

# A race against time: phenological sensitivity as a mediator of plant interactions

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## Motivation and Dissertation Framework

Phenology, the timing of annual life cycle events, allows organisms to synchronize important life cycle events with optimum environmental conditions (Forrest & Miller-Rushing, 2010). Phenology is an important mediator of ecosystem processes (Cleland *et al.*, 2007; Piao *et al.*, 2007) and species interactions (Leverett, 2017; Yang & Rudolf, 2010), and plays a major role in determining species' range limits (Chaine & Beaubien, 2001). Pronounced shifts in phenology observed across a broad range of taxa have been reported, with plant phenology shifting by 3-5 days on average per decade (Menzel *et al.*, 2006; Parmesan & Yohe, 2003; Root *et al.*, 2003). Phenological sensitivity to climate change varies among taxa, and there is evidence that within given communities species phenologies are shifting at different rates (Cleland *et al.*; Ovaskainen *et al.*, 2013). These differential sensitivities are likely to have far reaching effects on community interactions, but our ability to predict these second order effects remain limited.

In my proposed dissertation, I heed this call to advance our understanding of the effects of global change on species interactions as mediated through phenology. Sitting at the nexus of traditional community ecology and global change biology, my proposed dissertation will explore 1] how differences in sensitivity to environmental conditions can produce significantly different phenological patterns and 2] how differential phenological responses alter community interactions.

In **Chapter I**, I will examine flower-leaf sequences in temperate woody plant species, using experimental manipulations and statistical modeling to evaluate the currently evolutionary hypotheses for this phenological trait, and investigate the differential phenological sensitivity between flower and leaf buds as a potential mechanism for this variability.

In **Chapter II**, I turn my attention to seed germination phenology, where I probe the effect of variable stratification periods and incubation temperature on germination of a large suite of temperate, herbaceous plants, to determine interspecific differences in responses to changing climate, and evaluate the probability of germination rank changes under future climate scenarios.

In **Chapter III**, I expand the scope of my inquiry in chapter II, compiling a global database of experimentally manipulated germination trials, and use meta-analysis techniques to better understand the reaction norm of germination phenology in response to environmental manipulations.

In **Chapter IV**, I perform a direct test of the impact of phenological shifts on community interactions, by using alternate climatic treatment to manipulate the germination phenologies of two species growing in a pairwise competition experiment.

# Background

**Ecophysiology and Evolution of Spring Phenology** Plants sense and interpret a complex set of environmental cues that signal the changing of the seasons, and can respond by fine-tuning their phenological transitions accordingly

The same selective forces determining the optimum timing for transition from dormancy to growth have been suggested for both spring germinating seeds and bud phenology, with the adaptive benefits of early phenological transition, an extended growing season, predator avoidance, and reduced competition for resources balanced by the higher risk of mortality due to biotic and abiotic factors (Rathcke & Lacey, 1985). For flower buds, the availability of pollinators may be an additional selection factor. As such, the phenological optimum evolves in relation other functional traits and life history tradeoffs.

While the selective forces, environmental conditions and conceptual framework for the transition from dormancy to growth may be quite similar for seeds and buds, there is evidence that the physiological mechanisms regulating these processes are quite different. In buds, short day conditions and the end of the season induce dormancy by isolating meristematic cell interactions through heavy deposits of callose in the plasma membrane (Rinne *et al.*, 2011; Sager & Lee, 2014). Winter chilling degrades the callose, reengaging cellular integration for the transition to growth under suitable conditions.

In seeds, Absciscic acid (ABA), a hormone upregulated during seed maturation is generally thought to initiate and maintain dormancy as its concentration tends to decrease as seeds approach germination though the actual direct role of ABA in dormancy induction remains unclear (Baskin 2002). Environmental treatments such as cold or warm stratification and afterripening, have been shown to contribute to the degradation of ABA, and an upregulation and increased sensitivity to the growth hormone gibberellic acid ( $GA_3$ ), as well as ethylene and brassinosteroids, which promotes germination (Kucera *et al.*, 2005).

