

RH: Interactive cues and spring phenology

**Concept paper on understanding interactive cues and climate change (with growth chamber studies)**

- (1) How interactive cues will shape climate change responses
- (2) Limiting cues: How spring warming, winter chilling and daylength will shape climate change responses
- (3) Spring warming, winter warming or daylength: What cue will be most limiting in future tree phenology?

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## Abstract

Climate change has shifted plant phenology globally, with average shifts of 4-6 days/°C and some species shifting several weeks. Globally, such shifts have been some of the most reported and most predictable biological impacts of climate change. This predictability comes from decades of research, which have outlined the major cues that drive most studied plant phenology: temperatures (including spring warming and winter chilling) and daylength. Further simplifying predictions, spring temperatures are often the dominant cue in nature, making linear models of heat sums often excellent at predicting interannual variation in phenology. Yet as climate change has marched on, new research has uncovered failures to predict the current observed changes, with many shifts appearing more muted over certain time periods or in certain locations. Here we argue that such inaccurate predictions are most likely due to simple models that neglect to consider other major cues—especially winter chilling and daylength, which moderate and shape plant phenological responses to spring warming. We highlight how over 60 years of research in controlled environments can improve predictions for when, where and how the interactive effects of other cues will impact simple linear predictions. Finally, we discuss how a new generation of controlled environment experiments could rapidly improve our predictive capacity for woody plant phenology in coming decades.

*Main message (and, really, it's important):* if you want to project climate change impacts, you need to focus on relevant changes in all three cues. The relevant changes part is about comparing cues, the all three cues is about interactive cues.

*Keywords:* phenology, climate change, spring warming, forcing, chilling, daylength, photoperiod, non-linear responses, leafout, budburst

**Questions**, which are in addition to notes in orange throughout and general thoughts/ideas for improvement! Thanks for all your help!

1. Can we suggest where cues other than forcing are most critical? Perhaps at least for our focal spp.? If so, where would we add this (1.c)?
  - (a) If we know where a non-linearity in a response to a cue is (e.g., from experiments of models we know that the response to photoperiod gets bigger after 16 hours), then wherever you're near that on a range, you should expect bigger effects of that cue.
  - (b) Where chilling will change to above versus below the threshold that plants can sense
2. Is the intro too long? If so, please suggest ways to cut and/or re-arrange. (I have moved our PEP725 species outside of the intro, please let me know if you think it works).
3. I wrote this below (it's commented out just now): Unlike budset phenology, research suggests spring phenology is fairly plastic (without high local adaptation of cues across a range); this means species need a set of cues that work across their range ... which got me to wondering: can we explain why cues show so little local adaptation across species ranges? Relevant lit:
  - (a) Keeling et al. 2003: the impact of yearly variation in temperatures in genotype selection
  - (b) Someone must have said this but high variation in spring climatic conditions makes temporal variation in many ways as high as spatial and thus may slow local adaptation (see also Legave et al. 2013)
  - (c) How to see local adaptation? What is the appropriate phenotype, if not leafout?

## OUTLINE

1. Introduction
  - (a) Shifts in spring phenology are one of the most reported and most predictable changes with climate change
    - i. Review the shifts across space and time and how coherent they are
    - ii. Outline some studies showing how predictable they are (??)
  - (b) Recently however predictions have started to fail in certain places or over certain time periods
    - i. ??
    - ii. The main hypothesis for this failure is that most observational studies have ignored cues beyond simple forcing ones

- (c) There has been a lot of focus on forcing but really it's more complicated
  - i. For many species three major cues drive spring phenology: forcing, chilling, daylength
  - ii. These cues may create critical non-linear responses that most current methods cannot predict.
- (d) However, measuring these cues and thinking about how they will interactively produce future phenology is hard because:
  - i. They vary across species (and possibly within species across the range, but see below) Refs: Harrington and Gould 2015, *Frontiers in Plant Science*; Vitasse et al, 2009, *The Canadian Journal of Forest Research*
  - ii. They are expected to interact; cues may compensate for other cues; meaning they mask one another (e.g., chilling cue not fully being met could look like a photoperiod requirement that has not been met) \*Isabelle says 'for me this is two different things' – to discuss.
  - iii. They are hard to measure.
  - iv. To some extent (because of how they interact), we haven't really had to measure these other cues to get decent predictions for lots of places and years
- (e) But if evidence is rising that these cues are critical, how do we integrate them more into phenological research? Step 1 is clearly to figure out how to robustly measure them.
  - i. Methods especially lame at understanding these cues (and thus predicting non-linearities): models from long-term observational data ... somehow mention experiments maybe?
  - ii. Comment on the two issues at play here: the data type (e.g., long-term) versus the model type (e.g., linear and sans interactions?)
  - iii. The one method designed to look at all these cues is controlled environment (generally growth chamber) studies (Isabelle: this is clearly the most robust way to look at it, look at Satake et al 2013 (Satake A, Kawagoe T, Saburi Y, Chiba Y, Sakurai G, Kudoh H. 2013. Forecasting flowering phenology under climate warming by modelling the regulatory dynamics of flowering-time genes. *Nat. Commun.* 4:2303), but see also Nagano et al. 2012 (Nagano AJ, Sato Y, Mihara M, Antonio BA, Motoyama R, Itoh H. 2012. Theory deciphering and prediction of transcriptome dynamics under fluctuating field conditions. *Cell* 151(6):135869))
- (f) Growth chamber studies
  - i. Can manipulate all three cues (and even more, humidity etc. nod?)
  - ii. Are often focused on interactions (unlike other methods)
  - iii. Have been done *forever*. But oddly, never really reviewed.

