

Vegetative Phenology: Mechanistic Basis, Research Methodology and Anthropogenic Climate Change

1. Introduction

Since the 10th century B.C.E. humans have tracked phenological shifts in their environment and endeavored to understand them. Plant phenology is the study of the timing of recurring lifecycle events in biotic organisms (Forrest and Miller-Rushing, 2010; Flynn and Wolkovich, 2018). Historically, plant phenology has been rigorously monitored in agriculture, where anticipating the commencement of seasonal monsoons or late spring frosts played a pivotal role in food production (Piao *et al.*, 2019). However, plant phenology encompasses a far wider range of topics, spanning both contemporary and evolutionary time (Zhang, 2012; Forrest and Miller-Rushing, 2010). Because it concerns the timing of lifecycle events commensurate with changes in environment, occurrences such as vegetative bud formation, budburst (see Appendix 1-7), flowering, fruit production and leaf-drop are all key indicators of vegetation phenology (Brearley *et al.*, 2007; Gallagher and Campbell, 2017; Flynn and Wolkovich, 2018). Additionally, it is now well-documented that the timing of phenological events, such as vegetative budburst, has shifted in concert with rapid anthropogenic climate change (Forrest and Miller-Rushing, 2010; Glaum *et al.*, 2021). This essay aims to elucidate the following areas pertinent to plant phenology: (1) the mechanistic basis of phenology, (2) phenological research methodology and (3) phenological alterations due to anthropogenic climate change.

2. The mechanistic basis of phenology

The proximate drivers of plant phenology are temperature, photoperiod, and precipitation (Forrest and Miller-Rushing, 2010; Hänninen *et al.*, 2019). Within temperature, there are two primary factors: forcing and chilling, or warming temperatures in spring and duration and intensity of cold winter temperatures (Flynn and Wolkovich, 2018). Temperature can alternatively be grouped into soil temperature and air temperature, the effects of which differ depending on habitat. In boreal forests, for instance, Hänninen *et al.* (2019) noted that air temperature is the primary factor in vegetative budburst. Another effect of temperature forcing is the release of endodormancy, or the physiological state where growth is inhibited even in the advent of ordinarily suitable growing conditions (Jewaria *et al.*, 2021). In boreal and temperate forests this release from endodormancy into the state of ecodormancy and was found to be triggered by sustained temperatures of 4°-8° C (Jewaria *et al.*, 2021).

The second major factor affecting plant phenology is photoperiod, and in particular changes in day-length (Caffarra *et al.*, 2011). According to Caffarra *et al.* (2011), short days (ShDs) are one of the primary triggers for plants to enter endodormancy and begin to downregulate their metabolism for winter. Finally, there is precipitation. In a fascinating 10-year study (1990-2000) by Brearley *et al.* (2007), it was found that in the three years following drought— 1991, 1994 and 1997— more than half of tropical trees (primarily dipterocarps) underwent

general flowering (GF) events. Interestingly, this reproductive activity was synchronized and correlated to recurring changes in the El Niño Southern Oscillation (ENSO). Flynn and Wolkovich (2018) examined phenological factors such as photoperiod and temperature forcing and found that they often work in confluence. Bale *et al.* (2002), however, found they did not always work in tandem. To gain a broader perspective, scientists have increasingly adapted new research methodologies.

Phenological technology and research methodology

With a clear understanding of the proximate drivers of plant phenology, the role of technology and research methodology can be elucidated. The core methodologies employed to study plant phenology can be grouped into two designations: (1) in situ observations and (2) remote sensing (RS) (Liang and Schwartz, 2009). However, these methodologies contain both limitations and advantages. The primary limitations of in-situ observation are its incomprehensiveness. As Donnelly *et al.* (2022) noted, in-situ studies are limited by incomplete spatial coverage, uneven focus on dominant species, and temporal limitations including an overemphasis on start of season (SOS) and end of season (EOS) events. The strengths of in-situ methodologies are acuity of resolution, individual species identification and the ability to implement on-the-ground technology like PhenoCam for physical monitoring, Kriging estimation for temperature/ precipitation and LiDAR DEM for microtopography. More traditional in-situ observation has been used to monitor budburst via photography (see Appendix 1-11). However, due to the limitations of this methodology, researchers have turned to RS technology.