**Model of Spring Phenology** Many models have been developed to use temperature to predict phenology in woody plants (Chaine *et al.*, 2002), while seed science most commonly uses a single model, the thermal time cardinal, temperature model, or its variant the hydrothermal time model which includes water potential as a parameter (Bradford, 2002). The thermal time model of germination describes the relationship between time, temperature and germination fraction. [insert model here] If not observed experimentally,  $T_b$  can be inferred through statistical methods by regressing the reciprocal of germination time against a given germination fraction and determine the x-intercept (Pritchard *et al.*, 1999). While this model is widely noted for its biological accuracy in predicting the germination phenology of non-dormant seeds (Bradford, 2005), the standard thermal time model is less effective in phenological predictors for dormant species (Battla & Banech-Arnold, 2015). Several attempts have been made to modify this modeling framework to better incorporate a dormancy module. Conceptually, dormancy break treatments reduce  $T_b$  or ( $\theta_{tb}$  in the hydrothermal time variant) allowing for a more rapid accumulation of thermal time and more rapid germination. This framework has been applied to include afterripening (Meyer *et al.*, 2000), and cold stratification (Battla & Banech-Arnold, 2003; Pritchard *et al.*, 1996), but has not been broadly applied outside of agriculture or horticulture, and its effectiveness for a diversity of taxa remains unknown (Steadman & Pritchard, 2004). The model formulation is below:  
[insert second model here]

# chapter I: The significance of flower-leaf sequences in an era of global climate change

## Introduction

Why do some tree species seasonally flower before leafing out? This sequence, known as hysteroanthly, proteranthly, or precocious flowering is readily apparent in many ecologically and commercially important species and has been described as the characteristic flower-leaf sequence (FLS) of temperate deciduous forests (Rathcke & Lacey, 1985). Questions regarding the evolutionary origins and functionality of FLS are go beyond simple observational curiosity. Most of the current hypotheses regarding FLS's suggest they critical to the reproductive or physiological functioning of woody plants (Gougherty & Gougherty, 2018). Several authors suggest that the hysteroanthous FLS is a trait critical for wind-pollination efficiency (Friedman & Barrett, 2009; Whitehead, 1969). Others suggest that flowering first is an adaptation to reduce water stress and maintain floral hydration (Franklin, 2016), though this hypothesis has emerged primarily from the dry-deciduous tropics where hysteroanthly is also common (Franklin, 2016; Janzen, 1967). Still others suggest the hysteroanthous FLS is an adaptation to allow for extremely early flowering and is correlated with other early flowering traits such as seed size, dispersal time and cold tolerance (Bolmgren *et al.*, 2003; Gougherty & Gougherty, 2018; Primack, 1987). It is also possible that FLS's are highly conserved trait, and the preponderance of hysteroanthly in the temperate zone is a product of phylogenetic representation of the region rather than an adaptive quality to the trait.

Despite the rich theoretical attention FLS has recieved in the literature, data about FLS is limited. The most comprehensive source of data we have regarding FLS comes from catagorical, qualative descriptions in regional flora and guide books. A few long term empirical datasets in which FLS can be properly descibed as a continuous variable can be found, but these are rare when compared with the larger body of phenological data as flower and leaf phenology have generally been observed separately (Wolkovich & Ettinger, 2014). In part I of this chapter I ask, given the available data:

1. What is the associations between FLS and several other life history traits (pollination syndrome, shade tolerance, plant height, flowering time, duration of fruit maturation) pertinent to the established hypotheses? Are these results sensative to data quality, observational ambiguity and modeling choices? Does treating FLS as a continuous rather than catagorical varaiable change the model inference?

Treating FLS as catagorical masks important characteristics of FLS such as the range varibablity of FLS offset between species, individuals, populations and years. As far as I know, there have been no attempts to empircally quantify this variability. Improving our understanding of the variability of this pattern would aid significantly in evaluating the evolutionary hypotheses for FLS, and serve to generate hypotheses for the eco-physiological mechansims behind these patterns. In part II of this chapter I ask: In this part II I ask:

1. Is variability in FLS a product of a differntial sensitivities to environmental cue combinations between flower and leaf buds?