- iv. ...and are often poorly integrated into current climate change literature. Including debates where they are critical, like about photoperiod.
- (g) Our aim is to:
  - i. *Briefly* review how three major phenological cues for woody plant phenology will shift in coming decades with anthropogenic climate change (see Menzel & Primack on a similar topic in Ann Bot. 2015 Nov;116(6):889-97)
  - ii. Review of the three major phenological cues from growth chamber studies over the past 60 (70?) years to understand how much of the cue-space has been studied
  - iii. Compare treatments from controlled environment studies to predicted shifts in cues with climate change.
  - iv. Showcase how growth chamber studies can be best designed to better understand these interactive cues (paths forward).
- 2. We focus on woody species ...
  - (a) Research in the cues underlying phenology has been especially strong in model systems (e.g., *Arabidopsis*, *Populus*) and crops—with the exact phenophase of interest varying (potentially by a species’ life history: more focus on germination and flowering in *Arabidopsis*, and more on leafout and budset in *Populus*).
  - (b) Our focus here is on leafout, and thus we focus on woody species phenology: for which leafout has been widely studied across species, though much of what we say could apply to non-woody species and/or other phenophases with underlying similar cues.
- 3. To understand cues, it helps to think about the environmental variation a species experiences across its range
  - (a) Think about two example tree species: *Fagus sylvatica*, *Betula pendula*
  - (b) Look at their distributions
  - (c) In the spring there is selection for species to track the start of resources, and thus they need cues that work across the interannual variation in climate *across a species’ range*
  - (d) Thus, cues are adapted to high climate variation.
  - (e) A species range limit and phenology are intertwined: a species’ current range defines the range of cues it may see, but phenology also shapes those limits (CITES Chuine/Morin).
  - (f) This is why most temperate species probably have responses to all three cues: forcing, chilling, photoperiod, with the importance of each cue varying across a range (e.g., chilling in coastal versus continental, check also Legave paper)

4. Review how cues will shift with climate change (here we show the figures that Nacho has produced for two PEP725 spp.)

(a) Forcing: the world will get warmer

- i. Higher altitude and arctic places will warm more
- ii. Give range of warming depending on different scenarios
- iii. Minima (night-time temps) generally warm more than maxima (but not everywhere, see what Yann mentioned)
- iv. Piao et al 2014 Nature Communications - found that daytime forcing temperatures (Tmax) are more important for leaf out than nighttime temperatures (Tmin).
- v. Different seasons may warm differently

(b) Chilling, see forcing but ...

- i. Chilling only occurs between certain temps so some places accumulate more chilling with warming
- ii. And there is so much we don't know about how chilling works and interacts with forcing (sequential model, parallel models etc.)

(c) Photoperiod: Shifts with phenology

- i. Changes in forcing and chilling will alter the photoperiod that matters so to speak
- ii. Note that although daylengths themselves won't change with cc, the photoperiods experienced by organisms are likely shift as ranges shift and phenology shift (cite our other paper?)

5. Compare treatments from controlled environment studies to predicted shifts in cues with climate change: Part I: Review of the three major phenological cues from growth chamber studies over the last 67 years

(a) Be sure to note that most studies were *not* done for climate change research, they were done for fundamental science or agricultural purposes

(b) Quick intro to the data, how long, which cues ....

- i. Fig: Number of studies by year (OSPREE)
- ii. Fig: Map of studies, color coded or such by which of the three cues they manipulated

(c) For each of the three cues:

- i. X% of studies manipulated that cue
- ii. Variation across latitude (and hemispheres?), continents, and time (and species)?
- iii. Fig: Variation in treatments across space (photo/chill/force)

Any other reasons for WHY many woody species phenology growth chamber studies were conducted?

