Temperature and photoperiod interactively drive spring phenology across all species in a temperate forest community

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Abstract

The crucial role that phenology plays in ecosystem processes, and the wealth of observational data highlighting how rapidly plant and animal phenology are advancing has led to increased interest in better understanding and prediction of how plant phenology will shift with continued climate change.

Plant phenology—the timing of recurring life history events, such as leafout and flowering— is critical to the structure and function of ecosystems. Plant phenology determines the timing of the basal resource in most systems, and thus shapes food webs and mutualistic networks (Cleland et al., 2007). Additionally, spring plant phenology drives local ecosystem properties, from the length of the growing season to energy balance between land and atmosphere, and scales up to impact global carbon cycles (Richardson et al., 2009).

Phenology is also one of the major biological indicators of climate change, with plant phenology shifting across the globe 4-6 days/°C with warming (IPCC, 2014; Menzel et al., 2006). While this average response is strikingly consistent when considered across diverse datasets (Wolkovich et al., 2012), it masks tremendous variation. Variation is extreme when examined across species (Wolkovich et al., 2014), but additional variation can be seen within species across time (Fu et al., 2015; Yu et al., 2010; Zohner et al., 2017). Understanding this variation has been the goal of much recent work (Laube et al., 2015; Rutishauser et al., 2008), with research focusing on two major linked aims: (1) identifying and quantifying the environmental cues that drive spring phenology (i.e., leafout and budburst), and (2) identifying what drives variation in cues between different species.

Decades of study on wild species spring phenology—mainly focused on temperate woody species—show that three major cues drive budburst and leafout: warm spring temperatures (forcing), length and intensity of winter temperature (chilling), and changing daylength (photoperiod). Across studies increasing temperatures in the spring appear to be a dominant factor that controls spring phenology, yet many of these studies have been observational—making it nearly impossible to tease out the generally co-varying effects of longer days and reduced cold temperatures, which generally reduce chilling (Chuine, 2000; Cook et al., 2012). In contrast studies from controlled environments (e.g., growth chambers or greenhouses) have highlighted the additional importance of photoperiod and chilling (Caffarra et al., 2011; Falusi and Calamassi, 1996; Foley et al., 2009; Ghelardini et al., 2010; Heide, 1993), with longer days and increased chilling leading to more rapid leafout (Caffarra and Donnelly, 2011). Many of the cues are known to interact and possibly modify one another in some species. For example, insufficient amount of chilling may be offset by additional forcing; photoperiod and forcing are known to interact in driving spring phenology—especially through their complex impacts on dormancy

release (Chuine, 2000).

Yet, while such complexities have been identified in some species, a growing body of hypotheses and experimental studies, focused on woody species, has suggested many species are dominated by one cue and may lack any response to other cues (Körner and Basler, 2010). If true, this would have critical implications for predicting responses to climate change, as a species dominated by a forcing cue could march forever earlier in their leafout with continued warming, while species with strong photoperiod cues could stop advancing at some threshold point (Körner and Basler, 2010). Alternatively, if all three cues—temperature, photoperiod, and chilling—are interchangeable then a species experiencing a mild winter with insufficient chilling (as predicted with climate change) could still break bud given sufficiently long photoperiods and warm temperatures (Heide, 1993).

Research to date shows cues clearly vary across species, and recent efforts have focused on understanding and predicting this variation. Studies have focused on attributes of species: origin of species on shorter and longer timescales (Willis et al., 2010; Zohner et al., 2017), the successional stage (pioneer or climax communities) to which species traditionally belong (Basler and Körner, 2012; Laube et al., 2014), and a variety of possibly related traits (Lechowicz, 1984; Polgar et al., 2014). Most of these studies hinge on an often implicit assumption that phenology, by helping define the temporal niche of a species, is a critical axis of plant species assemble within one community (Gotelli and Graves, 1996). Support for this hypothesis comes from work showing that phenology is often staggered within one community and from the special case of plant invasions, where research has suggested climate change has provided open temporal niche space for new species to occupy (Willis et al., 2010; Wolkovich et al., 2013).

