Differences in flower and leaf bud responses to the environment drive shifts in spring phenological sequences of temperate woody plants

D.M. Buonaiuto [1,2,a], E.M. Wolkovich[3]

Introduction

One of the most widely documented biological effects of anthropogenic climate change are shifts in phenology, the timing of life cycle events, in plants (). While phenology is generally advancing with climate change, the strength of these phenological shifts can vary substantially among specific phenological phases (). These differences alter the timing of phases relative to each other, changing the the duration of inter-phase periods that make up phenological sequences (). Phenological sequences are a major driver of plant fitness that impact plant life history, resource allocation, demography and ecosystem processes (). Shifts in phenological sequences will likely alter many of these processes, but the effects these shifts depend both on the direction (whether distinct phases are shifting closer together or farther apart) and magnitude (how much they are shifting relative to each other).

Among deciduous woody plants, the relative timing of flower and leaf phenology, or flower-leaf sequences (FLSs), may be particularly consequential to fitness in temperate regions where flowering prior to leaf development is common (**??**). Long-term phenological observations over the last several decades indicate that, like other phenological sequences, FLSs are shifting due to anthropogenic climate change (**?**) suggesting that some of the critical functions of FLSs may become compromised. However, observed FLS shifts vary among species, which may put some species at greater risk while benefiting others (?).

For example, in wind-pollinated taxa, flowering before leaf development may be a critical adaptation for pollination efficiency by eliminating pollen interception by the forest canopy (?). In insect-pollinated taxa, flowering-first may increase the visibility of flowers to pollinators (??). Species with decreasing FLS interphases with climate change may expeience increased pollen limitation as more wind pollen is intercepted by vegetative structures and flowers are obscured by developing leaves. Conversely, pollination effeciency could improve for species with lengthening FLS interphases (direction). A change in the FLS interphase of just a few days would likely have little impact on these processes, but if shifts were on the order of weeks, the impact on the pollination biology of a species could be highly significant (magnitude).

Predicting the direction and magnitude of any FLS shifts requires identifying the underlying mechanisms that drive the difference responses to climate change among these phenophases for a diversity of woody plant species. Decades of research suggests that for woody plants in temperate regions, cool winter temperatures (chilling), warm spring temperatures (forcing) and day-length (photoperiod) are the primary drivers of both reproductive and vegetative phenology (??). However, observed FLS shifts indicate that there must be differences in how these cues influence phenological activity in floral and leaf buds.Identifying these differences is a necessary step for predicting the direction and magnitude, and ultimately fitness impacts of FLS shifts with climate change.

Most of the studies that have attempted to identify the differences between reproductive and vegetative phenology in woody plants have focused on crop species and two common, yet competing findings have emerged:

What we call the **precocity hierarchy hypothesis (PHH)** suggests that reproductive and vegetative buds respond similarly to most environmental cues, but have consistently different forcing requirements for the commencement of phenological activity (**???**). By contrast, what we call the **differential sensitivity hypothesis (DSH)** suggests that flower and leaf buds differ in the strength of their phenological responses to the multiple environmental cues (**?????**).

While these mechanisms may produce similar phenological patterns under historic climate conditions, they have different implications regarding the potential for FLS shifts with climate change. The PHH suggests that FLS variation is largely a product of climate variation during the interphase (**?**). If spring temperatures increase with climate change, the second phenophase of the FLS with be accelerated relative to the first and the FLS interphases will decrease, but given the relative auto-correlation of spring temperatures (), these shifts should be relatively muted.

The DSH suggests that with significant cue use differences among bud types, there will be strongly localized effects of climate change on FLSs. While on average the climate is warming, chilling and forcing may increase or decrease at different locations and on different time scales (**?**). Shifts in FLS variation will depend on the direction and rate of change in cues at specific locations and the differential sensitivity of reproductive and vegetative phenology to cue combinations. This hypothesis allows not only for larger magnitude shift in FLS, it also suggest that the magnitude of shifts may be highly divergent among populations of the same species.

In this study we test these hypotheses by comparing the phenological response to changing environmental conditions between flower and leaf buds for a suite of temperate shrubs and trees. We leverage these data to to make generalized projections for how FLSs may shift with climate change and discuss these shifts may affect plant function in the future.