Version dated: April 7, 2018

RH: Interactive cues and spring phenology

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

How interactive cues will drive climate change responses

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. Where to add potential new PhenoFit figure?
2. 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)?
3. Is the intro too long? If so, please suggest ways to cut and/or re-arrange.

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 (Spring Index? Primack linear paper)
      What other citations/examples can we add?
   (b) Recently however predictions have started to fail in certain places or over certain time periods
      i. Fu paper, Tibet etc.,
      other citations?
      ii. The main hypothesis for this failure is other cues most observational studies have ignored
   (c) There has been a lot of focus on forcing but really it's more complicated
      i. Think about two example tree species: *Fagus sylvatica, Betula pendula*
      ii. Look at their distributions
      iii. Cues are adapted to high climate variation!
      New term: Cue range limits. What do you think? As in the limits of cues as seen over a species' range, what do you think?
      iv. For many species three major cues drive spring phenology: forcing, chilling, daylength
      v. Research in this has been especially strong for woody species phenology: this is where we understand things best and thus our main focus here, though much of what we say could apply to non-woody species with similar cues (cite *Arabidopsis*).

what other herbaceous species

(d) These cues may create critical non-linear responses that most current methods cannot predict.

(e) However, measuring these cues and thinking about how they will interactively produce future phenology is hard because:

   i. 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)

   ii. They vary across species and possibly within species across the range

   iii. They are hard to measure.

   iv. To some extent, we haven't really had to measure these other cues to get decent predictions for lots of places and years

(f) 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

(g) 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.

(h) Our aim is to:

   i. Review how three major phenological cues for woody plant phenology will shift in coming decades with anthropogenic climate change

   ii. Review of the three major phenological cues from growth chamber studies over the past 60 (70?) years

   iii. Highlight their critical relevance to climate change research

   Should we cut this? Already covered above?

   iv. Compare treatments from controlled environment studies to predicted shifts in cues with climate change.

v. Showcase how growth chamber studies can be best designed to better understand these interactive cues (paths forward).

2. 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 warm more than maxima (night-time temps)
      iv. 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. Need a little more here ...
      Help appreciated on what to add for daylength

3. 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

   Any other reasons for most woody species phenology growth chamber studies?

   (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 space, continent and time (and species)?
      iii. Fig: Variation in treatments across space (photo/chill/force)
      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.)

4. 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) [1]

      ii. Add potential PhenoFit figure here? 3D of all three cues and how they shifted?

5. Paths forward (showcase how growth chamber studies can be best designed to better understand these interactive cues in regards to climate change forecasting)

   I think this section needs the most help! We have a lot of points and I think we need to clarify them and cut some probably.

   (a) Consider the following when designing experiments:

      i. Consider the cues with the current vs. future range of a species (as we did above) to inform experiments

      ii. If you don't work within the range or projected cue range limits of a species, then consider working on informative extremes...

      iii. So consider thermal tolerances/limits (and where is the species optimum?) ...These could be especially useful for understanding range limits: look at treatments beyond the variation seen within a species' range and see if there is abrupt change or you see continuous change, if no abrupt change then it may suggest that something else must limit range (e.g., biotic cues, minima temperature after which species)

      iv. After you carefully select the cues to study, make your reasoning clear

         do we need this?

   (b) Manipulating one cue may be less 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?

[1] We used daily min/max, as they're most directly comparable to OSPREE.

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?

ii. A better option than just long-term data are more efforts to integrate long-term data with growth chamber studies.

A. Studies that test the extremes are needed to parameterize models (ideally you need to know where the zeros are).

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.

D. Improving models means more back-and-forth worth 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)

(d) 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.

6. Wrap-up.... Climate change: it means all that work on phenology comes due ... now!

7. Now that climate change is here, experiments that want to claim climate change relevance must address what the cue impacts of climate change will really be

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.)