Drier soils delay plant phenology across temperate forest and grassland systems

A.K. Ettinger[1,2,a], J.S. Dukes[3,b], M.R. Johnston[4,c], C.R. Rollinson[5,d], and E.M. Wolkovich[1,4,6,e]

[1] Arnold Arboretum of Harvard University, Boston, Massachusetts 02131, USA

[2] The Nature Conservancy,Seattle, Washington, USA

[3] Carnegie Institute

[4] University of Iowa

[5] The Morton Arboretum, Lisle, Illinois 60532, USA

[6] Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada

[a] Corresponding author; email: ailene.ettinger@tnc.org; phone: 781-296-4821; mailing address: 74 Wall Street. Seattle, WA 98121, USA

October 19, 2024

Data Accessibility The data reported in this paper are from the MC3E and the new ExPhen databases, which are both available at KNB (Ettinger and Wolkovich, 2018, 2022).

Running title Drier soils delay phenology

Abstract

Previous meta-analyses of phenology responses to climate change have focused largely on temperature as a driver of observed shifts. Yet climate change also affects soil moisture, which is limiting to many biological responses. Here we synthesize microclimate and phenology data from climate change experiments in temperate systems—both forests and grasslands—to quantify how soil moisture interacts with temperature to affect plant phenology. We find that phenology (budburst, leafout and flowering) delays in drier soils, with the largest delays seen in budburst (0.42 days per percent reduction in soil VWC). Effects of soil moisture were much smaller than for temperature (-1.7 versus -7.9 in standardized units), with interactive effects of temperature x moisture even smaller (0.5). However, there was high variability in the response across species. Forecasting shifts in soil moisture with warming, we find that soil moisture declines of 10% would have important effects on the phenology of some species, potentially muting advances due to warming alone. Our results show that soil moisture plays an important role in the phenology of temperate systems, with varying effects across species, and thus is likely to affect ecosystem functions tied to phenology at fine spatial scales. Incorporating local context, including relevant species and downscaled climate change projections, will be critical for relevant for management and conservation.

INTRODUCTION

Climate change is affecting organisms by altering temperature and soil moisture around the world (Parmesan, 2006; Chen et al., 2011). Some of the most widespread biological responses to climate change are shifts in phenology, the timing of recurring biological events, which have occurred at rates of 2.3-5.1 days per decade (Parmesan, 2006; Poloczanska et al., 2013; Root et al., 2003). Shifts in plant phenology are the most widely documented, with spring phenology (budburst, leafout, and flowering) occurring earlier in recent years (Wolkovich et al., 2013), and senescence occurring later (Taylor et al., 2008; Delpierre et al., 2009).

Phenological shifts are typically attributed to warming temperature, a known and well-studied driver of plant phenology. The timing of spring budburst, for example, depends on temperature through both chilling (the prolonged exposure to cold temperatures after growth cessation in the fall) and forcing (exposure to warm temperatures). Forcing effects are typically considered more dominant, so much so that many models use only forcing to predict phenology. These include common models of 'growing degree days' (GDD) in which phenological events are triggered after a certain thermal sum is reached (e.g., Olsson and Jönsson, 2014). Recent trends of advancing spring phenology may be due to increases in chilling and/or forcing with global warming (Fujisawa and Kobayashi, 2010; Ibanez et al., 2010; Cook et al., 2012).

Effects of altered precipitation and soil moisture on plant phenology have received less attention, but are likely to be important drivers. Many experiments have now focused on the effects of altered precipitation regimes, with meta-analyses highlighting the diversity of findings (Lu et al., 2023), and the importance of interactive effects of precipitation shifts with global change drivers (Zhou et al., 2023). In particular, recent work (Zhou et al., 2023) suggests warming combined with drought treatments may slow advances in phenology. Budburst can be slowed by water stress through inhibiting cell elongation (Essiamah and Eschrich, 1986), and growing season start may be delayed by drought in grasslands Cui et al. (2017). Conversely, flowering phenology can be advanced by drought conditions (Hamann et al., 2018). Effects of soil moisture on phenology have been most well- quantified in arid and grassland ecosystems (e.g., Essiamah and Eschrich, 1986; Reich and Borchert, 1984; van Schaik et al., 1993; Tao et al., 2019); the role of soil moisture on phenology in other ecosystem types, especially more mesic ones, is less explored.

