Phenological sequences: how early-season events define those that follow

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Abstract

Premise of the study

Plant phenology is a critical trait; the timing of phenophases such as budburst, leafout, flowering, and fruiting, is important to plant fitness. Despite much stufy, little is known about how these phases relate to one another across an entire growing season. We test the extent to which early phenological stages constrain later ones, throughout a growing season and across 25 angiosperm tree species.

Methods

We observed phenology (budburst, leafout, flowering, fruiting, and senescence) of 118 individual trees across 25 species, from April through December 2015.

Key results

We found that early phenological events constrain later events, with the strongest relationships between consecutive stages. We also found that inter-phenophase duration constrains reproductive phenology for flowering and fruiting.

Conclusions

Our findings highlight that a shift in one phenophase could have cascading effects on later phases, so accurate forecasts of climate change impacts should include multiple phenophases within and across years.

Key words

plant phenology, climate change, budburst, leafout, flowering, fruiting, senescence, angiosperm, tree, arboretum

Introduction

Plant phenology, the timing of recurring life-events such as leafout and flowering, is a critical trait that affects individual fitness, population abundance, agricultural and natural productivity, and global climate, through its role in carbon sequestration (Cleland et al., 2007; Miller-Rushing and Primack, 2008; Primack and Miller-Rushing, 2009; Willis et al., 2010; Miller-Rushing et al., 2010). Advancement of budburst, leafout, and other phenophases are some of the most widely documented biological impacts of anthropogenic climate change, and phenology is likely to be further altered by future climate change (Parmesan, 2006). Because of its important role in many ecosystem services and in the global climate cycle, improved understanding and forecasting of tree phenology would aid in planning and preparing for climate change impacts.

Despite the observation that spring phenology generally shifts earlier with warmer temperatures, dramatic variation exists in phenological responses to climate. Temperature is thought to be a major factor controlling phenology of temperate tree species (Parmesan, 2006; Morin et al., 2010; Schwartz et al., 2013), but some populations and species have not shifted their phenology with recent warming (Wolkovich et al., 2012). In addition, different tree species vary widely in the timing of leafout and other phenological processes, even when exposed to the same environmental conditions (Lechowicz, 1984; Primack et al., 2009). For example, spring leafout can span weeks among coexisting tree species (Lechowicz, 1984).

The drivers of these variations are poorly understood, even though phenology has been long-observed (Wolkovich and Ettinger, 2014). Phenological patterns of temperate trees have been related to environmental factors, mainly seasonal and annual temperature (e.g. Richardson et al., 2006; Clark et al., 2014). In addition to these external drivers, it has been proposed that sequences of plant phenology are "endogenous;" that is, they are affected by changes in internal tree functions that may not be related to climate or other environmental factors (Borchert, 1992; Marco and Páez, 2002). For example, inflorescence architecture is a trait that may affect the sequence of leafout to flowering in trees (Marco and Páez, 2002).

One important, but often overlooked, feature of plant phenology is that events are sequential: leaf budburst comes before leafout, flowering comes before fruiting, and so on. This ordering is an endogenous factor that may constrain phenological responses to climate change. For example, if flowering cannot occur before leafout in a given species, and leafout date has not shifted earlier with recent climate change, then flowering time may also be static, even if warmer springs have caused pollinator activtiy to shift earlier. The extent of such constraints between phenological events is unknown, however, because few studies have integrated across consecutive events throughout a growing season (Wolkovich and Ettinger, 2014). Instead, researchers generally focus on one or two phenophases per study. Early season events (budburst and/or leafout) have been extensively studied, often using climate-controlled growth chambers (e.g., Basler and Körner, 2012; Laube et al., 2014). A separate group of studies, comprised of long-term observational data, focus primarly on flowering only (e.g., Fitter and Fitter, 2002; Miller-Rushing and Primack, 2008). Interest has surged in senescence, which had been less studied historically (Parmesan, 2006), but many of these studies focus *only* on senescence (e.g. Taylor et al., 2008; Archetti et al., 2013; Jeong and Medvigy, 2014). A recent meta-analysis highlights the lack of data on multiple phenophases with the finding that only five out of 51 (9.8%) phenology studies included data on both leaf and flower phenology wolkovich2012.

When research has looked across stages, important links have been found. For example, later leafing in a given year may be associated with later flowering, and fall senescence is correlated with fruit maturation for some species (Lechowicz, 1995). In addition, recent studies have found that the timing of autumn senescence is affected by spring phenology (Keenan and Richardson, 2015; Liu et al., 2016). These insights highlight the need to better understand how phenological stages relate to one another across an entire growing season (Wolkovich and Ettinger, 2014).

