Supplemental materials for Spatial and temporal shifts in photoperiod with climate change

A.K. Ettinger, D. Buonaiuto, C. J. Chamberlain, I. Morales-Castilla, E. Wolkovich

September 26, 2019

Supplemental Methods

The Observed Spring Phenology Responses in Experimental Environments (OSPREE) database

The OSPREE database is a compilation of 72 controlled environment studies of budburst responses to temperature and photoperiod, and spans 39 years and 203 woody plant species (Wolkovich et al., 2019). To identify studies for the database, we searched ISI Web of Science and Google Scholar with the following terms:

- 1. TOPIC = (budburst OR leaf-out) AND (photoperiod or daylength) AND temperature*, which yielded 85 publications
- 2. TOPIC = (budburst OR leaf-out) AND dorman*, which yielded 193 publications

 The initial searches yielded 201 papers, which were reviewed. OSPREE includes the subset of those studies that focus on temperate woody plants, tested for photoperiod and/or temperature effects on budburst, leafout, or flowering, and for which we could quantitatively identify forcing, photoperiod, and chilling treatments.

Quantifying and mapping differences in green-up across the United States and Europe (Figure 2)

Satellite images can be combined with algorithms—e.g. MODIS Land Cover Dynamics—to identify the dates on which phenophases transition from one to the next. Using data from the MODIS sensor (available at: https://lpdaacsvc.cr.usgs.gov/appeears/), we extracted spatial data for North American and Western European green-up—the beginning of seasonal greening—for the years 2009 and 2012. Green-up dates are calculated on the basis of the onset of the Enhanced Vegetation Index (Huete et al., 2002). From green-up maps for each year, we derived the photoperiod corresponding to each pixel (according to its geographic coordinates and day of the year), using the R function "daylength" in package geosphere (see Fig. 2a,b in main text). Finally, we mapped spatial patterns of temporal shifts in green-up by comparing an early and late spring years. To do so, we subtracted the 2013 green-up map from the 2009 one. Thus, a negative difference signifies earlier green-up in 2012 versus 2009; a positive difference is the result of later green-up in 2012 compared with 2009. The spatial resolution corresponding to the maps is 0.1 x 0.1 degrees.

Nonlinearities in phenological responses to daylength (Figure 3)

To explore to what extent spring phenology responds linearly (or non-linearly) to photoperiod, we selected OSPREE publications that had three or more photoperiod treatments, and, after reading the methods of these papers in detail, identified three that used three or more photoperiod treatments in the same experiment:

Ashby et al. (1962); Heide (1993) and Caffarra et al. (2011). The Ashby et al. (1962) study used two North American populations of *Tilia america*. Heide (1993) studied populations of *Fagus sylvatica* from Basel, Switzerland; Copenhagen, Denmark; As, Norway; and the Carpathian Mountains, Poland. The ? study used plant material of *Betula pubesens* from Wexford, Ireland. These experiments all used forcing temperatures of 21 or 22°C. Chilling varied considerably across experiments, and chilling level was categorized as follows:

- <1 Chill Portions = None
- 1-44 Chill Portions = Low
- 45-69 Chill Portions = Medium
- 70-106 Chill Portions = High
- >106 Chill Portions = Very High

Although our sample is limited—e.g. taxonomically, few forcing treatments, only three papers—emerging patterns suggest non-linear responses that differ across species and that may interact with varying chilling.

Mapping temporal and spatial shifts in space and time (Figure 4)

To examine the range of photoperiod treatments imposed in growth chamber experiments of woody plants, and compare these treatments to shifts in photoperiod that may be expected due to climate change-induced spatial and temporal shifts, we identified all experiments in the OSPREE database with at least two photoperiod treatments; this resulted in 30 experiments (Table S1, Wolkovich et al., 2019).