Recent studies have suggested that moisture may play an important—but complicated—role in the phenology

of temperate ecosystems as climate change progresses (e.g., Seyednasrollah et al., 2018; Wang et al., 2022). Wang et al. (2022) found that decreasing precipitation frequency correlates with earlier leafout in many regions, while others have found variation in moisture sensitivity across ecoregions (Seyednasrollah et al., 2018). Increasing research using large-scale observational phenology data (e.g., remote sensing products such as NDVI) have documented an important role for soil moisture from forests to grasslands (Lian et al., 2020; Shen et al., 2022; Liu et al., 2024), and suggested temperature may play a role through moderating soil moisture (Liu et al., 2024). Teasing out the role of soil moisture from temperature is challenging through long-term climate trends alone, however. Perhaps unsurprisingly then, many studies have attempted to manipulate moisture via experiments (e.g., Morin et al., 2010; Hoeppner and Dukes, 2012; Rollinson et al., 2012; Clark et al., 2014) though few experiments have directly reported on moisture effects of phenology in temperate, non-arid and non-crop systems. Effects in more arid systems are diverse, often with no overall shift in phenology (e.g., Sherry et al., 2007; De Kauwe et al., 2017; Howell et al., 2020), suggesting that identifying clear trends from single experiments may be difficult.

Field-based climate change experiments that warm plots to different levels and apply precipitation or drought treatments are valuable tools to study effects of temperature and moisture on plant phenology. Experiments can combine temperature and precipitation treatments to decouple them compared to what may be observed in nature, allowing their effects to be more robustly quantified. Further, these treatments allow for studying effects of "no-analog" climate scenarios forecasted for the future, particularly when they employ active-warming methods, such as forced air heaters, soil warming cables, or infrared heaters (Shaver et al., 2000; Williams et al., 2007; Aronson and McNulty, 2009). Climate change experiments often monitor daily soil moisture and air temperature at the plot-level, allowing detailed quantification of how microclimate affects plant phenology. While previous meta-analyses of phenology in climate change experiments have focused primarily on effects of temperature (e.g., Wolkovich et al., 2012), there has been little synthetic work on moisture effects across experiments.

Here we use measured microclimate and phenology data across experiments to test how soil moisture and above-ground temperature together affect plant phenology (budburst, leafout, flowering). Our aims were to: (1) quantify the effects of soil moisture versus temperature alone and synergistically across species; (2) test how consistent effects were across species, functional groups and biomes (forest versus grassland), and (3)

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forecast effects to understand future implications of moisture shifts with warming.

MATERIALS AND METHODS

Data– To investigate how soil moisture interacts with temperature to affect phenology, we used two databases that compiled data from climate change experiments. Microclimate data came from the MicroClimate from Climate Change Experiments (MC3E) database (Ettinger and Wolkovich, 2018; Ettinger et al., 2019). Phenology data came from a ExPhen, a new database of phenology from climate change experiments (Ettinger and Wolkovich, 2022).

Both databases were created by first identifying published, active-warming field experiments, many of which included precipitation manipulations. We focused on *in situ* active-warming manipulations because recent analyses indicate that active-warming methods are the most controlled and consistent methods available for experimental warming (Kimball, 2005; Kimball et al., 2008; Aronson and McNulty, 2009; Wolkovich et al., 2012). We carried out a full literature review to identify potential active-warming field experiments, following the methods and search terms of Wolkovich et al. (2012) for their Synthesis of Timings Observed in iNcrease Experiments (STONE) database (Wolkovich et al., 2013), but restricting our focus to active-warming experiments. Further, because our goal was to tease out variation in microclimate (including temperature and soil moisture), we focused on warming studies that included multiple levels of warming and/or precipitation treatments. These additional restrictions constrained the list to 11 new studies published after the STONE database, as well as six of the 37 studies in the STONE database. We contacted authors to obtain daily microclimate and phenological data for these 17 studies and received data (or obtained publicly available data) for 10 of them, as well as datasets from five additional sites offered or suggested to us over the course of our literature review and data analysis. The daily temperature and soil moisture data from these 15 experiments comprise the MC3E database (Ettinger and Wolkovich, 2018; Ettinger et al., 2019). Of these, were able to obtain plot-level phenology data from 14 experiments, which comprise the ExPhen database of experimental phenology, available at KNB (Ettinger and Wolkovich, 2022).