## Methods:

**Part I:** I obtained species level descriptions of floral-foliate sequences and trait information from the regional guidebook Michigan Trees (Barnes & Wagner, 1981,2004) and its companion volume Michigan Shrubs and Vines (Burton V. Barnes, Christopher W. Dick, 2016) (hereafter: MTSV) and the Unites States Forest Services Silvic Mannual Vol.2 (Burns *et al.*, 1990) (hereafter: USFS). All catagorical traits were reclassified as binary (FLS, shade tolerance, pollination syndrome). I developed two, alternative classifications for FLS, physiological (only taxa with "flowers before leaves" hysteroanthous) and functional (taxa with "flowers before

leaves”, ”flowers before/with leaves” and ”flowers with leaves” considered hysteranthous). In total, 196 and 82 woody species, in MTSV and USFS respectively, were included in my analysis. To investigate the phylogenetic signal of hysteranthous and control for phylogenetic structure in our dataset, we used a published angiosperm phylogenetic tree (Zanne *et al.*, 2013) pruned to match the species list from the MTSV and USFS data. Species not in the tree were added at the generic root. I used phylogenetic generalized linear modeling framework (Ives & Garland, 2010) to build a logistical regression model corrected for phylogenetic structure using the R package phylolm (Ho & Ane, 2014). The model was run with 599 bootstrapped re-sampling iterations for each dataset (Wilcox, 2010). Continuous predictors were rescaled by subtracting the mean and dividing by two standard deviations to allow for a reasonable comparison of effect sizes between the binary and continuous predictors in this model, and odds ratios were calculated to aid in interpretation of model coefficients (Gelman & Hill, 1997). Models were run on each dataset for each classification of FLS for sensitivity analysis.

For the model with FLS as a continuous response, I used a long term phenological dataset from Harvard Forest in Petersham, MA (HAFO) (O’Keefe, 2015) and calculated the average FLS lag time for 21 species which overlapped the MTSV species list. With same modeling framework, I modeled the association between the original MTSV predictors and the Harvard forest continuous FLS data. **Part II:** I first determined descriptive statistics (mean, standard deviation and range) of FLS offset in the HAFO dataset using the R base statistical package to establish a basic understanding of the typical variability in FLS. In October of 2017, I obtained cutting of dormant twigs from 12 woody plant species from Harvard Forest in Petersham MA. Twigs were transported to the Weld Hill Research Building in Boston, MA, where they were recut in water at the base, and placed into 250 ML erlenmeyer flasks. 6 replicates of each species were randomly assigned to different growth chamber temperature and photoperiod combinations. Twigs received 1 of 2 levels of chilling (4 or 8 weeks at 4 degrees), combined with 1 of 2 forcing treatments (24/18 or 18/12 day/night temperatures on 12 hour cycles) and 1 of 2 photoperiod treatments (8/16 or 12/12 day/night) for a 12 way full factorial design. Flasks were moved between chambers every 2 weeks to reduce the influence growth chamber effect artifacts on the results. Twigs were monitored for flower and leaf phenology using the bbch scale (Finn *et al.*, 2007) every 2-3 days for four months.

I currently use a multilevel, Bayesian, survival analysis framework to analyze these data. Survival analysis is the appropriate framework for these experiments as there were a considerable number of twigs that did not burst buds by the end of the experiment, but were determined to be living. Dead twigs, or those which were determined to have had no flower buds at the outset of the experiment are excluded from the analysis. I predicted that the FLS offset will vary significantly between treatment combinations and that this variation will be traceable to flowering and leaf phenology being differentially sensitive to the environmental factors. My initial model is a varying slope/intercept model by species with the following predictor and response formulation:

Days to event Photo:phase+Chill:phase+Force:phase

Where the interaction between phase and each predictor will reveal differences in response to the predictors between floral and leaf phenophases.

## Status and Preliminary Results:

**What are the associations between FLS and several other life history traits? Are sensitivity of the above analysis to data quality, observational ambiguity and modeling choices?:** In the categorical models, only flowering time is a consistently strong predictor of FLS, with the effect size of

pollination syndrome, seed development time and phylogenetic signal varying in significance depending on data source and modeling choices. There was no strong signal from height or shade tolerance. [See figure]. In the continuous model, pollination syndrome was the strongest predictor of FLS with shade tolerance and early flowering significant as well. [See figure]. These findings support the pollination syndrome, early flowering. It is not surprising that multiple hypotheses find support in this analysis, as FLS is a complex trait that may have developed independently in different selection environments.