Improved understanding and predictions of phenology with climate change would benefit from a fuller understanding of the interacting environmental cues that drive phenology within (and eventually across) communities. To this aim we studied how forcing, photoperiod and chilling cues vary across a community of 28 woody plant species from two temperate forest locations, separated by 4°latitude. We used clipped dormant branches, which have been shown to approximate whole plant responses (Vitasse and Basler, 2014), and forced them in controlled environments that varied forcing temperatures, photoperiod and chilling. We predicted that: (1) Cues would vary across species, driving staggered leafout across the spring, and (2) within

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species cues would trade-off, such that some species would be dominated by one or another cue, while others would show a mix of cues. To our knowledge this is the first multi-species study to assess all three cues in one experiment through a controlled environment approach, while several studies have done this for one species (Skuterud et al., 1994; Søgaard et al., 2008; Sønsteby and Heide, 2014; Worrall and Mergen, 1967), all other studies of all three cues have used multiple experiments (e.g., Caffarra and Donnelly, 2011) or relied on field sampling to asses one or more cues (e.g, Basler and Körner, 2012; Laube et al., 2014; Zohner et al., 2016).

Results & Discussion

In total we monitored 2,136 clippings and took over 19,320 observations of phenology (budburst and leafout as assessed by the BBCH scale) in an experiment that ran 82 days. Higher forcing temperatures, longer photoperiod, and more chilling all caused large advances in budburst and leafout (Fig. 1).

Forcing temperatures and chilling caused the largest advances in budburst and leafout, and these two effects offset one another, as shown by their interactive delayed response (Fig. 1). The interactive effects of forcing and chilling has been noted repeatedly before (e.g., Caffarra et al., 2011; Heide, 1993) and highlights that insufficient chilling can be overcome by additional forcing—a hypothesis suggested by recent studies that have found shifting temperature sensitivities in observational data over time (Fu et al., 2015; Yu et al., 2010). We found similar effects of chilling across two different base temperatures, with only minor differences: responses to more colder (1.5°C) chilling was similar or more muted compared to responses to a higher temperature (4°C) of chilling (Fig. 1-2). This could indicate that either plants cannot assess chilling temperatures below some threshold (Guy, 2014; Harrington et al., 2010) or that both our chilling treatments met the chilling requirements for our studied species and thus produced similar results.

The two forest sites showed very similar responses, with only a minor delay in overall timing for the more northern site (Fig. 1) and a more pronounced effect of site through its interaction with chilling. The full effect of chilling depended on site, with a larger impact of site on the lower chilling temperature (1.5°C). This could indicate that chilling requirements vary across populations due to local adaptation, or it could be due to the field chilling experienced before we took

cuttings for our experiments (see Table S4). Effects of forcing temperatures and photoperiod were comparatively less impacted by site.

At the community level we found that all species were responsive to all cues (forcing temperatures, photoperiod and chilling, Fig. S2-3), and cues were generally staggered such that each species would budburst and leafout at a distinct time compared to other species (Fig. S4). This provides support for the idea that spring phenology is an important component of the temporal niche (Gotelli and Graves, 1996; Loreau and de Mazancourt, 2008) for temperate forest species.

In contrast to our expectations that within a species cues would trade-off (i.e., a species could be dominated by one cue over all others), we found that species tended to show coordinated cues, especially between forcing and photoperiod (Fig. 2). Thus, a species with a strong response to forcing temperature generally also had a strong response to photoperiod, and similarly a species with a comparatively weak response to forcing also had a weaker response to photoperiod. This was also seen somewhat with chilling (Fig. 2), though we have fewer species with which to assess the relationship (see Methods).