Here, we analyze phenology data from the eight experiments in ExPhen that contain both regularly monitored plot-level soil moisture and above-ground temperature data (Table S1). Because we wished to examine

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variation among species and across sites, we focus on the most common three phenophases monitored, which were measured in three or more different experiments: budburst, leafout, and flowering. Two of the eight experiments were located in grassland ecosystems; the remaining six were in forests (Table S1). The database is species-rich, including 41 species monitored for budburst, 137 for leafout, and 124 for flowering, for a total of 190 species. These species span grasses (16 species), forbs (109 species), shrubs (29 species), and trees (36 species).

***Analysis*–** To understand how soil moisture interacts with temperature to affect phenology, we fit models with microclimate predictor variables of measured soil moisture, measured above-ground temperature, and their interaction to phenology response data (budburst, leafout, flowering). We excluded conifers from the analysis, because their phenology has distinct differences from angiosperm phenology Polgar et al. (2014) and conifer data existed from only one site in the database. For all phenophases, the response variable was day-of-year of the phenological event.

Predictors for our primary models were measured plot-level above-ground temperature, soil moisture, and their interaction. We chose to use measured microclimate as explanatory variables, rather than categorical treatment levels or target warming level, in our meta-analysis because experimental treatment effects from warming and drought can interact to alter microclimate conditions, in part due to feedbacks between temperature and soil moisture conditions (Ettinger et al., 2019; McDaniel et al., 2014).

We used hierarchical Bayesian models to test for effects for each species, as well as an overall effect, while accounting for site, year and plot-level effects. Grouping factors (often called 'random effects') for all phenology models were species (with random slopes and intercepts), site (random intercept), and year nested within site (random intercept). We fit models using the programming language `Stan` (Carpenter et al., 2017) (`www.mc-stan.org`), accessed via the `brms`(Bürkner, 2021) package in R (R Core Team, 2022), version 4.1.3. For each model fit, we ran four chains simultaneously, each with 4 000 iterations (2 000 of which were used for warm-up). Equations for these models can be found in the Supplemental Methods.

Given our aim to directly compare moisture and temperature effects, we used standardized predictors, which have an added benefit of improving model stability (Gelman and Hill, 2007). Standardizing predictors is a common technique in regression analysis; here we z-scored predictor variables (subtracting the mean and dividing by the standard deviation) and report coefficients from standardized predictor models as per SD

125 (standard deviation), alongside estimates of coefficients in their natural units.

RESULTS

127 We found that both higher soil moisture and higher temperatures advance phenology, meaning two common

128 effects of warming experiments—soil drying and warming—have contrasting effects on phenology. We found

129 that soil drying delays phenology and warming temperatures advance phenology. For budburst, wetter soils

130 and warmer temperatures alone advanced phenology by -1.7 per SD of soil moisture (or -5.22 days per 10

131 percent increase in volumetric water content) and Sexprtempeff.bbcent per SD of temperature (-3.4 per

132 degree Celsius), respectively. Together, wetter and warmer conditions delayed phenology a small amount

133 (interaction effect of 0.5 per SD or 3.7 natural units).

134 The magnitude of soil moisture effects varied across phenophases, with effects on budburst being stronger than

135 those on leafout (-0.4 per SD of soil moisture) and flowering (-1.3 per SD). Similar to budburst, temperature

136 effects were stronger than soil moisture for leafout (for which the temperature effect was -10.3 per SD) and

137 flowering (for which it was -7.9 per SD), across all species (Fig 1).

138 These overall effects varied widely across species (Fig 1). Species-level variance for the effect of moisture

139 was 2.7 standardized units for budburst, 4.5 for leafout, and 4.30 for flowering. Species-level variance was

140 even greater for temperature effects: 16.3 for budburst, 10.7 for leafout, and 5.9 for flowering. Variability

141 across species, however, was not predictable by life form (trees, shrubs, herbs, grasses, Fig S2) or ecosystem

142 (grassland versus forests, Fig S3).