**Is variability in FLS a product of differential sensitivities to environmental cue combinations between flower and leaf buds?:** As seen in the plots of HAFO phenology, there is considerable interannual and interindividual variation in FLS. Preliminary analysis of my experimental results seem to support the hypothesis that this variability is a product of differential sensitivity between flowering and leafing, but because of many non-response values in the data, spread unevenly across species and treatments, this finding has low confidence and other model approaches need to be attempted. Below I present other modeling frameworks I will attempt:

1. Rather than modeling flowering and leafing sensitivities as interactions, use offset (as determined in part I) as a response variable.
2. Use a logistic regression framework with phenology as a binary response.
3. Run individual species models for only the species with the most data.

## Chapter II: The germination response to varying stratification regimes of a suite of temperate herbaceous species

### 0.1 Introduction

The cold stratification requirement for dormancy release has been identified in a large number of taxa North American temperate plants, and stratification treatments are employed widely in both plant science and industry (Hartmann *et al.*, 2011). The duration of stratification needs has also been shown to differ between species, ranging from just a few days to many months (), and may vary significantly depending on temperature (Steadman & Pritchard, 2004) and between seed populations. While cold stratification is commonly found as an experimental treatment in the literature, and has been shown to advance germination, studies which evaluate the germination response across a range of stratification periods or temperature are more rare (Batlla *et al.*, 2009). As a result, the kinetics of the germination response to variable stratification regimes is poorly characterized in the vast majority of plant species.

Cold stratification in the lab, serves as a proxy for natural exposure to chilling conditions a seed would experience overwintering in the field. With global climate change, changes to the severity and duration of winter will alter the natural stratification period experienced by seeds (Walck *et al.*, 2011). While winters are generally predicted to be warmer and shorter (?), the number of days which the stratification conditions are met may increase, decrease, or shift temporally, differentially affecting the germination phenology plant species depending on their geographic position, and the dynamics of their response to temperature (Walck *et al.*, 2011). These shifts in germination may in turn alter plant competition through priority effects () and plant demography through seed bank dynamics, and multi-trophic interactions. To better predict the effect of warming winters on seed germination, it is imperative to better characterize the germination response to variable stratification regimes for a more broad range of plant species. In this chapter I ask:

1. How does varying stratification periods effect the germination time courses of plant species?
2. How do stratification periods and incubation temperatures interact in germination time course?

3. Is the stratification requirement best characterized by an optimum (Can seeds get over stratified) or a threshold?
4. To what degree is germination rank between species affected by varying stratification regimes?

## Proposed methods

**Experimental Protocols:** In the summer of 2018, seed of 24 temperate Eastern North America herbaceous plant species of both native and non-native origins were procured from plant nursery stock or collections (see figure X for species and provenances) and dry-stored until the start of the experiment. In mid-August 2018, all seeds were checked for the presence of an embryo using a float test (Baskin & Baskin, 2014), and imbibed in distilled water for 24 hours. Seeds of each species were then randomly divided into cohorts of 20-40, depending on seed availability and placed onto wetted filter paper in 8 cm plastic petri dishes. Each cohort was then assigned to a combination of stratification duration (10 levels: 0, 10, 20, 30, 40, 50, 60, 70, 80, 100 days) and incubation (2 levels, low temperature: 20 day/10 night or high 25 day/15 night) treatments, making for a 20 level fully factorial treatment design. For stratification, petri dishes were wrapped in aluminum foil and placed in a X germination chamber in the dark at 4 degrees C. At the end of each stratification duration, cohorts were transferred to incubation conditions in growth chambers. Germination fractions were observed every other day for 25 days, and petri dishes were checked daily and moistened as needed. By measuring the germination fraction over time, I will generate germination time courses for each species and each treatment.

