

Do early phenological events constrain later phenology?

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Goal

We aim to test the extent to which previous phenological stages constrain later ones, as this is poorly understood. We plan to submit this paper as a “brief communication” at American Journal of Botany (“short (3000-5000 word) research articles reporting exciting, significant new findings. They include no more than 4 figures and tables, combined. Manuscripts, and their abstracts, should be organized as described for Research articles.”) or a “rapid report” at New Phytologist.

Abstract

Premise of the study

Methods

Key results

Conclusions

Key words

Introduction

Phenology has

Phenological events are sequential (e.g. leaf bud-burst comes before leaf-out, flowering comes before fruiting). This ordering may constrain phenological events but the extent of constraints between phenological events is poorly understood, because few studies have integrated across events.

Hypotheses

Hypothesis 1: Previous phenological events constrain later events; e.g., late-fruiting species set fruit late in the season because they leaf-out late (Figure 1).

Hypothesis 2: Inter-phenophase time constrains phenology; e.g., late-fruiting species set fruit late in the season because they require longer development time (Figure 1).

Materials and Methods

Study site and focal species

This study was conducted at the Arnold Arboretum of Harvard University, a 281-acre park in Boston, Massachusetts, established in 1872. It contains a living collection of trees, shrubs, and vines that are native to New England, as well as others from around the world. Arboreta are great resources for studies across many species, particularly in temperate areas, since they may contain a higher diversity of tree species growing in one location than nearby natural areas. In addition, there is often high variation in phenology in the species planted in arboreta, for public enjoyment. For this study, we selected 25 focal angiosperm species that varied in their flowering times (Table 1). We selected up to five individuals of each species for the study, yielding a total of 118 individuals.

Phenology data collection

Phenology was quantified following the National Phenology Network (NPN) protocols (USA-NPN National Coordinating Office, 2012). The budburst phase is characterized by the green leaf tips visible at the tips of buds. Leaf out phase is characterized by visible fully unfolded leaves and petioles that have completely emerged from the buds. Leaf senesce phase is characterized by leaves changing from green to fall colors. Flowering phase is when open flowers are visible. Fruiting phase is when developing fruit are visible.

We visited each individual once every 6-10 days throughout the growing season. Phenology observations in the spring began on April 6, 2015, and fall phenology observations ended on December 2, 2015. From the phenology data, we extracted the day of the year (DOY) of the first observed occurrence of a given phenological phase. Budburst DOY was defined as the first day when three or more leaf buds were seen bursting. Leaf out DOY was defined as the first day when 5% or more of the individual was leafing out. Flowering DOY was defined as the first day when 5% or more of the flower buds were open. Fruiting DOY was defined as the first day when three or more developing fruits were observed on the individual. Leaf senescence DOY was defined as the first day when 5% or more of the individual showed fall colors. (These definitions follow NPN protocols.)

Statistical analyses

To understand the extent to which previous phenological events constrain later events (Hypothesis 1, Figure 1), we fit linear models with each phenological stage that we observed (except budburst, the earliest stage we quantified) as the response variable (i.e. species-level mean day of year of leaf-out, flowering, fruiting, or senescence). We fit 10 different models, each with one of the previous phenological stages as the explanatory variable. R^2 and p -value for each model are shown, with solid lines representing model fit when $p < 0.05$ and dashed lines representing model fit when $0.05 < p < 0.10$. Full model results are summarized in Table S1.

To understand the extent to which inter-pheno phenological events constrain later events (Hypothesis 1, Figure 1), we fit linear models with each phenological stage that we observed (except budburst, the earliest stage we quantified) as the response variable (i.e. species-level mean day of year of leaf-out, flowering, fruiting, or senescence). We fit 10 different models, each with one of the previous phenological stages as the explanatory variable. R^2 and p -value for each model are shown, with solid lines representing model fit when $p < 0.05$ and dashed lines representing model fit when $0.05 < p < 0.10$. Full model results are summarized in Table S1. All analyses were conducted in R version 3.2.4.

Results

Our results suggest that earlier phenological stages constrain later phenology in many cases (Figures 2, 3). The strongest correlations occurred between adjacent stages (i.e. those along the diagonal in Figure 3, such as leaf-out and budburst, fruiting and flowering). Senescence was the only phenological stage not well-correlated with an earlier phenological stage.

The data also suggest that inter-phenophase duration constrain phenology for reproductive stages (flowering and fruiting time, Figure 4). Reproductive phenology appears to be constrained by both earlier inter-phenophase times (e.g. time between flowering and budburst, time between fruiting and flowering) and later interphase times (e.g. time between senescence and flowering).

In general, our results suggest that growth phenology was not strongly constrained by inter-phenophase time, inter-phenophase time was not a strong predictor for growth phenology in most cases (Figure 4). The exception to this was budburst day of year, which was most strongly related to inter-phenophase time between leafout and budburst.

