

Woody plant phenological responses are strongly associated with key functional traits- Outline

January 14, 2022

Authors:

The Wolkovich Lab in 2021 ^{1,2,3,4}

Author affiliations:

¹Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4;

²Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

³Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

⁴Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

*Corresponding author: deirdre.loughnan@alumni.ubc.ca

Climate change is altering the timing of species phenologies, with such changes in temporal niches reshaping ecological communities and interactions between species. In temperate systems, the observed advances in plant phenological events, such as budburst, leafout, and flowering times, are associated with changes in seasonal temperatures, particularly warming winter and spring conditions (Menzel et al., 2006; Fitter and Fitter, 2002). But despite this strong general trend, phenological responses vary across species and geographically, and we have yet to fully understand the underlying mechanisms driving observed differences (Chuine et al., 2010; Morin et al., 2009). As the effects of climate change become more pronounced, understanding these relationships is of increasing importance if we are to predict and preserve the diversity and services found in temperate forest ecosystems.

Over several decades of work has identified three cues – chilling, forcing, and photoperiod – to be the

primary proximate drivers of budburst and leafout in temperate deciduous species (Chuine et al., 2016). For budburst to occur, species must experience extended period of cold temperatures to break dormancy (Cooke et al., 2012), with species with higher chill requirements budbursting later in the season. Spring forcing temperatures, or the temperatures needed to cue species to initiate growth after dormancy release, are also changing as temperatures warm and the timing at which suitable temperature thresholds are met occur earlier within the season (citation). Photoperiod cues can also determine some species ability to initiate growth (Basler and Körner, 2014; Zohner et al., 2020), however, species with strong photoperiod requirements are expected to be more constrained in their ability to track changes in temperature and may face fitness costs and novel species interactions as a result (?). Previous studies support the general trend of advancing budburst in response to each cue (Flynn and Wolkovich, 2018), but with considerable variation in the relative importance of different cues across species (Chuine et al., 2016; Flynn and Wolkovich, 2018). Some woody plant species, for example, require less forcing to budburst after experiencing a cool winter with more chilling, while also having the ability to compensate for low chilling with high forcing conditions or longer photoperiods (Laube et al., 2014; Harrington and Gould, 2015; Flynn and Wolkovich, 2018; Caffarra and Donnelly, 2011; Basler and Körner, 2014; Zohner et al., 2016). Evidence for the role of photoperiod is largely species specific (Heide, 1993; Basler and Körner, 2014; Singh et al., 2017; Zohner et al., 2016), with few studies testing for its importance across species in a community (but see Flynn and Wolkovich (2018)). Species that are less dependent on photoperiod cues and able to track trends in temperatures may benefit from greater intra-annual phenotypic plasticity resulting in greater fitness outcomes under increasingly variable climates (citation). Despite the insights that identifying these proximate drivers have provided, we still lack the generalizable and mechanistic understanding of why species and populations differ in their cue use that is needed to predict future changes in species sensitivities and community structures.

In our efforts to understand variation spring phenologies, several potential mechanisms have been tested to identify the drivers of species cue use. Work exploring drivers of intraspecific cue use, for example, has found age or the development stage of woody plants to be an important factor. Younger life stages, including both seedlings and younger understory trees both budburst earlier than mature individuals in the canopy (Vitasse, 2013; Seiwa and Kikuzawa, 1991). These trends reflect both differences in the temperature sensitivities across life stages and effects of ontogenic changes as trees mature (Vitasse, 2013; Seiwa and Kikuzawa, 1991). Interspecific differences in cues in contrast have been studied in relation to species' phylogenetic relatedness. Work on this topic has found strong evidence for events like flowering-time and budburst to be consistent within taxonomic families, suggesting conservatism in the genetic and physiological mechanisms that determine species phenologies (Kochmer and Handel, 1986; Davies et al., 2013; Gougherty and Gougherty, 2018). Studies of woody plant phenologies across species ranges have also highlighted the importance of local adaptations, with the presence of gradients in phenological responses and presumably cue use at northern range

limits (Lechowicz, 1984; Chuine and Beaubin, 2001; Chuine et al., 2010). In temperate systems for example, greater temperature variation in North America was associated with higher chilling requirements and more conservative phenological responses (Zohner et al., 2017). Across species latitudinal ranges, stronger responses to photoperiod cues have been observed at lower latitudes (Zohner et al., 2016). Exploring these potential drivers of plant phenologies have illustrated the nuanced nature of phenology in shaping diverse communities, but they are still limited in the degree to which they explain the variation we observe across species and ecosystems.

