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

February 2, 2022

Authors:

The Wolkovich Lab in 2021 [1,2,3,4]

Author affiliations:

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

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

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

[4]Edificio 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 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.

While we have yet to identify all drivers of selection on phenologies, considerable work has shown the im-

portance of three abiotic cues – chilling, forcing, and photoperiod – as the primary drivers of budburst and leafout in temperate deciduous species (Basler and Körner, 2014; Chuine et al., 2016; **?**; Flynn and Wolkovich, 2018). For budburst to occur, species must experience extended period of cold temperatures to break dormancy (Cooke et al., 2012), where species with higher chill requirements budburst 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 a species ability to initiate growth (Basler and Körner, 2014; Zohner et al., 2020). Species with strong photoperiod requirements are, however, 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, 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 a generalizable and mechanistic understanding of why species and populations differ in their cue use that. Further insight on this topic is needed to predict future changes in species sensitivities and community structure.

In our efforts to understand variation in spring phenological timing, researchers have tested several potential mechanisms to identify the drivers of species cue responses. Work exploring drivers of intraspecific cue use, for example, has found age or the development stage of woody plants to be important. 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, however, 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). Studies testing for trends in cues responses across species latitudinal ranges have also observed stronger responses to photoperiod cues 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 could help 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, common growth strategies, and different niche space (Westoby, 1998; Wright et al., 2004; Chave et al., 2009). The resulting leaf-height-seed scheme and the more extensive 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 reproductive phenological traits have been identified as ecologically important for many years (**??**), few studies have explored their role in the larger trait framework. Spring phenological traits, such as budburst and leafout, define the beginning of the growing season and period of photosynthesis, and therefore also have the potential to correlate with established growth strategies. Support for the existence of trade-offs in budburst dates and traits related to growth and resource use have been observed across plant functional groups and habitat types in a handful of studies. For example, several studies have found deciduous woody species with smaller vessel diameters and diffuse or semi-ring-porous xylem structures to leaf out earlier than species with larger vessels, 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, while (Sun et al., 2006) 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. Variation in leafout can also relate to species heights, both intraspecifically and across functional groups, with shorter individuals or understory species leafing out earlier than taller individuals or canopy species (**??**). To date, however, research in this area has focused on individuals at local scales, or few traits for a small number of species, limiting our ability to draw more general and causal inferences. There is also a lack of studies linking traits directly to cue sensitivity rather than phenological date. The likely associations between cue sensitivity, phenological events,

and growth strategies may allow for more generalizable trends across species and sites, and better account for species variability in key environmental cue use.

To date, there have been numerous studies investigating the relationships between climate and functional traits and a wealth of literature on the separate effects of climate cues as drivers of phenology. However, the selective pressures shaping species traits under variable temperatures are also likely to also act on species responses to phenological cues and define a species temporal niche. Species with a more acquisitive life-strategy 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. Such species face a lesser cost in triggering phenological events too early, because they can recover more quickly from early season damage (citation?). For example, acquisitive species produce leaves with high leaf nitrogen content and Specific Leaf Area (SLA) and so can take advantage of greater light availability by having higher rates of photosynthesis (Wright et al., 2004; Pereira and Des Marais, 2020), while also limiting the costs of tissue production (**???**). Acquisitive-strategy species also invest less in height and stem density (Laughlin et al., 2010), so will need to trigger the growing season with fewer cue units so they experience less competition for light during budburst. Earlier budbursting species also tend to have lower responses to cues, meaning they they require less spring forcing and winter chilling, and shorter days to trigger the beginning of the season (**cite Flynn & Wolkovich, 2018**). This suite of traits contrasts with more conservative life-strategy species with slower, more competitive growth strategies that benefit from slower rates of return on resource investment and the longer retention of leaf tissue. A greater requirement for cue unit accumulation to trigger phenological events should align with a more conservative life-strategy as such species seek to avoid damage due to premature development.

In this study, 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 experimental forcing, chilling, and photoperiod cues. Drawing on previous work and the broader trait literature, we predict that species that respond less strongly to chilling, forcing, and 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 are more responsive to chilling, forcing and photoperiods will have traits more associated with conservative growth and higher competitive abilities, such as low SLA, low LNC, greater heights and heavier seeds.

1 Methods

For our analysis, we combined phenological data from the OSPREE database (**?**) with functional trait data from the TRY(cite) and BIEN (cite) trait databases.

The OSPREE database contains woody, deciduous species phenological data for which experimental data on phenological cues is available, and for which the phylogenetic relationship is well known. 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 37 focal species, with the data originating from 28 unique studies.