**Statistical analysis:** Using the germination time courses for each species, I will calculate the rate of change for  $T_b$  given as a function of stratification duration. From these data, I will assess each species' sensitivity to stratification, and use

## 0.2 Status/preliminary results

**Project Status:** The experimental procedures are underway, and expected to conclude in December 2018.

# OEGRES: A meta-analysis of Observed environmental germination responses in experimental settings

## Introduction and Questions:

Seed germination is a critical life history stage for plant life, and as such, there is a long history, dating back to 300 years before the common era, of germination research (Baskin & Baskin, 2014). This work has produced a large body of literature detailing the germination requirements and dormancy classes for a vast number of taxa across an array of taxonomic and geographic space. Many comprehensive books and review papers have been written on the subject and germination research continues at a rapid pace around the globe, but there are still large gaps in our knowledge (Baskin & Baskin, 2014). As mentioned above, our understanding of dynamics of germination response to environmental state remain in its infancy. Without a better understanding of a more complete range of germination responses to different environmental conditions, it is difficult to predict the extent of climate change impact on plant regeneration. While few individuals systematically investigate responses to a wide range of environmental conditions, in addition to the experimental work I proposed in chapter 2, the large body of germination literature could be leveraged to this end. In this chapter, I propose a meta-analysis to more broadly address the questions I laid out in chapter II:

1. How does varying environmental treatments effect the germination time courses of plant species?
2. How do various environmental treatment interaction to effect seed germination?
3. Do we detect any broad pattern in the germination response to variable environmental conditions on a phylogentic, geographic, or life-history level?

In addition to these fundamental biological question I will also use this project to address several important questions about germination research methodologies including:

1. Which environmental cues are most commonly manipulated?
2. What treatment levels most commonly utalized in research, how often are multiple treatment levels applied within one experiment?
3. Do treatments decisions correlate with other factors such as geography, institution, or taxa studied?

## Proposed methods:

Due to the acknowledged importance of temperature in mediating seed dormancy and germination, my primary interest is to evaluate the effects of stratifaction and incubation treatments on germination, but I intend to also include other environmental factors, such as water status, soil properties, afterripening, and scarification treatment in my analysis. The details proposed my data collection, study inclusion criteria and analysis are found below.

**Data collection:** I performed search of the Web of Science datebase using the key words "germination" and "stratification", and excluding meeting abstracts, abstracts of published items and proceedings papers. The search return 1,200 papers. I then read the abstract, methods and figures of these papers to identify studies that fit for inclusion in my analysis.

**Inclusion criteria:** To be included in the study, papers were required to:

- Report an temporal germination response in addition to a final germination percentage.
- Manipulate a temperature variable (cold or warm stratification).

Papers that were not fully accessible were also excluded from my analysis. Because of the large volume of papers, I will randomy sample 2000 papers that meet the selection criteria, and use them to build a database using ImageJ to scrape data from the relevant figures. The response variables I will capture include any measurement or index of germination rate as well as final germination percentages. The predictors I capture in addition to the specific environmental treatments in the paper will include:

- seed provenance (continent, latitude, longitude, altitude, biome)
- seed age
- year of collection and maternal environmental
- dormancy class (if applicable)
- non-environmental treatments (chemical application)
- life history
- population native status

**Analysis:** Upon completion of the database, I will use a multilevel, Baysian modeling framework to assess the impact of varying temperature regimes on germination behavior. I intend to run several models with differnt grouping factors, including taxonomic, regional. I will also query to database to address the methodological questions addressed above.

## Project status:

As of August 16, I have evaluated 610 papers of which 241 were determined fit for inclusion. Assuming this 39.5 percent inclusion rate remains consistent, I expect that 450-500 studies will be fit for inclusion.

