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INTRODUCTION TO THE SPECIAL ISSUE ON PHENOLOGICAL PATTERNS IN THE FLORA OF WESTERN NORTH AMERICA

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If there were ever a time to study plant phenology, the time is now. Change is upon us in every regard and as a Society focused on the natural history of the flora of western North America, this special issue is focused on understanding the phenological responses of plants in our region. Western North America contains a diverse and highly endemic flora (Burge et al. 2016) that is also highly endangered. There are many threats to the flora, including rapid land use changes and anthropogenic climate change, which pose a heightened threat to California's endemic flora and beyond. Rising temperatures, predicted by climate models, are being observed in the West (Parmesan and Yohe 2003; Kelly and Goulsten 2008), and precipitation patterns are becoming more variable (Swain et al. 2018). These changes are already impacting plants in this region, as shown in many of the articles presented here. Understanding how plant species, populations, and communities change over time and across space is critical to directing conservation efforts, land management, and future scientific inquiry.

Plant phenology—or the timing of life history events, such as bud break or flowering—is a critical component of an organism's biology, and links it to a myriad of other interacting organisms (such as Olliff-Yang and Mesler 2018; Mulder et al. 2021 *this issue*). What triggers plant phenological responses is a fundamental question of organismal biology and ecology, yet for most species, this remains a mystery. Recent advances in available data have made studying phenology of plants much more feasible, and we are pleased to have brought together a group of articles that advance our knowledge of the phenological patterns of our flora (Fig. 1).

At its core, phenological research asks a basic question about an organism: “What environmental factors (e.g., temperature or precipitation) induce changes in the timing of a life history event (e.g., leaf drop, bud burst, flowering, fruiting, or senescence)?” The availability of climate data for the entire United States via Climate NA and PRISM provides many environmental variables with which to look for correlations with the phenological trait of interest (PRISM Climate Group 2004; Wang et al. 2016).

Phenological data has traditionally come from *in situ* observations of plants in the field. However, to understand plant responses to *in situ* environmental conditions, observations must span many years, making these datasets rare. In this issue you will see the results of a 5-yr study of *Dirca occidentalis* (Graves and Gimondo 2021 *this issue*), a 10-yr study of *Calochortus plummerae* (Williams et al. 2021 *this issue*), a 30-yr dataset for six desert taxa (Zachmann et al. 2021 *this issue*), and a 30-yr study in *Quercus* (Koenig et al. 2021 *this issue*). Common gardens are also incredibly valuable for understanding how plants from different populations vary with respect to phenological responses. Two papers featured here present results from 30-yr old common gardens in *Quercus* (Papper and Ackerly 2021 *this issue*; Wright et al. 2021 *this issue*). These long-term projects require sustained effort over long time periods, and we are excited to present their findings in this issue.

A more recent way to generate phenological data is to engage the public in the process of making *in situ* observations of plants. The National Phenology Network empowers people to make phenological observations of species in the field and, as a network, volunteers currently monitor over 1,000 plant species with data going back to the early 2000's (USA National Phenology Network 2021). These are recorded and aggregated for research use. Armstrong-Herniman and Greenwood (2021 *this issue*) use these data to understand the flowering phenology of five oak species. Other networks, like the Winterberry Network in Alaska, provide data on fruit availability during the harsh winters of northern regions (Mulder et al. 2021 *this issue*). These crowd-sourcing approaches provide robust datasets to answer questions on larger spatial scales.

Herbarium specimens preserve phenological data of plants across time and space. Although most herbarium specimens were not generally collected with the purpose of conducting phenological research, the phenological status of a specimen can be seen by visually inspecting the specimen. The use of herbarium specimens to track the relationship between local climatic conditions and the collection dates of flowering specimens has a relatively short



FIG. 1. Examples of plants included in this Special Issue on phenology, in order of appearance. (A) *Eschscholzia californica*, photo: Katelin Pearson; (B) *Calochortus plummerae*, photo: Kimberlyn Williams; (C) *Lasthenia gracilis*, photo: Emily Cox; (D) *Lasthenia californica*, photo: Alexander C. Yang; (E) *Clarkia unguiculata*, photo: Susan Mazer; (F) Bodega congeners *Camissoniopsis cheiranthifolia* (top) and *C. micrantha* (bottom), photos: Sharon Strauss and Keir Morse (respectively); (G) *Dirca occidentalis*, photo: William R. Graves; (H) *Quercus douglasii*, photo: Prahlad Papper; (I) *Quercus lobata*, photo: Walt Koenig; (J) *Quercus kelloggii*, photo: Wendy Armstrong-Herniman; (K) *Arctostaphylos andersonii*, photo: Tom Parker; (L) *Ceanothus cuneatus*, photo: Tom Parker; (M) *Fouquieria splendens*, photo: Rhonda Spencer; (N) *Ohneya tesota*, photo: Mark Dimmitt; (O) *Empetrum nigrum*, photo: Anne Ruggles; (P) *Vaccinium vitis-idaea*, photo: Anne Ruggles.