We wanted to compare experimental photoperiod treatment levels in these 30 experiments to temporal shifts that would be required for species to experience equivalent photoperiod shifts with climate change. To do this, we identified the dates between the winter and summer solstices on which daylengths at the latitude of the experiments matched treatment levels. When no date matched the experimental treatment level exactly, we chose the date with the most similar daylength, as long as it was within 0.5 hours of the photoperiod treatment level. For studies with only two photoperiod treatment levels, we identified matching dates for both levels. For studies with more than two daylength treatments, we identified matching dates for the lowest treatment level and the second lowest treatment level (e.g., if treatment levels were 10, 12, 14, and 16 hours of daylight, we identified dates with 10 and 12 hours of daylength only). This provided an estimate for the minimum temporal shift required during the spring that would equal the difference between the two treatments; that is, the minimum difference, in days, between dates with the lower daylength treatment and dates with higher daylength treatment. In 11 out of 30 cases, the experimental treatment differences exceeded what the difference in photoperiod experienced across the entire year at a given latitude (Xs in Figure 4).

To compare differences between experimental photoperiod treatment levels to differences in photoperiod species would experience with spatial shifts, we identified the daylength on the summer solstice for the latitudes of all 30 experiments in Table S1. To get potential changes in daylength experienced, we compared the summer solstice daylength at each latitude to the daylength on latitudes up to 40 degrees poleward (in continuous increments of 0.1°). Because latitudinal variation in daylength is greatest during the solstices, this provides a maximum possible shift in daylength, at a constant day of year. We then matched the experimental change in photoperiod between two treatments levels to the latitudinal shift that provided an equivalent change in photoperiod. In 13 out of 30 cases, the experimental treatment differences exceeded the photoperiod change that would be experienced with a latitudinal shift of up to 40°(Figure 4). Thus, although the analyzed experiments may not have originally aimed at assesing the effects of climate change on the phenological responses, the treatments are often well-outside the expected range of change and future efforts should take this into account.

Comparing shifts in experienced photoperiod in experiments to those in the natural world with climate change (Figure 5)

We took current budburst estimates (1981-2000) from PhenoFit (Duputié et al., 2015) and projected budburst (2081-2100) using the A1Fi Phenofit scenario for two species – $Fagus\ sylvatica$ and $Quercus\ robur$ – and compared these points to data obtained from OSPREE. The OSPREE data points were collected from experiments and days of budburst were calculated from the start of the experiment, rather than from the start of the year. In order to render these points comparable to the current estimates and projections, we scaled the days to budburst by adding the day of budburst from the first Phenofit observation to all of the OSPREE data points. We only used Phenofit estimates that had both current and projected estimates. Note that the three OSPREE data points for $Quercus\ robur$ with extremely high days to budburst (right panel of Fig. 5 in the main text) were from an experiment with very low forcing temperatures (Morin et al., 2010, 3.8-5.7°).

Supplemental Box S1. Dominant models of how photoperiod affects spring woody plant phenology

The molecular mechanisms and pathways underlying photoperiod sensitivity are poorly understood for most organisms, even in relatively well-studied phenophases such as spring budburst in woody plants (Ding and Nilsson, 2016). Spring budburst in woody plants is thought to be controlled by three main cues: chilling, forcing, and photoperiod, as well as interactions between them (Flynn and Wolkovich, 2018; Heide, 2008; Zohner et al., 2016). Our understanding of how plants interpret photoperiod comes largely from studies of flowering in the model plant *Arabidopsis thaliana* (e.g., Suárez-López et al., 2001) and fall budset in woody plant species (e.g., Howe et al., 1996).

Plants sense light inputs by blue light receptors and phytochromes, which have been found in nearly all organs throughout the plant. Plants are thought to interpret photoperiod through a coordinated response to light in relation to the time of day. When the internal circadian rhythm coincides with an external signal (light) under certain conditions (e.g., warm days), a response is induced (Lagercrantz, 2009). This "external coincidence model" has been most widely studied in *Arabidopsis*, and is thought to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species (Bünning, 1936; Davis, 2002; Bastow and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Petterle et al., 2013; Singh et al., 2017). The model proposes the existence of a circadian rhythm of light sensitivity, in which the night-phase is sensitive to light and the day-phase is insensitive to light. As days get longer in the spring, daylight illuminates the light sensitive phase, triggering a response.