143 We applied the above budburst model to forecast possible effects of climate change on phenology. Based

144 on the estimated effects, wetter soils advanced spring budburst at a rate of 5 days per 10% increase in soil

145 volumetric water content (VWC). Thus, if soil moisture is reduced by 10% of its current state, as is expected

146 over the next 50 years in areas where many of the experiments were conducted (the northeastern United

147 States) (Berg et al., 2017) (moving from, e.g.,21.5% VWC– the mean value for January-March across all

148 sites for which budburst was monitored– to 19.4%), budburst would be delayed by approximately 1 day on

149 average, due to changes in soil moisture alone (Fig 2).

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DISCUSSION

Here we synthesize experimental studies to find that soil moisture can strongly affect phenology in temperate non-arid ecosystems, in addition to the arid ecosystems where effects of water availability on phenology have been more often reported (e.g., refs). This offers new insight because, though increasing large-scale research suggests an important role for soil moisture in phenology, and small-scale experiments have found impacts of precipitation on phenology, there has been little work to understand cross-site impacts of soil moisture from experiments, despite the reality that many experiments collect these data. Soil moisture has not been a focus of previous phenology meta-analyses (e.g., Wolkovich et al., 2013), nor of most multi-species phenology studies in temperate mesic grasslands and forest ecosystems (e.g., Vitasse et al., 2021). Our findings highlight that, in mesic grasslands and forests, too, plants need water to advance budburst, leafout, and flowering; the delaying effect that dry soils seem to suggest that moisture can be a hidden, but potentially limiting, factor affecting phenology temperate systems not typically thought to be water-stressed.

Soil moisture is and will continue to shift with climate change (Berg et al., 2017), so while we found soil moisture had smaller effects than temperature it could have a big impact. Some areas, such as the northeastern United States (where many of the experiments were conducted) are getting wetter, and other places are expected to get drier (Berg et al., 2017). Overall, our forecasting suggests that temperature will continue to be a dominant controller of phenology, but that soil moisture also matters, especially for certain species.

High variation in responses to soil moisture across species and phenophases

Despite the overall effects of delays in phenology with soil drying, our results suggest that forecasts will need to contend with high variation in species responses, as well as differences across phenophases. We do not find strong differences in soil moisture effects across broad functional types (Figure S2), but there may be traits associated with these species-level differences in soil moisture effects.

-Add a ref or two about phenology-relevent-traits associated with responses to soil moisture?

Our findings of variation in soil moisture effects across species and phenophase may explain inconsistencies observed in previous studies. For example, Wolkovich et al. (2013) found that exotic species advance with precipitation, whereas native species delay at one site (Fargo).

176   1. Variance in soil moisture effect varied across phenophases and was lowest for budburst – perhaps
177   suggesting, across species, species need moisture for budburst? In contrast to temperature where the
178   variation is higher (though the overall effect of temperature is also higher...).

179   2. Interactions were weak for budburst and leafout, and stronger for flowering (Fig. 1).

180 Forecasting multiple drivers

181   1. Our work here shows that soil moisture affects the phenology of temperate grassland and forest systems.

182   2. Highly-cited phenology research in temperate grassland and forest systems has frequently ignored these
183   effects, focusing instead on temperature. Our finding that soil drying has an overall delaying effect
184   on phenology is consistent with Seyednasrollah et al. (2018), who found that moisture deficit generally
185   delays phenology in forest ecosystems, and with recent experimental (Liu et al., 2022) and observational
186   (Tao et al., 2020) studies in temperate grasslands.

187   3. Our results align within a larger literature from other systems that have found moisture matters to
188   phenology, including alpine systems dominated by snowpack (e.g., Dunne et al., 2004; Sherwood et al.,
189   2017), and arid/semi-arid ecosystems where precipitation is known to be more limiting (Tao et al.,
190   2019).

191   4. So we need to forecast both effects for phenology and possibly their impacts on other drivers and
192   limiting resources ...