Our finding that all species responded strongly to all three cues is at odds with some recently published work (Basler and Körner, 2012; Zohner et al., 2016) but is coherent with many other studies (e.g., Heide, 1993; Worrall and Mergen, 1967) and related process-based models of woody plant phenology (Chuine et al., 2016, 2000). The contrasting results may be due to varying methodologies. Our study used controlled environments to manipulate all three cues, while other studies have used multiple field sampling dates (i.e., sampling once from January to March in the northern hemisphere) to assess the effect of one cue, most often chilling (Laube et al., 2014; Weinberger, 1950; Zohner et al., 2017). While chilling increases across a winter season, forcing temperatures and photoperiod do as well, meaning it may be hard to fully assess any one cue using this method. Such methods may thus underestimate the full suite of cues that a species uses to control spring phenology. They may, however, have the advantage of providing more realistic environmental conditions by capturing realistic shifts in all three cues across the winter-spring season (Basler and Körner, 2012), and thus play an important role in helping predict near-term impacts of climate change. Our findings are probably impacted by collecting in January, when species had likely not had any cue fully met. Indeed, all methods using clipped end of tree branches are affected by the climate of the season when the experiment

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was conducted, which provides an additional confounding effect to all such experiments. An alternative reason we may have found contrasting results compared to previous studies could be differences in species sampling: our species list, however, includes a number of species classified as non- or low-responsive to photoperiod (i.e., *Alnus incana, Aronia melanocarpa* Zohner et al., 2016), thus this explanation seems less likely.

Responses to cues were qualitatively similar across both budburst and leafout, but quantitatively varied greatly between the two phenophases (Fig. 1-2), with responses generally greater to leafout (Fig. 1). This change was dramatic for the response to forcing and photoperiod where the advance in days more than doubled from budburst to leafout (Fig. 1, Table S2-3). Species cues varied depending on the phenophase considered, meaning species responses also shuffled between the two stages (Fig. 2). For example, shrubs tended to show weaker photoperiod effects to budburst (Fig. 2a) but this was not seen as consistently in the response to leafout (Fig. 2c). This also fundamentally means that the species that bursts bud first will not necessarily leaf out first.

These quantitatively diverging findings for each phenophase suggest complex dynamics in the early season within a community of species. Increasing evidence suggests the period between budburst and leafout is when plants are at greatest risk to tissue loss from frost (Lenz et al., 2013). For early season species in particular then, this period may be critical to their performance. Our results suggest that the cues for each stage are not identical and supports other work suggesting cues on bud swelling and budburst may be distinct from the cues governing the development afterwards (Basler and Körner, 2014). Understanding budburst is particularly difficult as it is the first observable event after a series of important physiological events required for budburst (endo and ecodormancy, Caffarra et al., 2011; Vitasse et al., 2014) and our results echo calls for increased research in this topic (Chuine et al., 2016), which spans both molecular, cellular and whole plant areas of study (Morin et al., 2009; Rinne et al., 2011; Singh et al., 2017).

Conclusions

Across the two communities we studied, our results suggest species within a community have paced budburst and leafout due to a mix of all three major environmental cues: forcing temperatures, photoperiod and chilling. In contrast to our and others' hypothesis (Körner and

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Basler, 2010), we found no evidence of any species being dominated by one or another cue; instead, species tended to show coordination across cues, especially between forcing and photoperiod cues. Thus accurately predicting the phenology of any one of our studied species under diverse environmental conditions would require considering how all three cues will change in concert. Shifting climate has already clearly altered forcing and potentially chilling across the globe (IPCC, 2014; Stocker et al., 2013) with trends expected to only continue and possibly accelerate; in contrast, photoperiod has not and will not shift. These trends combined with our results mean that all 28 species we studied could potentially show complex, non-linear responses in the future, with cascading community consequences.

Methods

Field sampling

Woody plant cuttings were made in January 2015 for 28 species which occurred in both Harvard Forest (HF, 42.5°N, 72.2°W) and the Station de Biologie des Laurentides in St-Hippolyte, Quebec (SH, 45.9°N, 74.0°W). The typical late January temperatures are -3.4 and -22°C, respectively; day length between these two sites differs by a maximum of 45 minutes. Weather station data from each field site was obtained for calculations of chilling units.