Both TRY and BIEN are large databases compiling plant trait data across many individuals, species, and studies. Initially, we began by selecting height, seed mass, LNC, SLA, stem specific density (SSD) and leaf dry matter content (LDMC) data for all 234 species represented in the OSPREE database.

We began by searching for trait data for all 234 species represented in the OSPREE database. Data was also obtained from the BIEN database using the BIEN R package (**?**). Data was requested or downloaded in December 2018. Our full trait datasets included data on x species .... (S Table x - a tabel only showing trait data for traits we actually used. Not all teh ones we requested.)

For our analysis we only included trait data from adult individuals with a minimum height of 1.42 m and we removed all data 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). Duplicated data across the datasets were removed (n= 434905). Finally, we subsetted the data to include only species for which we had a complete dataset for each species and trait. After our selection criteria, out data includes 26 species with at least one measurement for the following six traits: height, seed mass, LNC, SLA, SSD, & LDMC (n = 60740, n = 404, n = 243, n = 8524, n = 5474, n = 5101 for each trait, respectively). 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 the SLA and LDMC leaf traits, and similarly between stem specific density (SSD) and height, we further reduced the number of traits in our analysis to include only height, seed mass, LNC, and SLA. In doing so, we were able to increase the number of species we could include in our analysis, as 37 species had at least one measurement for our final four traits. Given the abundance of height data and overrepresentation of height measurements for six of our focal species, we

randomly sampled 3000 height measurements for each of these species to include in our analysis (n = 27318). 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

To test the relationships between functional traits and species cue responses, we developed a joint hierarchical bayesian model. Our model is composed of two sub-models that are co-estimated and linked by shared parameters. Because each trait varied in the number of studies in which it is included as well as the number of individuals for which it is measured, we chose to model each trait separately. The first part of the model is a hierarchical intercept only model (Equations 1, 2 & 3) estimating species mean trait value for species i ($trait_i$). This ($trait_i$) value is a combination of a species mean trait value $\alpha_{sp,i}$ and a hierarchical grouping term on the intercept for study to account for study level differences in the trait data ($\alpha_{study,i}$).

The second part of our models is a hierarchical linear model (Equation 4) regressing the date of budburst b ($pheno_b$) against a combination of chilling, forcing and photoperiod units. 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, °C, and hours for chilling, forcing, and photoperiod respectively). We test whether there is a link between phenological cue response ($\beta chill_{sp}, \beta force_{sp}, \beta photo_{sp}$) and mean traits by including the mean trait values from the previous model (α_{sp}) in the estimation of the cue slopes. Each cue slope is a combination of a species-specific slope value (αcue) independent of trait, and the species trait value (α_{sp}) (Equations 10, 9 & **??**)multiplied with an interaction parameter $\beta trait.cue$ (Equations 5, 6 & 7). A greater $\beta trait.cue$ value means trait is more strongly related to cue slope, and its sign dictates the direction of the interaction.

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 warmup iterations and 2,000 sample iterations. 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).

$$trait_i \sim N(\alpha_{sp,i} + \alpha_{study,i}, \sigma_{trait}) \tag{1}$$

$$\alpha_{sp} \sim N(\mu, \sigma Sp) \tag{2}$$

$$\alpha_{study} \sim N(0, \sigma Study) \tag{3}$$

$$pheno_b \sim N(\alpha pheno_{sp_b} + \beta force_{sp_b} * Forcing_b + \beta photo_{sp_b} * Photo_b + \beta chill_{sp_b} * Chill_b, \sigma_{pheno}) \tag{4}$$

$$\beta chill_{sp} = \alpha chill_{sp} + \beta trait.chill * \alpha sp_{sp} \tag{5}$$

$$\beta force_{sp} = \alpha force_{sp} + \beta trait.force * \alpha sp_{sp} \tag{6}$$

$$\beta photo_{sp} = \alpha photo_{sp} + \beta trait.photo * \alpha sp_{sp} \tag{7}$$

$$\alpha pheno \sim N(\mu_{pheno}, \sigma_{pheno}) \tag{8}$$

$$\alpha force \sim N(\mu_{force}, \sigma_{force}) \tag{9}$$

$$\alpha chill \sim N(\mu_{chill}, \sigma_{chill}) \tag{10}$$

$$\alpha photo \sim N(\mu_{photo}, \sigma_{photo}) \tag{11}$$

Finally, we used a phylogenetic grereralized 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 (?).