- iv. Fig: Variation in treatments across time (graph with year on  $x$ -axis or divide time in half or such?)
  - v. Say something about material (seeds/saplings/cuttings)? Can we tie to relevance of predicting future forest communities or such?
- (d) X% of studies manipulated which interacting cues? (i.e., how many studies manipulate 1 cues, 2 cues, 3 cues ... of those manipulating 1 cue, what is the breakdown by cue etc.)
6. Compare treatments from controlled environment studies to predicted shifts in cues with climate change: Part II: What cues will be most limiting with climate change? How do controlled environment studies compare?
- (a) Consider both the range of a species and the climate change projections ...
    - i. Take each PEP725 datapoint within our selected species' range and calculate:
      - A. Min daily temp for 1-2 months before leafout (Nacho's figures)
      - B. Max daily temp for 1-2 months before leafout (Nacho's figures) <sup>1</sup>
7. Paths forward (showcase how growth chamber studies can be best designed to better understand these interactive cues in regards to climate change forecasting)
- (a) If you want work to be most relevant to climate change, then consider the following when designing experiments:
    - i. The cues with the current vs. future range of a species (as we did above) to inform experimental range
    - ii. If you don't work within the range or projected cue range limits of a species, then consider working on informative extremes... but extremes are extremely difficult to reproduce in controlled environments (and this is something we technologically need to improve)
  - (b) Manipulating more than one cue may be most useful, esp. if we want to advance comparisons with long-term data
  - (c) Major need to better understand deviations in long-term data are: better non-linear models for more species. How best to do this?
    - i. Studies using only long-term observational data must test for and be up front about correlations in predictor variables (e.g., chilling, forcing and daylength often covary) and thus what they can and cannot rule out.

Do we need this? And/or are there any ways to untangle cues using long-term data?

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<sup>1</sup>We used daily min/max, as they're most directly comparable to OSPREE.

- ii. A better option than just long-term data are more efforts to integrate long-term data with growth chamber studies (cite Caffarra, Chuine suggestions: chuine & Regniere 2017 suggestion + see Nagano, Satake work, Ford et al. 2015)
  - A. Studies that test the extremes are needed to parameterize models (ideally you need to know where the zeros are) cite: Chuine & Regniere 2017
  - B. Traditional methods to hold-out data and test how well the model performs
  - C. Use growth chamber studies to test model predictions, especially in future climate scenarios where non-linearities are predicted, and vice versa, see Nagano et al. 2012
  - D. Improving models means more back-and-forth work between developing models based on both long-term data and experiments, then testing predictions with new experiments and as newer observational data are generated (i.e., more years and also data from new locations); cite Satake et al; Nagano et al.
- (d) Building species-rich predictions ...
  - i. Given how complicated this all sounds, how do we build up to multi-species predictions?
  - ii. Need more efforts to combine data
  - iii. Introduce Bayesian hierarchical modeling within this framework
  - iv. And need more efforts to publish studies in a way that makes synthesis possible ...
  - v. Studies not interested in climate change forecasting can still contribute—with little effort—to progress in this area by: Reporting all cues (even the ones you don't measure) so they can be used in modeling efforts.
- 8. Wrap-up: Climate change: it means all that work on phenology comes due ... now!
  - (a) If we could better harness the power of growth chamber studies it could... transform our understanding and forecasting
  - (b) Rule out or in hypotheses to explain observed discrepancies (move away from trying to tease out cues using only correlated long-term data)
  - (c) Contribute to more models being developed and improved, which could contribute to global land surface models, community predictions etc.
  - (d) While understanding, modelling and predicting interactions among cues and their effects on phenology is challenging, any advances on this should yield more accurate predictions, with valuable implications to more realistically assess the effects of climate change on plant biodiversity, including agricultural and forest species.

**Examples of how cues interact:**



1. OSPREE studies found that additional chilling, or even simply sufficient chilling, could lower the photoperiod requirement but when the chilling requirement wasnt fulfilled, increased photoperiod could compensate for the lack of chilling (Nienstaedt 1966, Myking1995, Falusi 1996, Hawkins 2012)

## FIGURES

1. PEP725 spp. 1980 figures
2. PEP725 spp. Future figures
3. Number of studies by year (OSPREE) *Other ideas?! Such as, number of species studied by year. Show crops or remove or show separately?*
4. Map of studies, color coded or such by which of the three cues they manipulated
5. Variation in treatments across space (photo/chill/force)
6. Variation in treatments across time (graph with year on  $x$ -axis or divide time in half or such?)
7. Not a figure, but analysis-related: X% of studies manipulated which interacting cues? (i.e., how many studies manipulate 1 cues, 2 cues, 3 cues ... of those manipulating 1 cue, what is the breakdown by cue etc.)