193   5. Multiple global change factors affect phenology (temperature and soil moisture here, also CO2?, nitro-
194   gen, photoperiod)

195   6. Soil moisture may actually mediate plant phenology responses to warming and nitrogen addition, too
196   (Liu et al., 2022)

197 Implications and next steps

198   1. To do this forecasting, we need to improve how we relate experiments to the 'real world'. This in-
199   cludes moving beyond treatments levels to analyze plot-level microclimate- closer to how plants may

be experiencing treatments. Our study differs from some because we used field-measured soil moisture – most studies use precipitation (e.g., Tao et al., 2020) or gridded moisture products (e.g., Tao et al., 2019). The problems with these proxies are widely known (REF). However, our use of measured soil moisture also created a data limitation, as we were able to use only a subset of all the climate change experiments included in the ExPhen and E3 databases. So, we need more people to measure this! Such new data could help understand how temperature is affected by soil moisture, and how soil moisture is affected by temperature treatments.

2. Scaling up to ecosystem? recent papers on nutrient cycling

   (a) Soil moisture as a key factor affecting nutrient cycling (N, CH4 uptake)(Liu et al., 2019)

   (b) Soil moisture affects resorption of nitrogen and phosphorus during foliar senescence(Estiarte et al., 2022).

   (c) "Species-specific biomass responses to the environment in the climate-corrected biomass were asynchronous, demonstrating the importance of species interactions in vegetation responses to global change. Biomass production was co-limited by climatic and soil drivers, with each species experiencing its own unique set of co-limitations." (Wilfahrt et al., 2021)

   (d) Anytihng from Grephon we want to include?

Conclusions

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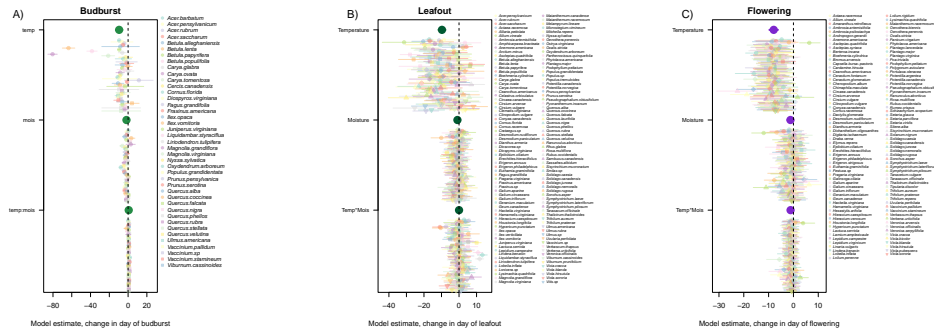351 Letters 26:1370–1381.

Figures

Figure 1: **Model coefficients from budburst, leafout, and flowering models (with centered predictors)** and including all species. We could show only the most common species here, to improve readability, and then show this version (with full species list) in the supplement. Thoughts?
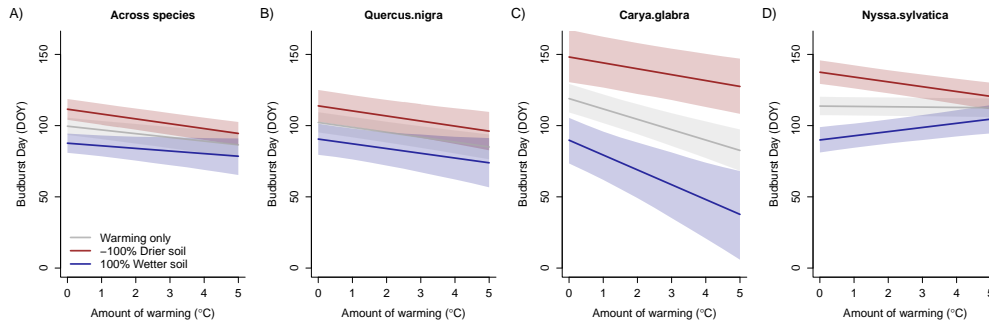

Figure 2: **Patterns of forecasted changes in budburst date with warming and shifts in soil moisture vary across species**. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and example species *Quercus nigra* in B); however, the magnitude of these effects, as well as the sign and magnitude of the estimated interaction between soil moisture and temperature, differed across species, resulting in divergent patterns with forecasted conditions under climate change. Budburst may occur much earlier in wetter vs drier soils with warming for species that have a synergistic interaction between soil moisture and temperature, such as *Carya glabra* (C). Whereas, other species with an antagonistic interaction, such as *Nyssa sylvatica*(D), may experience delayed budburst in wet soils but advance in dry soils.

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