Discussion

Leaf-out, flowering, and fruiting support hypothesis 1: their timing appears to be constrained by earlier phenological stages. Add references/studies that may explain physiology behind this, or have observed something that concurs with this? These constraints in phenological events likely create correlations among other traits (e.g. frost tolerance may critically control leaf-out date, which in turn affects flower, fruiting and seedset dates, and thus could create a correlation between frost tolerance and seed mass).

Flowering and fruiting also support hypothesis 2: their timing appears to be constrained by inter-phenophase time. Fruiting takes about 0-20 days for most species. Add references/studies that may explain physiology behind this, or have observed something that concurs with this?

Our two hypotheses are not mutually exclusive. Constraints on phenology may be species-specific.

Budburst and inter-phenophase time relationship suggests that earlier budburst does not always result in earlier leaf-out (although many species did that burst their buds early did also leaf out early, Figure 3). For some species, earlier budburst is simply associated with longer time between budburst and leaf-out (Figure 4). From our data, it is not clear if this pattern is due to variation in species' physiology and drivers of phenology, or to weather patterns. For example, many species leafed out after day 130, despite budburst days ranging from day 110 to 130. Weather conditions during the spring of 2015 were cold and wet, with warming occurring suddenly on day XXX (just an idea- i have no idea if this is true! need to look at the data). Multi-year studies will be critical.

Expect correlations could be strongest at biggest at end of season. Geometric constraint.

Conclusions

Next steps: Encourage a phylogenetic approach, collect data across years. We observed variation at whole organism level- may want to explore at individual flower/fruit level.

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Data Accessibility

The data set for this study available online at supplemental material in Appendix S1. OR better to have on KNB?

Authors's contributions

S.G., A.E., and E.W. conceived and designed the study together; S.G. conducted the field and lab work; S.G. and A.E. analyzed the data; S.G. and A.E. wrote the manuscript, with significant input from E.W.

1 Bibliography

Tables

Table 1: **Focal species.** Twenty-five angiosperm species were selected, based on their flowering phenology. The number of individuals of each species observed at the Arnold Arboretum from spring through fall 2015 is in parentheses.

Early season flowering	Mid season flowering	Late season flowering
<i>Aesculus flava</i> (5)	<i>Carya glabra</i> (5)	<i>Catalpa speciosa</i> (5)
<i>Betula alleghaniensis</i> (5)	<i>Carya ovata</i> (5)	<i>Kalopanax septemlobus</i> (3)
<i>Betula nigra</i> (5)	<i>Crataegus crus-galli</i> (5)	<i>Styphnolobium japonicum</i> (5)
<i>Gleditsia triacanthos</i> (5)	<i>Fagus engleriana</i> (4)	<i>Tilia americana</i> (5)
<i>Liriodendron tulipifera</i> (5)	<i>Fagus grandifolia</i> (5)	<i>Tilia japonica</i> (5)
<i>Phellodendron amurense</i> var. <i>lavalleyi</i> (4)	<i>Fraxinus chinensis</i> (5)	
<i>Populus deltoids</i> ssp. <i>deltoids</i> (5)	<i>Liquidambar styraciflua</i> (5)	
<i>Pyrus calleryana</i> var. <i>dimorphophylla</i> (3)	<i>Platanus occidentalis</i> (5)	
<i>Pyrus ussuriensis</i> var. <i>hondoensis</i> (5)	<i>Quercus glandulifera</i> (4)	
<i>Quercus alba</i> (5)	<i>Quercus rubra</i> (5)	

Figures

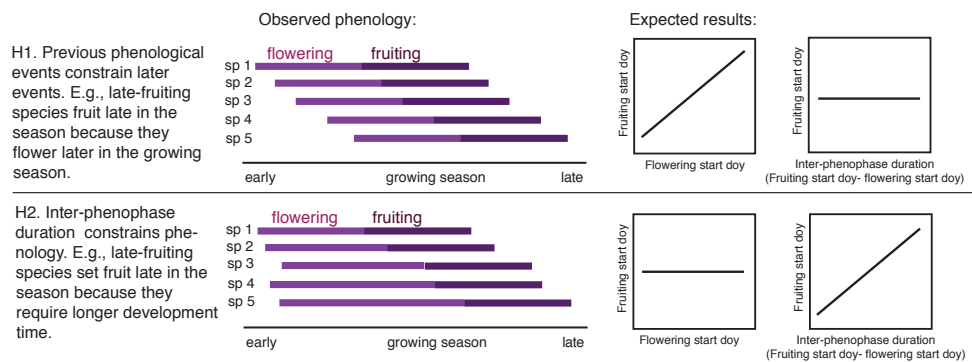


Figure 1: **Hypotheses.** We show flowering and fruiting as examples of consecutive phenological events. We expected the same patterns for other consecutive events, such as leaf bud-burst and leaf-out. Inter-phenophase duration is the time between phenological events, e.g., the number of days between the start of flowering and the start of fruiting.

