Titles
Chilling dominates tree budburst in controlled climate experiments, but not in the great outdoors
Chilling outweighs photoperiod and forcing cues in temperate trees in experiments, but not in natural systems

Abstract

Decades of research on woody species highlight how three major cues shape spring phenological events (e.g., budburst and leafout): forcing (warm temperatures, generally occurring in the late winter and early spring), daylength (photoperiod) and chilling (cool temperatures, generally occurring in the fall and late winter). How pervasive these cues are and whether some species are effectively governed by only one or two cues is a critical area of climate change biology research, as it would shape how complex responses to warming will be. Here we use a global meta-analysis of all published growth chamber studies to test for the relative effects of these three major cues across XX species. We find they almost all show these cues, making climate change responses complex.

1   Outline so far...

For decades, plant phenology has been one of the most reported and consistent biological imprints of climate change (IPCC, 2014), with many temperate plants leafing and flowering earlier with rising temperatures (cites). Understanding such shifts is important as phenology shapes a suite of ecosystem services, including pollination and carbon sequestration, and scales up to impact projections of climate change itself.

As research interest in phenology has progressed, critical discrepancies and uncertainties in our understanding have emerged. Though responses to warming are consistent on average (Wolkovich et al., 2012), they show high variation across species and sites (cites). Furthermore, long-term observational studies provide increasing evidence that sensitivities of phenology to temperature are weakening in recent decades (Yu et al., 2010). In Europe, recent work from some of the most well-studied tree species shows declining responses to temperature, suggesting that the long-term trend towards ever-earlier springs may be stalling (Fu et al., 2015). The authors, and others, suggest that complex cues—hypothesized to underlie spring phenology for most temperate species—underlie these declining temperature sensitivities.

Fundamental research in phenology outlines three major cues known to shape spring phenology (Chuine, 2000). These are: chilling (cool temperatures, generally occurring in the fall and late winter), forcing (warm temperatures, generally occurring in the late winter and early spring), and daylength (photoperiod) . A fundamental challenge of understanding the relative roles of these three cues is that they are often strongly correlated. During the transition from winter to spring at many temperate latitudes, air temperatures increase (i.e., forcing increases) at the same time that daylength is increasing.
Chamber experiments have been conducted for decades and offer a valuable methodology for understanding fundamental drivers of spring phenology. (Define Chamber experiments?) Chamber studies often attempt to break the correlation between chilling, forcing, and photoperiod to reveal mechanistic links between environmental conditions and budburst phenology. To date, chamber studies have revealed contrasting effects of the three major budburst cues. Some studies have proposed that photoperiod is likely to constrain species responses to climatic warming (Basler and Körner, 2012; Caffarra et al., 2011b; Caffarra and Donnelly, 2011), whereas others

report that photoperiod is not a strong cue for most species (Zohner et al., 2016; Laube et al., 2014).

Here, we use meta-analysis to integrate divergent studies of budburst responses to chilling, forcing, and photoperiod. We conducted a literature review to identify growth chamber studies of spring phenology in wood plant species; this search yielded a database of nearly 13,000 rows across 85 studies across 41 years and 227 species (reference map of studies). This database includes only studies for which we could identify forcing, photoperiod, and chilling treatments quantitatively. (Chilling was rarely reported and for studies missing this information, we estimated it ourselves when possible using climate data for the experiment cite. See Supplemental Materials). We used a Bayesian hierarchical model to estimate the effects of chilling, forcing, and photoperiod. This model partially pools for a robust overall effect, and for robust effects for species with lots of data (*Fagsyl, Betpen*) but pools towards the mean for species with fewer data (See Supplemental Materials- mention species complex)

Short paragraph: Our results show that budburst phenology is determined by forcing, chilling, and photoperiod – all three cues are important and all three advance budburst. Consistency across species – fairly consistent with some variation in forcing, and then chilling, not much for photoperiod.

Temperature, which is radically altered by climate change, was most important – chilling and forcing show large effects on budburst

1. Chilling is the strongest strongset and most consistent cue (ref Laube and anyone else?)

2. Then forcing, consisent with experimental studies (CITES), observational (CITES)

3. Chilling is rarely manipulated directly, thus we had to calculate most of the chilling (impossible to provide estimates with only experimental chilling... ref supp heat maps)

4. Weinberger methods is most common for chilling and this is not a super way to measure it.

5. How you measure chilling matters a bit ... Utah vs. Chill portions

Photoperiod

1. Photoperiod ... very consistent across species, suggesting all species do cue to it (ref Zohner, Caffara, Flynn ??)

2. The magnitude of photoperiod effects varies with latitude, with lower source latitudes generally having earlier budburst. Say provenance (population).

We did not estimate interactions. Why? .. Add in node to process based models here.

1. Very few studies actually design experiments to test for interactions, so there is little to build on

2. The few studies that do interactions often use the weinberger method, which seems a little weird based on our results.