Here, we examine the extent to which early-season phenological events constrain later events, across multiple co-occurring tree species with varying phenology. Specifically, we test two hypotheses:

- *Hypothesis 1: Previous phenological events constrain later events;* e.g., late-fruiting species set fruit late in the season because they flower and leafout late (Figure 1). To be consistent with this hypothesis, we expected earlier events, such as flowering, would be strong predictors of later events, such as fruiting.

If so, then, across all species, previous events should predict later events with a slope of one, indicating that the later event happens a set number of days (represented by the intercept) after the previous event (Figure 1).

- *Hypothesis 2: Interphase duration constrains phenology;* e.g., late-fruiting species set fruit late in the season because they require longer maturation time (Figure 1). To be consistent with this hypothesis, we expected that the interphase duration between earlier and later events would be a strong predictor of the later event, regardless of the timing of the earlier event (Figure 1).

Testing these hypotheses addresses basic, critical questions about drivers of variation in temperate tree phenology. These questions remain unanswered despite decades of phenology research because no previous field studies, to our knowledge, have examined multiple phenophases spanning the entire growing season and across a large number of tree species.

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 3,825 woody plant taxa that are native to North America, Europe, and Asia. Arboreta are excellent resources for phenological studies across many species (e.g., Primack and Miller-Rushing, 2009), 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 of species planted in arboreta, for public enjoyment of foliage and flowers throughout the season. 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

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. We observed five phenological stages, which were quantified following the National Phenology Network (NPN) protocols (for a full description see Denny et al., 2014). The budburst phase was characterized by green leaf tips being visible at the tips of buds, and the leafout phase was characterized by visible fully unfolded leaves and petioles that had completely emerged from the buds. The flowering phase was when open flowers were visible, and the fruiting phase was defined by ripe fruit being visible. Leaf senescence was characterized by leaves changing from green to fall colors. On each observation day, we estimated the presence and abundance of each phenophase on each individual tree.

From the field observation data, we extracted the day-of-year (DOY) of the first observed occurrence of a given phenological phase. Budburst and fruiting DOY were defined as the first day when three or more burst leaf buds or ripe fruits, respectively, were observed on the individual. Leafout, flowering, and leaf senescence DOY were defined as the first day when 5% or more of the individual was leafing out, flowering, or showed fall colors, respectively (Denny et al., 2014). From these individual tree phenology observations, we calculated species-level mean start dates for all phenophases, for use in our statistical analyses.

Statistical analyses

To understand the extent to which previous phenological events constrain later events (Hypothesis 1, Figure 1), we fit linear models in which the response variable was phenological stage (i.e., the species' mean DOY

of leafout, flowering, fruiting, or senescence), and the predictor was previous phenological stage. Thus, budburst was excluded as a response variable, because it was the earliest stage we quantified, and senescence was excluded as a predictor variable because it was the latest stage we quantified. We therefore fit 10 different regression models, estimating the intercept of the relationship between later and previous phenological phases, and forcing the slope to be one (Hypothesis 1, Figure 1). In addition, we fit 10 models, with the same predictor and response variables, in which we estimated the slope and the intercept. Under Hypothesis 1, we expected that the models with forced slopes should provide similar fit to the data as the standard regression models that estimate both slopes and intercepts. We compared fit of these two model structures using r-squared values, as well as Akaike's Information Criterion (AIC).

To understand the extent to which interphase duration constrains later phenological events (Hypothesis 2, Figure 1), we fit linear models in which the response variable was phenological stage, and the predictor was the number of days between consecutive phenological stages. Thus, as above, budburst was excluded as a response variable budburst and senescence was excluded as a predictor variable. We therefore fit 10 different models, each with one of four phenological stages as the response variable and one of the four interphase durations as a predictor. To investigate the effect of interphase duration, separate from the constraint imposed by the inherent ordering of events, we fit models in which the interphase durations were randomized with respect to the timing of the earlier phenophase. We did this resampling of interphase duration 999 times for each model structure, then compared the mean slope of these resampled models to the slope of the fitted model.

All analyses were conducted in R version 3.2.4 (Team, 2016), and code is available in the Supplemental Materials.