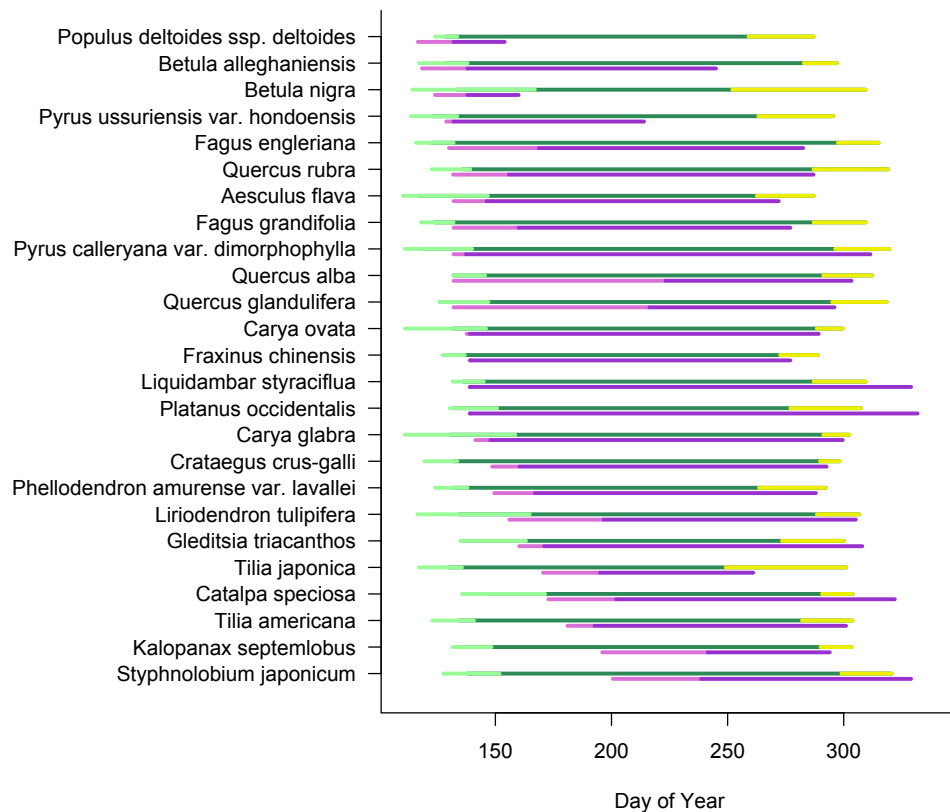


Figure 2: **Focal species' phenology during the 2015 growing season, sorted by their mean first-flower dates.** For growth phenology, light green represents the bud-burst phase (from its mean start day-of-year to the mean start day-of-year for leaf-out, across all individuals within a species), dark green represents full leaf-out (from the mean day-of-year when fully-expanded leaves were first observed through the start of senescence), and yellow represents the senescence phase (from the mean day-of-year when leaves first began changing color through the mean day-of-year when more than 95 percent of leaves on the tree had changed color). For reproductive phenology, light purple represents the flowering phase (from the mean day-of-year when flowers first appeared to the mean day-of-year when fruits first appeared, across all individuals within a species) and dark purple represents the fruiting phase (from the mean day-of-year when fruits first appeared to the mean day-of-year when more than 95 percent of fruits were first observed as ripe).