$$y \sim MVN(\mu, S) \quad \mu = \mu_{grand_{sp}} + \alpha study_{study_i}$$

2   Results

Our model estimated most mean trait values to be close to the simple geometric mean across the data. However, there were some cases were the effect of study was influential. This lead to differences between the simple geometric means and the species trait estimates without the effect of study (Fig1). Each of our trait models predicted most species cue responses to be negative, indicating that the average effect of forcing, chilling, and photoperiod cues were to advance budburst date. The exceptions to this were the photoperiod estimates from our height and SLA models, both of which showed a small positive or delaying effect, but considerable variation in the estimated value. The absolute effect of species cue responses was generally greatest for forcing cues, except in our models of LNC, for which chilling cues had the largest absolute response. Photoperiod cues had the smallest cues responses in three of our models, except for our model of tree height, in which the absolute effect of chilling was less than that of photoperiod. The effect of traits on cue responses were all negative and were greatest for forcing and chilling, while the effects of photoperiod cues were weaker across all our models. These trait effects on cue responses were variable across species and for some traits were also dependent on the trait values themselves (Figure 1 & 2).

In our model for SLA, we found all three cue responses to be affected by SLA as well as the trait value itself. Species with low SLA were more sensitive to increased forcing, chilling, and photoperiod cues when the trait effects were included (Fig 2). Species with leaves with high SLA , however, showed no difference in their cue responses when the trait effect was included in the model. Interestingly these high trait species only showed cues responses to forcing and chilling, and were relatively insensitive to changes in photoperiod cues (Fig 2). The effect of height and LNC on species cue responses were similarly dependent on the magnitude of the trait value. Taller species all showed a stronger trait effect relative to shorter individuals, with the response to both forcing and chilling changing from a positive slope, or delaying effect, to a negative slope when trait values were accounted for. The effect of photoperiod was less strong, and only noticeable for taller species. As we observed with SLA, shorter species showed a much smaller trait effect and only advanced in budburst dates in response to chilling and forcing. Similarly species that produce leaves with high LNC showed no difference in budburst with increased forcing and a slight delay in response chilling when trait effects were not included. However, with the trait effect these species had a negative cue responses, advancing their budburst with higher cue treatments. Species with low LNC consistently advanced their budburst with

increased forcing and chilling irrespective of trait effects, but to our surprise, there was no effect of LNC to photoperiod cues regardless of trait values.

Finally, our model estimates for the trait effects of seed mass on cue responses were all negative, however, given the nature of the log10 transformation and the resulting negative trait values, the inclusion of trait effects offset the effects of cue responses in the absence of traits. The inclusion of the trait effect in our model resulted in large seeded species to have no differences in budburst dates with increasing forcing, offsetting the delayed effect the model predicts in the absence of the trait effect. A similar, but stronger response was also estimated the response on large seeded species to chilling temperatures, while the magnitude of the response to longer photoperiods was negligible. Small seeded species produced similar estimates regardless of whether trait effects were considered, and only advanced their budburst dates in response to higher forcing cues.

PGLS suggests there are no strong phylogenetic effects

3 Discussion

– What do our results suggest for the relationship between cue use and traits? - Species responses to forcing, chilling, and photoperiod cues are influenced by species functional traits and the dependent on trait values. - generally in line with previous studies of phenological cues

  – Do we find relationships between cues and traits? - yes, but dependent on the trait value; species with hight SLA, Seed mass and heights had a stronger response when the effect of trait was included

  – Do these trends agree with a fast/slow tradeoff? - not really, only for height and seed mass - taller trees did have higher chill and forcing requirements - high SLA species required more chilling or higher forcing temperatures to bb earlier - contrary to our prediction - LNC really did not matter, minor increase in response for high LNC which is contrary to our prediction - larger seeds did bb earlier with higher chilling - as predicted

– How do our results relate to previous studies?

– What do our results suggest for the bigger picture?

  – How might traits constrain/facilitate future shifts in phenology?

  – How might ecosystem functioning shift if species track temperature? How to our results relate to seasonality and frost risk?

  – What does it mean if more competitive/invasive species respond to warming and start bb earlier - outcompete species and lead to compressed temporal niche?

– Relate our results to invasion success

– Limitations

   – we assume stronger cues mean earlier bb but really it's more complicated than this

   – broad approach means lose detail and compromise - traits come from different populations to the phenology data

   – disconnect between trait data - observational - and phenology data that is in a controlled environment

   – limited data may have reduced diversity of traits/strategies - may not be enough to detect predicted trends – reframe this as less of a limitation and more of a future direction

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, photoperiotls, and tree phenology. Science 329:277–278.

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. Bönisch, 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.

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.

Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aaasa, 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. Jatczak, 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.

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.

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. Cornellissen, 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.