Results

We monitored five phenophases, which varied in duration. First budburst date occurred over 32 days in the spring and first leafout date occurred over 30 days, across all focal individuals (Figure S1) and species (Figure 2). Flowering phenology occurred over a longer period than budburst and leafout, spanning 131 days from late April to September. The first observation of ripe fruit spanned 175 days, and the start of leaf senescence occurred over 56 days across all individuals and species. Most species (20/25) spent the majority of the growing season in the reproductive phenological phases (i.e. flowering and fruit development), and most species (23/25) began leaf budburst prior to flowering, though leaf development overlapped with flowering in some species (Figure 2). The majority of species (15/25) also produced ripe fruit prior to beginning senescence (Figure 2).

We found that the timing of early phenological stages did predict the timing of later stages, in many cases (Figures 2-3, Table S1), suggesting that earlier phenological stages constrain later ones. The strongest relationships (i.e., with the most variation explained) occurred between adjacent stages (those along the diagonal in Figure 3, such as leafout and budburst, fruiting and flowering). For adjacent phases, the forced slope model provided similar fit to the regression models, except in one case: the senescence vs. fruiting model (Figure 3, Table S1).

We observed strong relationships (e.g. $r^2>0.7$) between phenology and interphase duration for both reproductive phenophases (flowering and fruiting time, Figure 4, Table S2). Flowering DOY is strongly predicted by days between flowering and leafout ($r^2=0.93$), as well as by days between flowering and budburst ($r^2=0.87$). Fruiting DOY is strongly predicted by days between fruiting and flowering stages ($r^2=0.74$), by days between fruiting and leafout ($r^2=0.98$), and by days between fruiting and budburst ($r^2=0.97$).Senescence was predicted by days between senescence and budburst, days between senescence and leafout, and days between senscence and flowering; senescence was not affected by days between senescence and fruiting. Leaf-out was not predicted by interphase duration.

Discussion

All phenological stages we observed support Hypothesis 1: timing appears to be constrained by previous phenological stages. These findings are consistent with recent work suggesting that spring phenology can affect senescence time (Keenan and Richardson, 2015; Liu et al., 2016). Consecutive events were correlated across both growth and reproductive phenophases (i.e. flowering and leafout were correlated to a similar degree as fruiting and flowering, Figure 3). These associations may occur because of endogenous dependencies between the two phases, because of a shared external driver such as growing degrees, or a combination of endogenous and external factors (Lechowicz, 1995). Thus, environmental conditions in the winter or spring that may directly affect only early phenological stages, such as budburst, are likely to have cascading effects on later stages such as leafout, flowering, and fruiting. Our data suggest that, for most events, these effects are most apparent for consecutive stages (i.e., those along the diaganol in Figure 3), and are well-approximated by the forced slope model for three of the four later phenological events we studied (leafout, flowering, and fruiting, Figure 3).

Although some of the variation in reproductive phenology (flowering and fruiting) was explained by previous phenology (Hypothesis 1), much more variation was explained by inter-phenophase duration (Hypothesis 2). Later flowering species generally required more time between flowering and leafout. Similarly, late fruiting species had longer inter-phenophase duration between the first observation of ripe fruit and first flowering date. It may be that late fruiting species require longer fruit development times to produce larger fruits or more highly-provisioned seeds. This would be consistent with previous theories that trees investing more resources into their offspring (i.e., having larger seeds) require more time to build resources (Bolmgren and D Cowan, 2008; Sun and Frelich, 2011). There were notable exceptions to this general relationship, however. Several late-flowering species set fruit later than expected, given their intermediate interphase duration between flowering and fruiting (*Catalpa speciosa, Tilia americana, T. japonica*, Figure 4). These species also flowered later than expected, given their leafout DOY Figure 3. External ecological factors may be the cause; for example, these species are all insect-pollinated, so the timing their pollinator activity may also affect their floral phenology (Elzinga et al., 2007).

Interphase fruiting and senescence Leaf-out and senscence were less related than expected, given the ordering of these events (Figure 4). These relationships are expected, given the ordering inherent in flowering and fruiting (i.e. the gray lines from resampling show similar slopes to the black line, representing the fitted relationship, Figure 4). Add something about senescence vs fruiting being more weakly related than forced slope model? Need to think about how to interpret this.