Taking a functional trait approach to phenological research has also been proposed as a means to explain the variation in cue use across species and geographically (Flynn and Wolkovich, 2018; Osada, 2017). Early work on functional traits used trait data from diverse global assemblages of deciduous plants to identify associations between traits and common growth strategies and different niche space (Westoby, 1998; Wright et al., 2004; Chave et al., 2009). The resulting leaf-height-seed scheme and more extensive the leaf economic spectrum found direct associations between several trait values and gradients in species growth rates and competitive abilities (Westoby, 1998; Wright et al., 2004; Díaz et al., 2016; Chave et al., 2009; Funk et al., 2016). While phenological traits have been identified as ecologically important for many years (??), only a handful of studies have explored their role in the larger framework. The existence of trade-offs in plant phenology and traits associated with growth strategies and changes in climate have been observed across plant functional groups and habitat types. Deciduous woody species with smaller vessel diameters and diffuse or semi-ring-porous xylem structures have been shown to leaf out earlier, as this anatomy reduces the risk of embolism during freezing events (Lechowicz, 1984). In testing relationships between budburst and leaf traits of deciduous tree species in Japan, (Osada, 2017) found positive correlations between budburst date and leaf area, leaf mass, and nitrogen content by both mass and area. (Sun et al., 2006) also found deciduous species with high leaf mass per area (a trait that is the inverse of specific leaf area) to budburst earlier in deciduous oak forests in eastern China. While variation in leafout can also relate to species heights, both intraspecifically and across functional groups such as understory species verses canopy species, with shorter individuals leafing out earlier than taller ones (??). To date, research in this area has largely consisted of studies conducted within single sites, with few focal species or traits, limiting their ability to draw more general and causal inferences.

While there have been numerous studies investigating the relationships between climate and functional traits, and a wealth of literature on the effects of climate cues as drivers of phenology, the interrelatedness of traits, phenological responses, and climate drivers has yet to be widely tested. The same selective pressure shaping species traits under variable temperature are likely to also act on species responses to phenological cues and define a species temporal niche. Drawing on previous work and the broader trait literature, we predict that species that budburst early in the growing season should have shorter rates of return on resource investments

and the ability to take advantage of the greater abundance of soil nutrients and light early in the growing season. Plants that produce leaves with high leaf nitrogen content and SLA can take advantage of greater light availability with greater rates of photosynthesis (Wright et al., 2004; Pereira and Des Marais, 2020), while also limiting the costs of tissue (???). Earlier budbursting species also experience less competition for light and can invest less in height and stem density (Laughlin et al., 2010). This suite of traits should contrast species with slower, more competitive growth strategies that benefit from slower rates of return on resource investment and the longer retention of leaf tissue.

We test for associations between plant phenological responses to environmental cues and common functional traits. Budburst data for tree species in controlled environmental studies was selected from the Observed Spring Phenology Response in Experimental Environments (OSPREE) database and paired with functional trait data from the TRY and BIEN databases. This data was used to explicitly test for the relative differences in functional traits and the timing of budburst in response to variable forcing, chilling, and photoperiod cues. We predict that species that budburst under low chilling, low forcing, and short photoperiod conditions are more likely to have traits associated with acquisitive growth, but low competitiveness, as reflected by high SLA, high LNC, shorter heights, and lower seed mass. In contrast, species that budburst later under high chilling or high forcing temperatures, with long photoperiods may have traits more associated with conservative growth and higher competitive abilities, such as low SLA, low LNC, greater heights and heavier seeds.

1 Methods

To test for relationships between functional traits and species phenological cues, we combined trait data from the TRY and BIEN trait databases with data on phenological responses to temperature and photoperiod cues from experiments. We began by searching for trait data for all 234 species represented in the OSPREE database. We requested trait data for ten functional traits from the TRY database (Table S1). Data was also obtained from the BIEN database using the BIEN R package (?), and included data from 34 species and seven traits (Table S1). Data was requested or downloaded in December 2018. In our analysis we only included trait data from adult individuals of deciduous woody species, with a minimum height of 1.42 m. We removed all data denoted as being from experiments or growing in non-natural habitats. Traits were also grouped where appropriate, for example, separate entries for specific leaf area (SLA) values with petioles, without petioles, and for which no petiole presence was specified were all categorized as a single trait in our analysis (see Table S1). Data from studies duplicated in both the TRY and BIEN datasets were also removed (n= 434905). Finally, we subsetting the data to include only a complete dataset for each species and trait, resulting in a final dataset which includes 26 species with at least one measurement for the following six traits:

height, SLA, seed mass, LNC, SSD, & LDMC ($n = 60740$, $n = 8524$, $n = 404$, $n = 243$, $n = 5474$ for each trait respectively). Given the abundance of height data and overrepresentation of height measurements for 13 of our focal species, we randomly sampled 5000 height measurements for each of these species to include in our analysis ($n = XX$). This reduces the effect of trait values from these frequently measured species from overwhelming the partial pooling effect in our model. In addition we excluded seed mass data from the HE Marx dataset from BIEN, as it consisted of only one value, making it challenging to include the study level effect in our model.