Little is known about the genetic pathways responsible for the light-sensing apparatuses involved in spring budburst, and how they may vary across species or populations. Some genes have been identified that play a role in coordinating budburst in poplar (*Populus* spp.), and may occur in other woody species as well. Many similarities exist between the proposed regulatory networks of vegetative growth in *Populus* and those controlling floral initiation in *Arabidopsis*, (Ding and Nilsson, 2016). For example, vegetative growth and inhibition of budset are promoted by the FLOWERING LOCUS T2 (FT2) gene, a homolog of *Arabidopsis thaliana* gene FLOWERING LOCUS (FT). FT2 expression appears to be controlled by a pathway that is effective in long days and warm temperatures, marking the onset of the growing season (Hsu et al., 2011). Its loss of expression in autumn, when the days are getting shorter, is associated with the onset of dormancy (Glover, 2014).

There are large gaps in our understanding of how photoperiod sensing pathways affect budburst, the genetics behind these pathways, and the extent of species- and population-level genetic variation. Questions also remain about how photoperiod sensing interacts with temperature sensing to affect responses. For example, Figure 3 shows the most detailed data we were able to find of budburst responses across different photoperiod and chilling treatments. These data underscore how variable responses to photoperiod are, across species and populations, and with different chilling treatments.

References

- Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. Nature reviews. Genetics 13:627.
- Ashby, W., et al. 1962. Germination capacity in American Basswood *Tilia americana*. Transactions of the Illinois State Academy of Science 55:120–3.
- 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.
- Bastow, R., and C. Dean. 2002. The molecular basis of photoperiodism. Developmental cell 3:461–462.
- Bünning, E. 1936. Endogenous daily rhythms as the basis of photoperiodism. Ber Deut Bot Ges 54:590-607.
- Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011. Modelling the timing of *Betula pubescens* bud-burst. I. Temperature and photoperiod: A conceptual model. Climate Research 46:147.
- Davis, S. J. 2002. Photoperiodism: the coincidental perception of the season. Current Biology 12:R841–R843.
- Ding, J., and O. Nilsson. 2016. Molecular regulation of phenology in trees—because the seasons they are a-changin. Current opinion in plant biology 29:73–79.
- Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species adapt to climate change. Global Change Biology 21:3062–3073.
- Falusi, M., and R. Calamassi. 1990. Bud dormancy in beech (*Fagus sylvatica L.*). Effect of chilling and photoperiod on dormancy release of beech seedlings. Tree Physiology 6:429–438.
- ——. 1996. Geographic variation and bud dormancy in beech seedlings (Fagus sylvatica L). Pages 967–979 in Annales des Sciences forestières. Vol. 53. EDP Sciences.
- 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.
- Ghelardini, L., A. Santini, S. Black-Samuelsson, T. Myking, and M. Falusi. 2010. Bud dormancy release in elm (ulmus spp.) clones—a case study of photoperiod and temperature responses. Tree physiology 30:264–274.
- Glover, B. 2014. Understanding flowers and flowering second edition. OUP Oxford.
- Heide, O. 1993. Dormancy release in beech buds (Fagus sylvatica) requires both chilling and long days. Physiologia Plantarum 89:187–191.
- Heide, O., and A. Prestrud. 2005. Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. Tree Physiology 25:109–114.
- Heide, O. M. 2008. Interaction of photoperiod and temperature in the control of growth and dormancy of *Prunus* species. Scientia Horticulturae 115:309–314.
- ———. 2011. Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus* species. Journal of Experimental Botany 62:5397–5404.
- Heide, O. M., and A. Sønsteby. 2012. Floral initiation in black currant cultivars (*Ribes nigrum L.*): Effects of plant size, photoperiod, temperature, and duration of short day exposure. Scientia Horticulturae 138:64–72.
- Heide, O. M., and A. Sonsteby. 2015. Simultaneous dormancy induction interferes with short day floral induction in black currant (*Ribes nigrum* L.). Scientia Horticulturae 185:228–232.