RS has become increasingly common in the past 25 years. Integral to the function of LSP, a type of RS, are reflectance-based 'greenness' proxies that detect reflected solar radiation (Helman, 2018; Donnelly *et al.*, 2022). Plants emit or absorb solar radiation at different spectral frequencies, absorbing lower frequencies (~620 nm) and reflecting solar radiation at near infra-red (~800 nm) (Helman, 2018). This 'greenness' is detected using enhanced vegetation index (EVI) and converted into data sets used to monitor phenological shifts. Another benefit of RS methodology is the vast increase in both spatial and temporal scale. RS data also integrates topographical complexity, is easier to apply and quicker to gather (Donnelly *et al.*, 2022). However, interpretation of data—especially in landscapes containing multi-canopy layers—can pose real difficulties in RS data gathering. Additionally, the process of 'smoothing,' or removing erroneous visual data, can further confound RS datasets (Helman, 2018). In the past few decades, phenological data has formed a fundamental component of the Coupled Model Intercomparison Project (CMIP) implemented by the Intergovernmental Panel on Climate Change (IPCC).

4. Phenological alterations: anthropogenic climate change

Because phenological shifts can be used as bioindicators of anthropogenic climate change, plant phenology has come into sharp focus in the past two decades (Macgregor *et al.*, 2019). There is now incontrovertible evidence that the biogeochemical feedback loops set off by climate change have affected

population dynamics and breeding cycles throughout the world (Matthysen, Adriaensen and Dhondt, 2010). Because of this, phenology has been studied to anticipate future changes to ecosystems and the services they provide (Piao *et al.*, 2019). Events such as premature budburst, for example, increases the likelihood of the plants incurring damage from late season frosts (LSFs) (Zohner *et al.*, 2020; Hänninen *et al.*, 2019). Further well-documented examples include the mismatch of songbirds' first egg-laying dates compared with the availability of invertebrate food supply, the effect of which can deprive fledglings of their primary food source, thereby negatively impacting population abundance (Both *et al.*, 2009). A recent paper by Macgregor *et al.* (2019) also revealed that the range and distribution of 130 species of *Lepidoptera* shifted poleward in conjunction $\sim 0.5^\circ\text{C}$ mean temperature rise between 1995 and 2014. In another study spanning 29 years, the egg-laying dates of two sympatric species, *Cyanistes caeruleus* and *Parus major* were examined. The results showed that the first egg-laying date of these species retreated at rate of 0.1 day/yr^{-1} , or a total of ~ 3 days over the course of their study (Matthysen, Adriaensen and Dhondt, 2010). This research has led researchers like Vitasse *et al.* (2021) to conclude that current phenological shifts under climate change are having a profound impact on biodiversity loss and species redistribution.

5. Conclusion

Plant phenology addresses a wide range of areas from understanding plant-pollinators co-adaptations to global shifts in species abundance and distribution. (Zhang, 2012; Glaum *et al.*, 2021). Comprehending the mechanistic basis, research methodology and phenological alterations due to anthropogenic climate change has helped scientists and citizens better understand the present and project into the future. Because vegetative phenology can be used in a variety of fields, from agriculture and land use to conservation and climate modelling, it is imperative that researchers continue to develop an understanding of this important field of study.

Word Count: 1198

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Appendix: Phenological events in four vegetation layers (January-March 2023)

Canopy Layer:

1. Horsechestnut (*Aesculus hippocastium*)



1a. Winter bud



1b. Pre-budburst



1c. First bud burst



1d. Late-stage budburst

2. Sycamore (*Acer pseudoplatanus*)



2a. Winter bud



2b. Pre-budburst



2c. Pre-budburst



2d. First bud burst

3. Hawthorne (*Crataegus monogyna*)



3a. Winter bud



3b. Pre-budburst



3c. First bud burst



3d. Late-stage budburst

Sub-canopy Layer

4. Hazel (*Corlyus avellana*)



4a. Winter bud



4b. Pre-budburst



4c. First bud burst

4d. Late-stage budburst

5. Elderberry (*Sambucus nigra*)



5a. Winter bud



5b. Budburst



5c. First leaves



5d. Late-stage leaves

Shrub layer:

6. Blackberry (*Rubus fruticosus*)



6a. First leaves



6b. Late-stage leaves

Ground/Field Layer:

7. Bluebell (*Hyacinthoides non-scripta*)



7a. Winter bud



7b. Budburst



7c. First leaves



7d. Late-stage leaves

8. Sycamore seedling (*Acer pseudoplatanus*)



8a. Winter seed



8b. Seed-burst



8c. First leaves



8d. Late-stage leaves

9. Bulbous buttercup (*Ranunculus bulbosus*)



9a. First flowers

10. Common nettles (*Urtica dioica*)



10a. First leaves

11. Heath bedstraw (*Galium saxatile*)



11a. First leaves