Species were chosen based on the dominant forest vegetation at each site, aiming to maximize the number of shared species between the two sites. Of the 28 species, 19 occurred at both sites. Comparing only shared species, the mean days to bud burst and leaf out across all treatments for Harvard Forest and St. Hippolyte was 25.6/36.8 and 24.8/36.1 days, respectively (Table S1). For each species, up to 15 representative healthy, mature individuals with branches accessible by pole pruners from the ground were tagged in late summer and fall 2014. In winter 2015, six individuals were located and 4-16 cuttings taken from each individual, depending on size of the individual and number of treatments to be applied. Cuttings were kept cold and transported back to the Arnold Arboretum in Boston, MA.

Growth Chamber Study

Cuttings were placed in growth chambers at the Arnold Arboretum in Erlenmeyer flasks distilled water, with water changed every 7-10 days. The base of cuttings was re-cut at each water change under water to prevent callusing. For 11 of the 28 species, sufficient cuttings

were obtained from each individual tree to apply the full set of 12 experimental treatments: 2 temperature (20°C / 10°C warm vs. 15°C / 5°C cool) x 2 photoperiod (12 vs. 8 h) x 3 chilling (no additional chilling, additional 33 d at 4°C, or 33 d at 1.5°C) treatments. For the remaining 17 species, only sufficient cuttings were obtained to apply the temperature and photoperiod treatments, without the additional chilling levels. The total number of cuttings for a given species thus ranged from 24 to 144, depending on presence at each site and application of the chilling treatment. Lighting was a combination of halogen incandescent bulbs and T5HO fluorescent lamps with the lamploft adjusted to provide roughly 400 $\mu moles/m^2/s$ as measured by Apogee QSO-A5E quantum PAR light sensors in each chamber. Treatments were rotated across chambers every two weeks as well as flask position within chamber to remove any possible bias of chamber or flask position.

Phenology of the cuttings was assessed using a modified BBCH scale Finn et al. (2007), with observations on each of the 2,136 cuttings made every 2-3 days for the course of the 82-day experiment, a total of 48 observation days. The phenological stages assessed in the present study are bud burst, defined as beginning of sprouting or bud breaking or shoot emergence (Code 07 in Finn et al. (2007)) and leaf out, defined as first leaves unfolded (Code 11 in (Finn et al., 2007)). Additional stages up to flowering and stem elongation were also recorded. In total, we made 19,318 phenological observations at the cutting level.

Statistical analysis

For the two phenology responses measured, bud burst and leaf-out, we fit mixed effect hierarchical models using site, warming, photoperiod, and chilling treatments as predictors (fixed effects) and species as a modeled groups (random effects). For each model, two-way interactions for effects of site, warming, and each of the chilling treatments were included. The models were fit using a Markov Chain Monte Carlo sampling approach in the programming language `Stan` (Carpenter et al., 2016)(www.mc-stan.org), accessed via the *rstan* package in R www.r-project.org.

The model was fit using a Bayesian approach with five main effects and each of their two-way interactions, which allowed us to calculate the posterior probabilities of the effects for each of the abiotic drivers individually and interactively across all species sampled. The model was fit as follows:

$$y_i \sim N(\alpha_{sp[i]} + \beta_{site_{sp[i]}} + \beta_{temperature_{sp[i]}} + \beta_{photoperiod_{sp[i]}} + \beta_{chilling1_{sp[i]}} + \beta_{chilling2_{sp[i]}}$$

$$+\beta_{temperature \times photoperiod_{sp[i]}} + \beta_{temperature \times site_{sp[i]}} + \beta_{photoperiod \times site_{sp[i]}}$$

$$+\beta_{temperature \times chilling1_{sp[i]}} + \beta_{temperature \times chilling2_{sp[i]}}$$

$$+\beta_{photoperiod \times chilling1_{sp[i]}} + \beta_{photoperiod \times chilling2_{sp[i]}}$$

$$+\beta_{site \times chilling1_{sp[i]}} + \beta_{site \times chilling2_{sp[i]}})$$

Each of the 14 β coefficients was modeled at the species level, as follows:

1. $\beta_{site_{sp}} \sim N(\mu_{site}, {\sigma^2}_{site})$

...