history (Willis et al. 2017). Nevertheless, herbarium-based phenological studies are dramatically increasing the temporal scale of phenological research. The consortium of California Herbaria has a robust record of curating the state’s herbarium specimens and currently specimens are being imaged as part of the California Phenology Thematic Collections Network (Yost et al. 2019; <https://www.capturingcaliforniasflowers.org/>; NSF Project #1802163). Phenological status is being recorded on

each of these images. As of 2021, there are now over 1.3 million phenological records in the CCH2.org data portal, which are available for research use. These records will dramatically increase phenological research by creating a historical record going back to the 1800’s. Here, we present two papers that use phenological data from herbarium specimens. Mazer et al. (2021 *this issue*) used herbarium records spanning the last 115 yr for *Clarkia* species. Pearson et al. (2021 *this issue*) uses the historical record to

study how California's state flower, *Eschscholzia californica*, is responding across its range.

The variation observed in these papers and others clearly indicates that generalizations about shifts in phenology due to climatic changes are too early at this point. In this issue, Zachmann et al. (2021 *this issue*) find that for some desert taxa, warming promotes earlier flowering, yet individual species still varied in their response to several climate variables. Williams et al. (2021 *this issue*) find that for a rare geophyte, rainfall and time since fire, were most correlated with flowering. Armstrong-Herniman and Greenwood (2021 *this issue*) find that winter rainfall drives budburst in five long lived perennial tree species (*Quercus* spp.). Yet for one of the same species, *Quercus lobata*, warming temperatures were shown to advance flowering times (Koenig et al. 2021 *this issue*). For two other woody perennials, *Ceanothus* and *Arctostaphylos*, there was no evidence for an advance in flowering time over that last century (Parker 2021 *this issue*). For the winter flowering species *Dirca occidentalis*, fall rainfall and fall and winter temperatures drove flowering (Graves and Gimondo 2021 *this issue*). Water availability drove the intensity and duration of flowering of *Lasthenia gracilis*, a spring annual (Cox and Olliff-Yang 2021 *this issue*). In a second paper on *Lasthenia*, we find that germination date and competition from neighboring plants are important predictors of the flowering season of *L. californica* (Olliff-Yang and Ackerly 2021 *this issue*). In *Eschscholzia californica*, long term temperatures were more important than long term precipitation in predicting flowering time (Pearson et al. 2021 *this issue*). Plants may also exhibit a plastic response to flowering, whereby changes in the environment can be tolerated to a certain extent. We show here that responses are variable among close relatives, as Mazer et al. (2021 *this issue*) found in *Clarkia* and Strauss et al. (2021 *this issue*) found across a wide variety of taxa in a community context in Bodega Bay, California. We also see variation in phenological responses within populations of the same species, as in the Blue Oak (Papper and Ackerly 2021 *this issue*), and California Poppy (Pearson et al. 2021 *this issue*). Given this variation, future predictions across ecosystems are difficult to make at this time. More widely available data for a larger number of taxa and across more temporal and geographic scales will help to illuminate general trends, if there are any.

As more phenological studies are conducted, we can begin to make comparisons across taxonomic groups and across climates. Many papers in this issue are focused on plants in the Mediterranean climate of western California. These responses can be contrasted with responses from the far north (Alaska – Mulder et al. 2021 *this issue*) to those of the southwest (Sonoran Desert – Zachmann et al. 2021 *this issue*).

There has been extensive work done on phenology across the world, but we are still just beginning to

understand the complexity of timing that can occur within and between species, across landscapes and in different ecological contexts. This understanding is essential as climate change continues to alter the environmental cues that plants are responding to, and many species may need to shift rapidly to track optimal conditions.

Regardless of the drivers of a phenological event, the timing of plant resources—such as nectar, pollen, and fruit—strongly influence interacting organisms. For example, in this issue we see that when the fall season is extended and fruit ripen earlier, food resources in the winter and spring will be lower (Mulder et al. 2021 *this issue*). Environmental variables influence flowering season duration (Cox and Olliff-Yang 2021 *this issue*; Olliff-Yang and Ackerly 2021 *this issue*) and determine the conditions when flowers may be available for pollination (Graves and Gimondo 2021 *this issue*), which can result in higher or lower overlap in time with active pollinator species. Additionally, differences in timing between species and across habitats will have consequences for pollination and competition (Mazer et al. 2021 *this issue*; Strauss et al. 2021 *this issue*). For these reasons, shifts in phenology with climate change may have cascading effects within ecosystems, and will be important to continue to track.

In this issue, fourteen works are presented, covering a wide array of taxa representative of a small slice of our extremely diverse flora (Fig. 1). These manuscripts include historical, observational, and experimental studies of the timing of various plant stages, from leaf out and flowering to fruit set. Many authors from across western North America and beyond contributed manuscripts for this issue, and we are pleased to present a collection of papers spanning a diverse set of species.

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