- Howe, G. T., G. Gardner, W. P. Hackett, and G. R. Furnier. 1996. Phytochrome control of short-day-induced bud set in black cottonwood. Physiologia Plantarum 97:95–103.
- Howe, G. T., W. P. Hackett, G. R. Furnier, and R. E. Klevorn. 1995. Photoperiodic responses of a northern and southern ecotype of black cottonwood. Physiologia Plantarum 93:695–708.
- Hsu, C.-Y., J. P. Adams, H. Kim, K. No, C. Ma, S. H. Strauss, J. Drnevich, L. Vandervelde, J. D. Ellis, B. M. Rice, et al. 2011. Flowering locus t duplication coordinates reproductive and vegetative growth in perennial popular. Proceedings of the National Academy of Sciences 108:10756–10761.
- Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the modis vegetation indices. Remote sensing of environment 83:195–213.
- Kobayashi, Y., and D. Weigel. 2007. Move on up, it's time for change—mobile signals controlling photoperiod-dependent flowering. Genes & development 21:2371–2384.
- Lagercrantz, U. 2009. At the end of the day: a common molecular mechanism for photoperiod responses in plants? Journal of Experimental Botany 60:2501–2515.
- 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.
- 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.
- Myking, T., and O. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. Tree physiology 15:697–704.
- Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. Forest Science 12:374–384.
- Okie, W. R., and B. Blackburn. 2011. Interactive effects of light and chilling on peach flower and leaf budbreak. HortScience 46:1056–1062.
- Partanen, J., H. Hänninen, and R. Häkkinen. 2005. Bud burst in Norway spruce (*Picea abies*): preliminary evidence for age-specific rest patterns. Trees 19:66–72.
- Partanen, J., V. Koski, and H. Hänninen. 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). Tree Physiology 18:811–816.
- Partanen, J., I. Leinonen, and T. Repo. 2001. Effect of accumulated duration of the light period on bud burst in Norway spruce (*Picea abies*) of varying ages. Silva Fennica 35:111–117.
- Petterle, A., A. Karlberg, and R. P. Bhalerao. 2013. Daylength mediated control of seasonal growth patterns in perennial trees. Current Opinion in Plant Biology 16:301–306.
- Pettersen, H. 1972. effect of temperature and daylength on shoot growth and bud formation in azaleas. Amer Soc Hort Sci J .
- Sanz-Perez, V., P. Castro-Diez, and F. Valladares. 2009. Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring Mediterranean oaks. Plant Biology 11:142–51.
- Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. Photoperiod-and temperature-mediated control of phenology in trees—a molecular perspective. New Phytologist 213:511—524.
- Suárez-López, P., K. Wheatley, F. Robson, H. Onouchi, F. Valverde, and G. Coupland. 2001. CONSTANS mediates between the circadian clock and the control of flowering in *Arabidopsis*. Nature 410:1116.

Viherä-Aarnio, A., R. Häkkinen, and O. Junttila. 2006. Critical night length for bud set and its variation in two photoperiodic ecotypes of *Betula pendula*. Tree Physiology 26:1013–1018.

Wolkovich, E. M., A. K. Ettinger, D. Flynn, T. Savas, C. Chamberlain, D. Buonaiuto, and J. Samaha. 2019. Observed Spring Phenology Responses in Experimental Environments (OSPREE). doi:10.5063/F1QV3JQR.

Worrall, J., and F. Mergen. 1967. Environmental and genetic control of dormancy in *Picea abies*. Physiologia Plantarum 20:733–745.

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.