From the OSPREE database, we acquired data of spring phenological responses to forcing, chilling, and photoperiod cues in controlled environment studies. This database was constructed using a literature search of ISI Web of Science and Google Scholar using the following terms:

- (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature*
- (budburst OR leaf-out) AND dorman*.

First published in 2019, this database has since been updated, and now includes the review of an additional 623 and 270 new publications from each search term respectively. From this subsequent review, we added an additional 12 papers. For additional information on the construction of the OSPREE database and methods of cue estimates, see (?). Our analysis used all available budburst data for our 26 focal species, with the data originating from 28 unique studies.

To test for correlations in our six traits and further refine our trait selection, we performed a PCA. The principle component explained 32.2% of variation while the second explained 23.4% of the variation (Fig. S1). Given the strong association between SLA and LDMC, and similarly between stem specific density (SSD) and height, we further reduced the number of traits in our analysis to include only height, SLA, seed mass, and LNC.

We fit four models, with separate models for each trait. Using the following joint hierarchical bayesian models, we estimated the relative trait effect on cue responses and budburst date for each species:

$$\begin{aligned}
\hat{trait}_i &= \mu_{grand_{sp}} + \alpha_{study_{study_i}} \\
\mu_{grand_{sp}} &= \alpha_{grand} + \alpha_{sp_{sp_i}} \\
\alpha_{grand} &\sim N(0, \sigma_{grand}) \\
\alpha_{sp} &\sim N(0, \sigma_{sp}) \\
\alpha_{study} &\sim N(0, \sigma_{study}) \\
trait_i &\sim N(\hat{trait}_i, \sigma_{trait}) \\
\\
\hat{pheno}_i &= \alpha_{pheno_{sp_i}} + \beta_{force_{sp_i}} * Forcing_i + \beta_{photo_{sp_i}} * Photo_i + \beta_{chill_{sp_i}} * Chill_i \\
\beta_{force_{sp}} &= \alpha_{force_{sp}} + \beta_{trait.force} * \alpha_{sp_{sp}} \\
\beta_{chill_{sp}} &= \alpha_{chill_{sp}} + \beta_{trait.chill} * \alpha_{sp_{sp}} \\
\beta_{photo_{sp}} &= \alpha_{photo_{sp}} + \beta_{trait.photo} * \alpha_{sp_{sp}} \\
\alpha_{pheno} &\sim N(\mu_{pheno}, \sigma_{pheno}) \\
\alpha_{force} &\sim N(\mu_{force}, \sigma_{force}) \\
\alpha_{chill} &\sim N(\mu_{chill}, \sigma_{chill}) \\
\alpha_{photo} &\sim N(\mu_{photo}, \sigma_{photo}) \\
pheno_i &\sim N(\hat{pheno}_i, \sigma_{pheno})
\end{aligned}$$

Where i represents a unique trait values or budburst observations in the first and second section of the model respectively, sp represents the species level effects, $study$ represents studies level effects, alpha parameters are the intercepts for species level effects for trait differences and cue responses, beta parameters represent the slope estimates for cues responses, trait is the estimated trait value, and $pheno$ the estimated day of budburst since cues were applied. This value is incorporated into the second model as the beta trait.cue parameter, which is then used to estimate the day of budburst, denoted as $pheno$.

To explicitly compare the effects of chilling, forcing, and photoperiod, we used standardized z-scored values for the predictor variables which accounts for the differences in the scale of predictors across studies (?), as well as the natural units for the cues (including chill units, degree C, and hours for chilling, forcing, and photoperiod respectively). In the first section of this model, we estimate the relative trait effect for each species, while also accounting for study effects. We estimate the trait effect as a latent parameter, with values close to zero indicating small relationships between traits and cues values, while greater values represent high correlations between traits and phenological cues. Our model also includes partial pooling across species

and across studies, allowing use to account for differences in sample size, methods, and ecosystem types. Our model was first developed using test data and our priors validated using prior predictive checks. In our models, we used weakly informative priors, with four simultaneous chains of 1,000 sampling iterations and 2,000 posterior samples for each parameter. The models produced Rhat values close to 1 and neffs greater than 10% of the number of iterations, indicating that the model performed sufficiently well. We fit our models using the Stan programming language (Stan citation), interfaced with using the rstan package (version, citation).

Finally, we used a phylogenetic generalized least-squares regression model (PGLS) to test the relationship between day of budburst and individual traits. This analysis allowed us to test for phylogenetic non-independence in the phenology-trait relationship (?). We obtained a rooted phylogenetic tree by pruning the tree developed by (?) and performed the PGLS analysis using the mean trait values and mean posterior estimates of the cue responses from our joint model. The PGLS was run using the "Caper" package in R (?).