# Chapter IV: Seasonal priority effects: Germination phenology as a mediator of plant competition

## Introduction

Priority effects, a class of interspecific interaction in which the effect of species on one another depends on the order in which they arrive at a site, are a cornerstone of community assembly theory (Fukami, 2015). These historical contingencies have been shown to have the capacity alter the structure and function of communities driving communities to alternate stable states (Fukami & Nakajima, 2011). Recent theory has suggested that it is not just species' arrival times that determine the course of interactions, but significant priority effects can be determined by the phenological differences between species already resident to a site, a subcategory of historical contingency known as seasonal priority effects (SPE) (Wainwright *et al.*, 2012). Like traditional priority effects, SPE's can operate through niche preemption, in which the species with earlier phenology reduce the amount of resources available for species with more delayed phenological activity, or niche modification, in which earlier phenological initiators modify the environment, determining the growth conditions that the later species will experience. While niche modification effects can be facultative or detrimental, the effects of niche preemption on the later species is always detrimental (Fukami, 2015). Most of the evidence for seasonal priority effects, comes from observation studies correlating higher phenological sensitivity (earlier phenology), with competitive dominance or invasion success (Gioria *et al.*, 2018). However early phenology may be associated with other traits associated with superior competitive ability (Dickson *et al.*, 2012), and the strength of priority effects have been shown to vary based on the identities (Cleland *et al.*, 2015) and by environment (Kardol *et al.*, 2013). While some studies have succeeded experimentally linking seasonal priority effects with competitive dominance (Wainwright *et al.*, 2012), or inferred seasonal priority effects through sequential planting studies (Koerner *et al.*, 2008), to my knowledge, the relative strength of SPE is determine competitive relationships between species has yet to have been quantified in any systems. With the evidence for significant interspecific differences in phenological sensitivity to variable climates, it is likely that climate change will alter the lag time or germination rank between species. If SPE's do indeed significantly mediate species interactions, this phenological shifts would be expected to have strong implications for community dynamics. In this final chapter I ask:

- What is the effect of a stronger SPE on the competitive dynamics of pair-wise species interaction?

## Proposed Methods

Based on the results of from chapter II, two species will be selected for a pairwise competition experiment. The two species will be selected based on the following criteria:

1. They have similar growth requirements and would be likely to be found in the same habitat in nature.
2. Their germination rank changes or the lag between their respective germination phenology shifts by more than 10-15 days given different stratification/incubation combinations.

Seeds of each species will be sown in a soil medium at varying relative and overall densities following a response surface design detailed in Inouye (2001) [see figure]. This design has been shown to be the most



effective for differentiating between the effects of intra vs. interspecific competition and integrating data with theoretical models of competition. Replicants of each density will be randomly assigned to two different stratification/incubations regimes that have previously been shown to alter the germination rank of the species, thus manipulating the strength of the seasonal priority effects in the competitive system.

After the given stratification period and 25 days of incubation, all pots will be transferred to greenhouse for the duration of the experiment (16 weeks). Every 4 weeks, the height of each plant will be measured and standardized photos of each pot will be taken to allow for an estimation of percent cover of each species. The measurement will be applied for a biomass estimation using models found in Axmanová *et al.* (2012). At each measurement interval, 5 plants of each species, not included in the response surface will be measured, then harvested, dried and weighed to better calibrate the biomass models. At the conclusion of the experiment, all plants will be harvested, dried and weighed for a final biomass calculation.

**Analysis:** I will use the repeat measures of biomass to calculate and compare the relative growth rate (RGR) (Connolly & Wayne, 2005) of each species under the different priority effect manipulations. I predict that the first species to germinate in each treatment will have a higher relative growth rate and suppress the growth rate of the second species. If no switch in germination rank is possible, I expect more pronounced priority effect (great lag between germination), to produce a greater differential in relative growth rate than the weaker priority effect treatment.

# Timeline

Time	Task
<b>Fall 2018</b> ch.1 ch.2 ch.3 ch.4	Write article for part 1 Complete experiment data collection Complete OEGRES initial inclusion survey
<b>Spring 2019</b> ch.1 ch.2 ch.3 ch.4	Analysis of part 2 Data analysis Begin data scraping Select species and treatment for response surface
<b>Summer 2019</b> ch.1 ch.2 ch.3 ch.4	Write article for par 2 Continue data analysis Continue data scraping Continue preparations for response surface trials
<b>Fall 2019</b> ch.2 ch.3 ch.4	Continue data analysis Continue data scraping Initiate treatments, begin competition experiment
<b>Spring 2020</b> ch.2 ch.3 ch.4	Data analysis Data cleaning Continue experiment
<b>Summer 2020</b> ch.2 ch.3 ch.4	Conclude Data analysis Data cleaning Begin data analysis
<b>Fall 2020</b> ch.2 ch.3 ch.4	Write article Modeling Continue data analysis
<b>Spring 2021</b> ch.3 ch.4	Continue Modeling Continue data analysis
<b>Summer 2021</b> ch.3 ch.4	Write article Continue data analysis
<b>Fall 2021</b> ch.4	Write article 10
<b>Spring 2022</b>	Defense

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