Growth phenology (leafout and senescence phases) demonstrated little support for Hypothesis 2 (interphase time). If anything, we had expected that these two phases would demonstrate stronger constraints with interphase time becuase they occur the beginning and end of a bounded growing season (Letten et al., 2013). Instead, the low variation in leafout phenology explained by interphase duration and the weak or non-existent relationship between senescence and interphase time (in 2/4 cases) may mean that these phases are strongly constrained by environmental conditions, and endogenous factors are less important (Fenner, 1998), at least in some years. For example, the lack of a significant relationships between interphase duration and leafout may be due to the distinct weather patterns in 2015. Many species leafed out close to DOY 130 (May 10, 2015), regardless of leafout-budburst interphase duration, which ranged from 0 to 20 days (Figure 4). Temperatures during January through March were colder than average in 2015, with above-average snow-fall, but temperatures warmed considerably in late April and early May to above-average conditions (www.bluehill.org). Trees have species-specific chilling and forcing requirements that must be met prior to leafing out **??**. The temperature conditions specific to the year of our study (i.e. the long period of cold temperatures, followed by rapid warming) may have meant that chilling and forcing requirements were met for both species with high chilling requirements and those with high forcing requirements at a similar point in time, leading to a flush of leafout in early May, across diverse species.

Our results highlight that both Hypothesis 1 and Hypothesis 2 are operating. This is likely because species vary in which hypothesis primarily governs their phenology. For example, we found a positive relationship between fruiting and flowering (Figure 3); later fruiting is therefore associated with later flowering, as observed

in, for example, *Styphnolobium japonicum* and *Tilia americana*. However, later fruiting is not *always* the result of later flowering. Some species, such as *Quercus alba* and *Quercus grandifolia*, flower relatively early and fruit late; later fruiting for these species is instead associated with longer time between fruiting and flowering (Figure 4). Disentangling the ways that earlier phenology and interphase time interact with one another, and with environmental conditions, to determine later phenology will require multi-year field studies that observe phenophases across diverse species and throughout the growing season (e.g. Elmendorf et al., 2016). Experimental manipulations will also be beneficial for discerning the physiological and genetic bases for the relationships we observe (Flint, 1974).

Our findings have important implications for improved forecasting of climate change induced shifts in phenology. First, a shift in one phase may have cascading effects on later phases, since each phase is linked to phases that occur before and after it (Wolkovich and Cleland, 2014). This highlights a clear need to conduct future studies across entire growing seasons (Wolkovich and Ettinger, 2014), and begs the question of how phenophases may be linked across years, as well. For example, the timing of spring budburst in one year may be related to the timing of budset the previous fall (Mimura and Aitken, 2010). Although relationships between phenophases have not been widely studied, there is a growing ecological literature on the concept of "ecological memory," or the capacity of past states to influence present or future responses (Ogle et al., 2015). The ecological memory of phenology has not been quantified, but may be critical for accurate forecasting, particularly for species like *Quercus rubra*, which require more than one year for fruit maturation. Second, given the species-specific nature of phenological constraints, accurate forecasts of community-wide phenological shifts are likely to require species-specific information, such as fruit development time for fruiting forecasts, in addition to climate data (Diez et al., 2012).

Conclusions

We have shown that early and late phenological stages are strongly linked across the growing season, providing a new approach to explaining some of the dramatic variation in phenological responses observed to date. Many studies have sought to identify the particular environmental drivers of phenology (e.g. Morin et al., 2010; Schwartz et al., 2013). Our findings here suggest that timing and duration of previous phenological states should also be examined. In addition, identifying the appropriate temporal window for both environmental and endogenous drivers is essential (Teller et al., 2016). Because earlier phenophases define those that follow, the relevant time period for these drivers may extend further back in time than the single growing season we evaluated here. Multi-year studies will be critical to evaluate the extent to which phenological patterns are consistent among years that may vary in climate, as well as biotic conditions (i.e. pollinator or pest populations) (Lechowicz, 1995). A fuller understanding of phenological constraints and drivers of phenological variation offers the potential for improved forecasts of phenological shifts with climate change to help predict how ecosystem functions will be altered in the future.

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Data Accessibility

The data set for this study is available online at Knowledge Network for Biocomplexity (Gee et al., 2017).

Author contributions

All authors conceived of and designed the study and edited the manuscript; S.G. conducted the field and lab work; S.G. and A.E. analyzed the data and wrote the manuscript.

1 Bibliography

References

Archetti, M., A. D. Richardson, J. O'Keefe, and N. Delpierre. 2013. Predicting climate change impacts on the amount and duration of autumn colors in a new england forest. Plos One 8:e57373.

Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agricultural and Forest Meteorology 165:73–81.

Bolmgren, K., and P. D Cowan. 2008. Time–size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117:424–429.

Borchert, R. 1992. Computer simulation of tree growth periodicity and climatic hydroperiodicity in tropical forests. Biotropica pages 385–395.

Clark, J. S., C. Salk, J. Melillo, and J. Mohan. 2014. Tree phenology responses to winter chilling, spring warming, at north and south range limits. Functional Ecology 28:1344–1355.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology and Evolution 22:357–365.

Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. Enquist, P. Guertin, A. H. Rosemartin, M. D. Schwartz, K. A. Thomas, et al. 2014. Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. International journal of biometeorology 58:591–601.

Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen, and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. Ecology letters 15:545–553.

Elmendorf, S. C., K. D. Jones, B. I. Cook, J. M. Diez, C. A. Enquist, R. A. Hufft, M. O. Jones, S. J. Mazer, A. J. Miller-Rushing, D. J. Moore, et al. 2016. The plant phenology monitoring design for the national ecological observatory network. Ecosphere 7.

Elzinga, J. A., A. Atlan, A. Biere, L. Gigord, A. E. Weis, and G. Bernasconi. 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology and Evolution 22:432–439.

Fenner, M. 1998. The phenology of growth and reproduction in plants. Perspectives in Plant Ecology, Evolution and Systematics 1:78–91.

Fitter, A. H., and R. S. R. Fitter. 2002. Rapid changes in flowering time in british plants. Science 296:1689–1691. ID: 15; PT: J.

Flint, H. L. 1974. Phenology and Genecology of Woody Plants, pages 83–97. Springer Berlin Heidelberg, Berlin, Heidelberg.

Gee, S., A. Ettinger, and E. Wolkovich. 2017. Phenological sequences: a dataset of tree phenology from 25 species throughout one growing season.

Jeong, S.-J., and D. Medvigy. 2014. Macroscale prediction of autumn leaf coloration throughout the continental united states. Global ecology and biogeography 23:1245–1254.

Keenan, T. F., and A. D. Richardson. 2015. The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models. Global change biology 21:2634–2641.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biology 20:170–182.

Lechowicz, M. J. 1984. Why do temperate deciduous trees leaf out at different times? adaptation and ecology of forest communities. The American Naturalist 124:821–842.

———. 1995. Seasonality of flowering and fruiting in temperate forest trees. Canadian Journal of Botany 73:175–182.

Letten, A. D., S. Kathleen Lyons, and A. T. Moles. 2013. The mid-domain effect: it's not just about space. Journal of Biogeography 40:2017–2019.

Liu, Q., Y. H. Fu, Z. Zhu, Y. Liu, Z. Liu, M. Huang, I. A. Janssens, and S. Piao. 2016. Delayed autumn phenology in the northern hemisphere is related to change in both climate and spring phenology. Global change biology 22:3702–3711.

Marco, D. E., and S. A. Páez. 2002. Phenology and phylogeny of animal-dispersed plants in a dry chaco forest (argentina). Journal of Arid Environments 52:1–16.

Miller-Rushing, A. J., T. T. Hoye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B-Biological Sciences 365:3177–3186.

Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in thoreau's concord: A community perspective. Ecology 89. PT: J; TC: 92; UT: WOS:000254124200006.

Mimura, M., and S. Aitken. 2010. Local adaptation at the range peripheries of sitka spruce. Journal of evolutionary biology 23:249–258.

Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three european oak species in response to experimental climate change. New Phytologist 186:900–910.

Ogle, K., J. J. Barber, G. A. Barron-Gafford, L. P. Bentley, J. M. Young, T. E. Huxman, M. E. Loik, and D. T. Tissue. 2015. Quantifying ecological memory in plant and ecosystem processes. Ecology letters 18:221–235.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637–669.

Primack, R. B., I. Ibanez, H. Higuchi, S. D. Lee, A. J. Miller-Rushing, A. M. Wilson, and J. A. S. Jr. 2009. Spatial and interspecific variability in phenological responses to warming temperatures. Biological Conservation 142. PT: J; TC: 28; UT: WOS:000270203100022.

Primack, R. B., and A. J. Miller-Rushing. 2009. The role of botanical gardens in climate change research. New Phytologist 182.

Richardson, A., A. Bailey, E. Denny, C. Martin, and J. O'Keefe. 2006. Phenology of a northern hardwood forest canopy. Global Change Biology 12:1174–1188. PT: J; UT: WOS:000238352800004.

Schwartz, M. D., E. G. Beaubien, T. M. Crimmins, and J. F. Weltzin. 2013. North america. Pages 67–89 *in* Phenology: an integrative environmental science. Springer.

Sun, S., and L. E. Frelich. 2011. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. Journal of Ecology 99:991–1000.

Taylor, G., M. J. Tallis, C. P. Giardina, K. E. Percy, F. Miglietta, P. S. Gupta, B. Gioli, C. Calfapietra, B. Gielen, M. E. Kubiske, G. E. Scarascia-Mugnozza, K. Kets, S. P. Long, and D. F. Karnosky. 2008. Future atmospheric co2 leads to delayed autumnal senescence. Global Change Biology 14:264–275.