3. They're hard for a couple reasons: need more reps, and photothermoperiodicity.

4. And! We cannot fully disentangle forcing vs. chilling conditions. (Chuine et al. 2016 GCB).

5. Our results average over interactive effects.

One paragraph: A simple interpretation of our model – especially its chilling and photo effects – predicts declining sensitivities in long-term data with climate change. This is because even though forcing increases, chilling is expected to decreases and photoperiods should get shorter – both predicting delays, and thus an overall muted effect of temperature-only. (Ref exp conditions forecasting figure.) But how do experimental temperature and photoperiod compare to predicted ones in nature? (Ref experimental conditions forecasting figure)

But how do the conditions overlap with natural conditions? (PEP + experimental data figures)

1. Forcing isn't bad

2. Experimental chilling is generally lower than field chilling

3. Photoperiod differences are very big in experiments

4. Declining sensitivities in PEP data (need to check)

Forecasting with these semi-real data, however, do not predict a decline in sensitivity given the moderate amounts of warming already seen, instead they a suggest general advance of budburst until extremely high warming (ref. forecasting figure with PEP-based data)

1. Chilling often increases with small amounts of warming in some sites

2. Even if warming only happens in the winter, it takes a lot of warming to see a delay due to decreased chilling

3. At higher warming do see a leveling off or delay due to decreased chilling at some sites

4. Depends a lot on local climate... We also find that patterns of advancment with warming vary considerably depending on the current/background climate (e.g. how much advancement will continue with warming depends on how much chilling is currently experienced and whether that will increase or decrease with warming.)

5. (Compare advances in our models to PEP725 data?)

6. Photoperiod effects are minimal, even for *Fagus*

So why is PEP725 showing declining sensitivities?

1. Our results suggest few sites with delays before 3-4 degrees warming (CHECK)... and Germany has warmed X amount

2. Speeding up a biological process given sampling time resolution could lead to declining estimates of sensitivites, even if unchange

3. Say something about what to do about this and how to figure out if this is the issue or it's cues.

Our results suggest most or all studied species are responsive to these three cues

1. Our results are only for one region, but highlight how critical accurate forecasts of shifts in forcing and chilling will be at local scales

2. To do this, we desperately need to better understand chilling (dormancy release) so that we can predict it in the future (maybe say need better models for chilling across species).

3. Alongside this, we need more fundamental understanding of interactive cues, which requires larger studies across diverse species. Our results include these complexities but a finer understanding is needed in locations where cues do not change in concert.

4. These complexities are unlikely to alter our fundamental predictions of an increasing advance for many temperate trees in the future, even those with strong chilling or forcing cues (ref Gauzere) [Alt: An imrproved understanding of interactive cues, however, is unlikely to alter our fundamental predictions of an increasing advance for many temperate trees in the future, even those with strong chilling or forcing cues (ref Gauzere), unless cues are changing very asynchronously.]

Main text figures:

1. μ plots

2. μ forecasting figures: spring x winter warming – PEP climate range and experimental climate range

3. Species forecasting with PEP data: *Betula, Fagus* ... need to think on which ones to use (x sites x species focus etc). ... Maybe show photoperiod one?

4. PEP data figure with environmental conditions: as in Cat's figure + OSPREE data + maybe foercasting (at 2C or such?)

Supplemental figures/tables:

1. Map of study locations, shading or symbol coding for number of cues (Lizzie)

2. Map of species forecasting to justify sites

3. Tables, yes.

4. Heat maps for the main data, including by actual study design and by calculated chilling (our calculations)

5. Photoperiod x latitude effects figure

2 Reference list

A few categories:

Papers about contrasting results over what cues matter from growth chamber studies: Basler and Körner (2012, 2014); Caffarra et al. (2011*a*); Caffarra and Donnelly (2011); Caffarra et al. (2011*b*); Heide and Prestrud (2005); Koerner and Basler (2010); Laube et al. (2014); Vitasse and Basler (2013); Zohner et al. (2016). Get Nanninga *et al.* 2017: 'Increased exposure to chilling advances the time to budburst in North American tree species' and maybe Malyshev *et al.* 2018 'Temporal photoperiod sensitivity and forcing requirements for budburst in temperate tree seedlings.'

Papers about declining sensitivities (Ailene will update this list): Rutishauser et al. (2008); Fu et al. (2015). Also look for a Wang *et al.* article 'Impacts of global warming on phenology of spring leaf unfolding remain stable in the long run.' Vitasse paper on declining variation across elevation gradient. See Yu et al. (2010), but this is not temperate trees.

Papers about chilling units paper (Lizzie gets a list): Fu 2012 from OSPREE. Harrington and Gould (2015)Luedeling et al. (2011); Luedeling and Brown (2011); Luedeling et al. (2013)

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