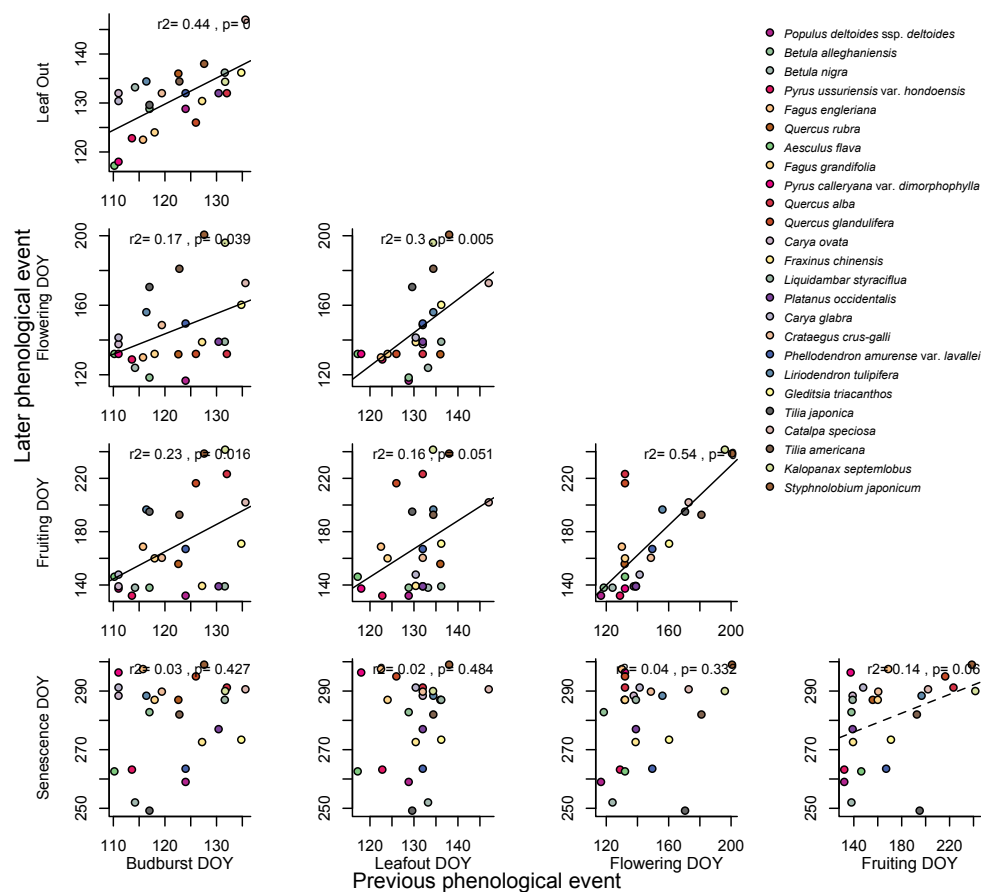


Figure 3: **Relationships among phenological stages across the 25 focal species.** Linear models were fit with the species-level mean day of year of the later phenological stages as the response variable, and mean day of year of earlier stage as the explanatory variable. R^2 and p -value for each model are shown, with solid lines representing model fit when $p < 0.05$ and dashed lines representing model fit when $0.05 < p < 0.10$. Species in the legend are ordered from early to late first flower dates, as in Figure 2.

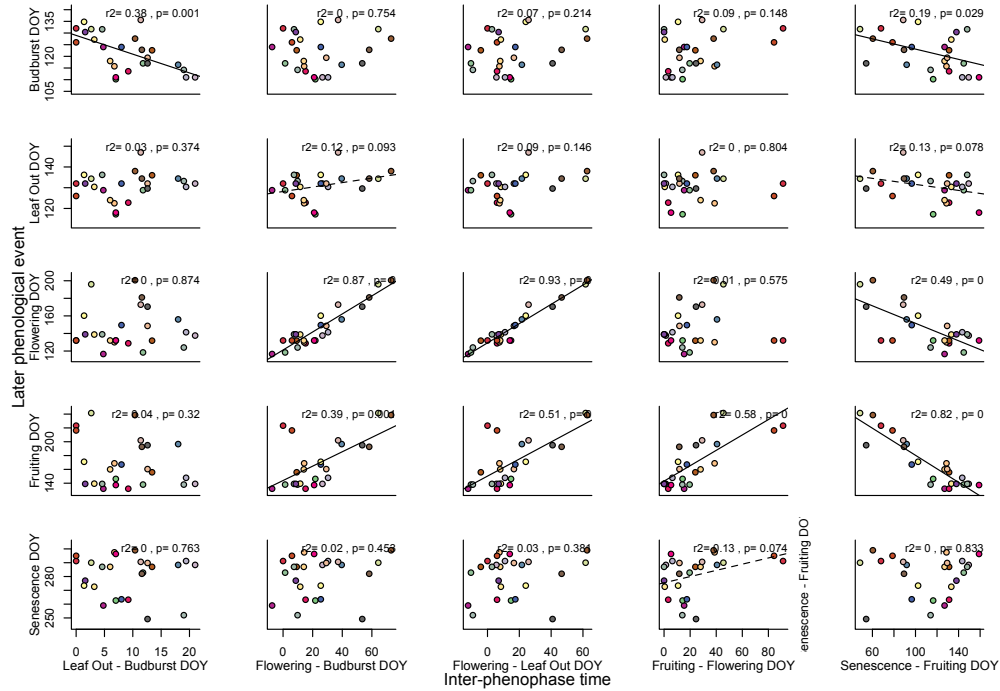


Figure 4: **Relationships among phenological stages and inter-phenophase duration across the 25 focal species.** Inter-phenophase duration is the time between the start of the earlier phenological event and the start of the later phenological event, e.g., the number of days between the species' mean start of flowering and its mean start of fruiting. Linear models were fit with the species-level mean day of year of the later phenological stages as the response variable, and interphenophase duration as the explanatory variable. R^2 and p -value for each model are shown, with solid lines representing model fit when $p < 0.05$ and dashed lines representing model fit when $0.05 < p < 0.10$.