Team, R. C. 2016. R: A language and environment for statistical computing.

Teller, B. J., P. B. Adler, C. B. Edwards, G. Hooker, and S. P. Ellner. 2016. Linking demography with drivers: climate and competition. Methods in Ecology and Evolution 7:171–183.

Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species' success in thoreau's woods. Plos One 5:e8878. PT: J; TC: 27; UT: WOS:000273896500007.

Wolkovich, E. M., and E. E. Cleland. 2014. Phenological niches and the future of invaded ecosystems with climate change. AoB Plants 6:plu013.

Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, J. Regetz, T. J. Davies, N. J. B. Kraft, T. R. Ault, K. Bolmgren, S. J. Mazer, G. J. McCabe, B. J. McGill, C. Parmesan, N. Salamin, M. D. Schwartz, and E. E. Cleland. 2012. Warming experiments underpredict plant phenological responses to climate change. Nature 485:494–497.

Wolkovich, E. M., and A. K. Ettinger. 2014. Back to the future for plant phenology research. New Phytologist 203:1021–1024.

Tables

Table 1: **Study species.** Twenty-five angiosperm species were selected based on their flowering phenology in long-term records of the Arnold Arboretum. The flowering patterns we observed during our one year of data collection did not always perfectly match these long-term patterns. 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**
Aesculus flava (5)	*Carya glabra* (5)	*Catalpa speciosa* (5)
Betula alleghaniensis (5)	*Carya ovata* (5)	*Kalopanax septemlobus* (3)
Betula nigra (5)	*Crataegus crus-galli* (5)	*Styphnolobium japonicum* (5)
Gleditsia triancanthos (5)	*Fagus engleriana* (4)	*Tilia americana* (5)
Liriodendron tulipifera (5)	*Fagus grandifolia* (5)	*Tilia japonica* (5)
Phellodendron amurense var. *lavallei* (4)	*Fraxinus chinensis* (5)	
Populus deltoides ssp. *deltoides* (5)	*Liquidambar styraciflua* (5)	
Pyrus calleryana var. *dimorphophylla* (3)	*Platanus occidentalis* (5)	
Pyrus ussuriensis var. *hondoensis* (5)	*Quercus glandulifera* (4)	
Quercus alba (5)	*Quercus rubra* (5)	

Figures

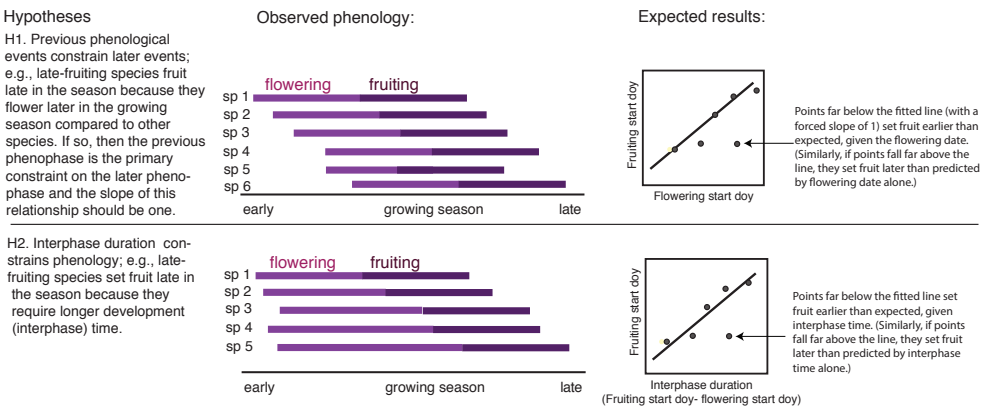

Figure 1: **Hypotheses.** We show flowering and fruiting as examples of consecutive phenological events. We expected the same patterns for other consecutive events, such as leaf budburst and leafout. Interphenophase duration is the time between phenological events, e.g., the number of days between the start of flowering and the start of fruiting.