2 Results

Our models PGLS suggests there are no strong phylogenetic effects

3 Discussion

Limitations: Only consider above ground traits

References

- Basler, D., and C. Körner. 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology* 34:377–388.
- Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species: Effects of light and temperature on bud burst. *International Journal of Biometeorology* 55:711–721.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Chuine, I., and E. G. Beaubin. 2001. Phenology is a major determinant of tree species range. *Ecology Letters* 4:500–510.
- Chuine, I., M. Bonhomme, J. M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global change biology* 22:3444–3460.
- Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. *Science* 329:277–278.
- 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.
- Cooke, J. E., M. E. Eriksson, and O. Junttila. 2012. The dynamic nature of bud dormancy in trees: Environmental control and molecular mechanisms. *Plant, Cell and Environment* 35:1707–1728.
- Davies, T. J., E. M. Wolkovich, N. J. Kraft, N. Salamin, J. M. Allen, T. R. Ault, J. L. Betancourt, K. Bolmgren, E. E. Cleland, B. I. Cook, T. M. Crimmins, S. J. Mazer, G. J. McCabe, S. Pau, J. Regetz, M. D. Schwartz, and S. E. Travers. 2013. Phylogenetic conservatism in plant phenology.
- Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönsch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. *Nature* 529:167–171.
- Fitter, A. H., and R. S. Fitter. 2002. Rapid changes in flowering time in British plants. *Science* 296:1689–1691.
- Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 219:1353–1362.

- Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, A. E. Sutton-Grier, L. Williams, and J. Wright. 2016. Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews* 92:1156–1173.
- Gougherty, A. V., and S. W. Gougherty. 2018. Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits , phylogenetics , and climate. *New Phytologist* 220:121–131.
- Harrington, C. A., and P. J. Gould. 2015. Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. *Frontiers in Plant Science* 6:1–12.
- Heide, O. M. 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* 88:531–540.
- Ishioka, R., O. Muller, T. Hiura, and G. Kudo. 2013. Responses of leafing phenology and photosynthesis to soil warming in forest-floor plants.
- Kochmer, J. P., and S. N. Handel. 1986. Constraints and Competition in the Evolution of Flowering Phenology. *Ecological Monographs* 56:303–325.
- 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.
- Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* 24:493–501.
- 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.
- Lenz, A., G. Hoch, C. Körner, and Y. Vitasse. 2016. Convergence of leaf-out towards minimum risk of freezing damage in temperate trees. *Functional Ecology* 30:1480–1490.
- Lopez, O. R., K. Farris-Lopez, R. A. Montgomery, and T. J. Givnish. 2008. Leaf phenology in relation to canopy closure in southern Appalachian trees. *American Journal of Botany* 95:1395–1407.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jactzak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in Thoreau’s Concord: A community perspective. *Ecology* 89:332–341.

- Morin, X., M. J. Lechowicz, C. Augspurger, J. O’keefe, D. Viner, and I. Chuine. 2009. Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology* 15:961–975.
- Osada, N. 2017. Relationships between the timing of budburst, plant traits, and distribution of 24 coexisting woody species in a warm-temperate forest in Japan. *American Journal of Botany* 104:550–558.
- Pereira, C. G., and D. L. Des Marais. 2020. The genetic basis of plant functional traits and the evolution of plant-environment interactions. *International Journal of Plant Sciences* 181:56–74.
- Seiwa, K., and K. Kikuzawa. 1991. Phenology of tree seedlings in relation to seed size. *Canadian Journal of Botany* 69:532–538.
- Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jonsson, and R. P. Bhalerao. 2017. Photoperiod- and temperature-mediated control of phenology in trees – a molecular perspective.
- Sun, S., D. Jin, and R. Li. 2006. Leaf emergence in relation to leaf traits in temperate woody species in East-Chinese *Quercus fabri* forests. *Acta Oecologica* 30:212–222.
- Suzuki, S., and G. Kudo. 1997. Short-term effects of simulated environmental change on phenology, leaf traits, and shoot growth of alpine plants on a temperate mountain, northern Japan. *Global Change Biology* 3:108–115.
- Vitasse, Y. 2013. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist* 198:149–155.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas, C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley, Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C. Thomas, M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Zohner, C. M., B. M. Benito, J. D. Fridley, J. C. Svenning, and S. S. Renner. 2017. Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe and East Asia. *Ecology Letters* 20:452–460.
- Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* 6:1120–1123.
- Zohner, C. M., L. Mo, T. A. M. Pugh, J.-F. Bastin, and T. W. Crowther. 2020. Interactive climate factors restrict future increases in spring productivity of temperate and boreal trees. *Global Change Biology* pages 1–14.

4 scrape

In testing for likely associations between phenological events and other commonly measured traits, this work would improve our understanding of ecosystem functioning and a trade-offs in resource use and conservation across species.