14. $\beta_{site \times chilling2_{sp}} \sim N(\mu_{site \times chilling2}, {\sigma^2}_{site \times chilling2})$

For the μ and σ parameters, weakly informative priors were chosen.

We ran four chains simultaneously, with 4 000 warm-up iterations followed by 3 997 sampling iterations, resulting in 15 998 posterior samples for each parameter. We used a non-centered parameterization on all interactions terms and assessed good model performance through $\hat{R}$ close to 1 and high $n_{effective}$ as well as visual consideration of chain convergence and posteriors.

Acknowledgements

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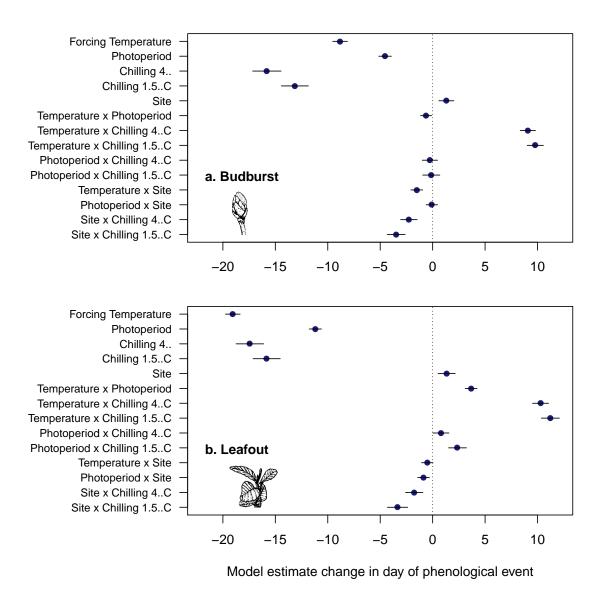
Figures

Figure 1: Effects of forcing temperature, photoperiod, chilling and site on budburst (a) and leafout (b) days across 28 species. Dots and bars show mean and 50% credible intervals from a Bayesian hierarchical model that also incorporated species-level variations (see Tables S2-3; Figs. 1, S2-3). Advances in phenology are show by negative numbers, while delays are shown as positive. Forcing temperatures and photoperiods were two levels each (forcing temperatures 20°C/10°C vs. 15°C/5°C; photoperiods of 8 and 12 hours), and chilling treatments were applied for 30 days. Budburst and leafout images from Finn et al. (2007).
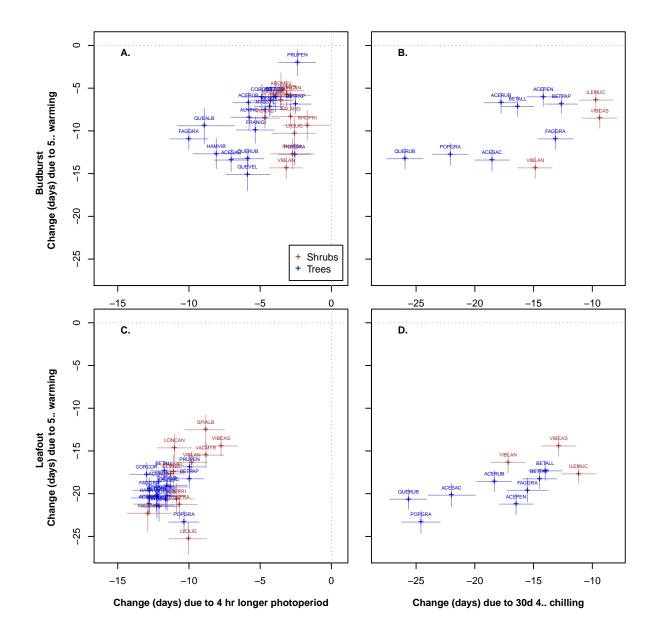
Figure 2: Coordinated effects of photoperiod, temperature and chilling across species: Dots and bars show mean and 50% credible intervals from a Bayesian hierarchical model (see Tables S2-3; Figs. 1, S2-3). For visualization purposes, species names are represented by the first three letters of the genus and first three letters of the species epithet (see Table S1 for full species names and Fig. S5 for additional version of figure).