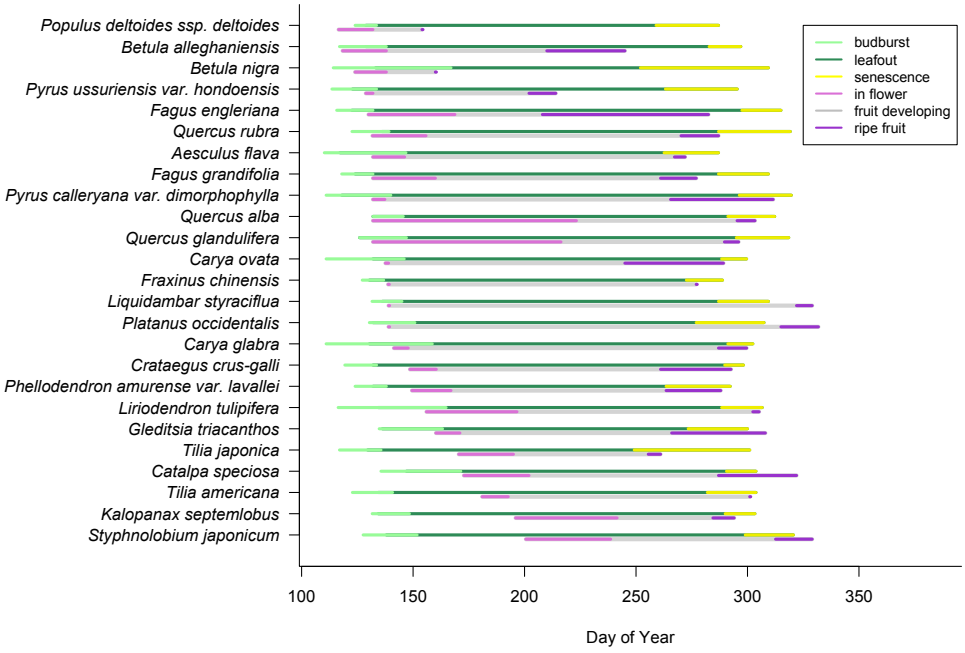

Figure 2: **Species' phenology during the 2015 growing season, ordered by mean first-flower dates.** Growth phenology is shown for budburst (from its mean start day-of-year to the mean start day-of-year for leafout, across all individuals within a species), leafout (from the mean day-of-year when fully-expanded leaves were first observed through the start of senescence), and senescence (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). Reproductive phenology is shown for flowering (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 fruiting (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).

