulation (Michaels, 2009). Although we now understand the genetic regulatory network for flowering time, at least for *Arabidopsis*, in great detail, we know very little about the genetic basis of natural phenological variation or how plants of identical age under identical conditions can flower at different times. Uncovering this source of variation is crucial, because this variation influences mating patterns within populations and gene flow among populations, and also is what selection can act upon to shift flowering time in populations.

Selection on flowering time is expected to act in some unique ways, which make the study of the evolution of flowering time particularly interesting. For example, selection on flowering time can be caused by both abiotic factors, such as temperature and moisture availability, and by biotic factors, including the availability of pollinators and the flowering times of other plants of the same species in the neighborhood (the social environment). The abiotic environment is expected to impose mainly hard selection (selection that imposes additional mortality above the background rate), while the social environment should impose soft selection (selection that substitutes nonselective for selective deaths, keeping overall mortality rate the same, or that influences reproductive output rather than survival) that is also density- and frequency-dependent (Weis et al., 2015). Selection on flowering time also has unique features such as strong asymmetry, with the negative consequences of flowering too late much more severe than the consequences of flowering too early, that provide exciting opportunities to apply novel tools of selection analysis (Weis et al., 2014) to investigate and predict evolution in phenology.

Future investigations into flowering phenology are likely to be informative on a variety of fronts, only a few of which have been mentioned here. Databases containing long-term and spatially extensive records of plant phenology, such as those created through Project Budburst (http://budburst.org/) and the National Phenology Network (https://www.usanpn.org/), will be especially helpful in facilitating such studies. Herbarium records and long-term seed collections, such as Project Baseline (http://www.baselineseedbank.org/) are also critical in this regard. Flowering phenology is rapidly changing, as is our understanding of this highly influential and centrally important trait.

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