Supplemental Tables

Table S1: Locations, photoperiod treatments, and whether or not photoperiod had an effect on budburst, in studies in the OSPREE database with at least two photoperiod treatments. These studies span 176 different woody species and are mapped in Figure 4. In the 'photoperiod effect' column, 'yes' denotes studies in which authors report significant photoperiod effects on at least one focal species; 'no' which denotes nonsignificant effects of photoperiod.

| reference | study | continent | latitude | longitude | daylength range | ge photoperiod |
|-----------------------------|-------|---------------|----------|-----------|-----------------|----------------|
| | | | (°) | (°) | (hrs) | effect? |
| Ashby et al. (1962) | exp1 | North America | 42.99 | -89.41 | 8-16 | yes |
| Basler and Körner (2014) | exp1 | Europe | 46.31 | 8.27 | 9.2-16 | yes |
| Caffarra et al. (2011) | exp2 | Europe | 52.32 | -6.93 | 10-16 | yes |
| Falusi and Calamassi (1990) | exp1 | Europe | 46.03 | 10.75 | 9-13 | no |
| Falusi and Calamassi (1996) | exp3 | Europe | 38.27 | 15.99 | 9-13 | yes |
| Ghelardini et al. (2010) | exp1 | Europe | 43.72 | 11.37 | 8-16 | no |
| Heide and Prestrud (2005) | exp1 | Europe | 56.18 | -4.32 | 10-24 | yes |
| Heide (2008) | exp1 | Europe | 48.40 | 11.72 | 10-24 | yes |
| Heide (2011) | exp1 | Europe | 59.67 | 10.67 | 10-20 | no |
| Heide and Sønsteby (2012) | exp1 | Europe | 56.50 | -3.06 | 10-24 | yes |
| Heide and Sonsteby (2015) | exp2 | Europe | 56.50 | -3.06 | 10-15 | yes |
| Heide (1993) | exp1 | Europe | 59.50 | 10.77 | 8-24 | yes |
| Heide (1993) | exp1 | Europe | 59.67 | 10.83 | 8-24 | yes |
| Heide (1993) | exp3 | Europe | 47.50 | 7.60 | 13-16 | yes |
| Howe et al. (1995) | exp1 | North America | 40.55 | -124.10 | 9-24 | yes |
| Laube et al. (2014) | exp1 | Europe | 48.40 | 11.71 | 8-16 | no |
| Myking and Heide (1995) | exp1 | Europe | 56.10 | 9.15 | 8-24 | yes |
| Nienstaedt (1966) | exp1 | North America | 44.17 | -103.92 | 8-20 | yes |
| Okie and Blackburn (2011) | exp1 | North America | 32.12 | -83.12 | 0-12 | yes |
| Partanen et al. (2001) | exp1 | Europe | 61.93 | 26.68 | 6-16 | yes |
| Partanen et al. (2005) | exp1 | Europe | 61.82 | 29.32 | 5-20 | yes |
| Partanen et al. (1998) | exp1 | Europe | 60.03 | 23.05 | 8.66-12 | yes |
| Pettersen (1972) | exp1 | Europe | 59.66 | 10.77 | 10-24 | no |
| Sanz-Perez et al. (2009) | exp1 | Europe | 40.40 | -3.48 | 10-16 | yes |
| Viherä-Aarnio et al. (2006) | exp1 | Europe | 60.45 | 24.93 | 16-17 | yes |
| Viherä-Aarnio et al. (2006) | exp1 | Europe | 67.73 | 24.93 | 20-21 | yes |
| Viherä-Aarnio et al. (2006) | exp2 | Europe | 60.45 | 24.93 | 15-19 | yes |
| Viherä-Aarnio et al. (2006) | exp2 | Europe | 67.73 | 24.93 | 22-23 | yes |
| Worrall and Mergen (1967) | exp3 | North America | 41.31 | -72.93 | 8-16 | yes |
| Zohner et al. (2016) | exp1 | Europe | 48.16 | 11.50 | 8-16 | yes |