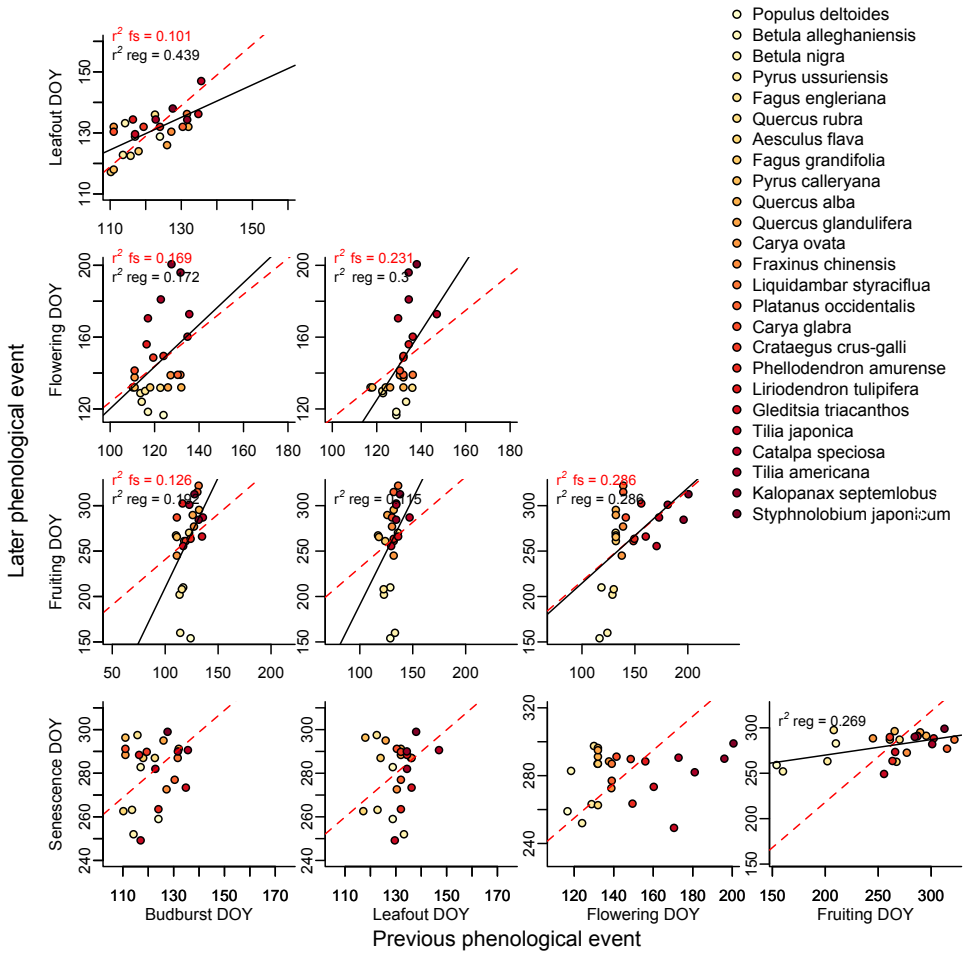

Figure 3: **Relationships among phenological stages across the 25 focal species.** Linear models were fit with the species-level mean day-of-year (DOY) of the later phenological stages as the response variable, and mean day-of-year of earlier stage as the explanatory variable. Models with a forced slope of 1 are shown by dashed red lines, and r^2 is given when ^{2}>0.10. ("fs", in red). r^2 for standard regression ("reg," in black) and lines for these models are shown by solid black lines, when r^2>0.10. Full model statistics are summarized in Table S1 in the Supplemental Materials. Species in the legend are ordered from early to late first-flower dates, as in Figure 2.

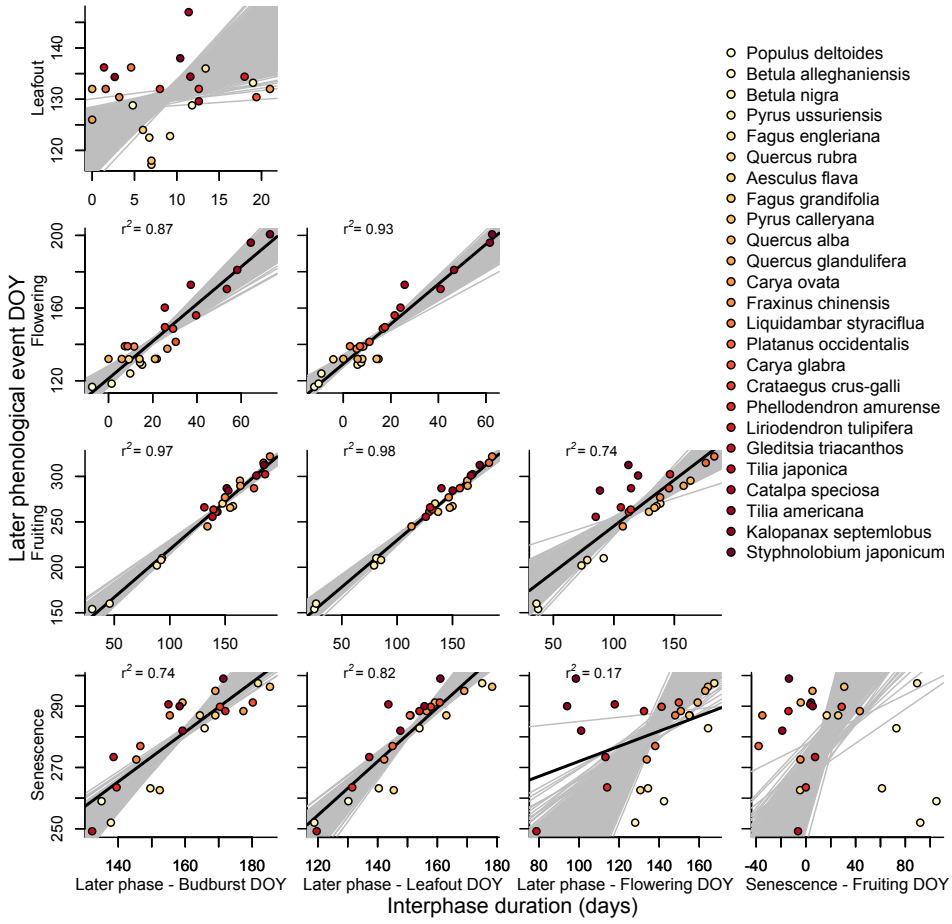

Figure 4: **Relationships among phenological stages and interphase duration across the 25 focal species.** Interphase duration is the time between the start of the earlier phenological event and the start of the later phenological event, e.g., the number of days between the species' mean start of flowering and its mean start of fruiting. Linear models were fit with the species-level mean day-of-year (DOY) of the later phenological stages as the response variable, and inter-phenophase duration as the explanatory variable. Solid lines (representing model fit), r^2, are shown $r^2>0.10$). Gray lines represent model fits when interphase was randomized with respect to the timing of the earlier phenophase. Full model statistics are summarized in Table S1 in the Supplemental Materials. Species are color-coded as in Figure 3.