Drier soils delay plant phenology across temperate forest and grassland systems

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

Running title Drier soils delay phenology

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Paper type GCB

Abstract

Previous meta-analyses of phenology responses to climate change have focused largely on temperature as a driver of observed shifts. However, soil moisture is also affected by climate change and likely to alter 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 -7.8 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 with warming alone. Our results show that soil moisture plays an important role in the phenology of temperate systems and may be critical for accurate projections. Quantifying phenological sensitivity to changes in soil moisture will therefore likely improve forecasts of shifts in phenology with future climate change at the fine spatial scales 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 is 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 phenology have received less attention, but are likely to be important drivers of plant phenology. For example, budburst, flowering, and leaf drop are affected by tree water status in dry ecosystems (e.g., Essiamah and Eschrich, 1986; Reich and Borchert, 1984; van Schaik et al., 1993). 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). Flowering phenology, on the other hand, can be advanced by drought conditions (Hamann et al., 2018). When effects of soil moisture on phenology have been quantified, this has occurred largely in arid and grassland or meadow ecosystems (e.g., Cleverly 2016, Tao et al 2019, Ganjurjac et al 2020); its role in other ecosystem types is less explored.

Recent studies have suggested that moisture may play an important—but complicated—role in the phenology of temperate ecosystem 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). These studies, however, are observational, where correlations between moisture and temperature make robustly teasing out effects of moisture challenging. 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 offer 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., 2013), 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) 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., 2013). We carried out a full literature review to identify potential active-warming field experiments, following the methods and search terms of Wolkovich et al. (2013) 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 14 experiments comprise the MC3E database (Ettinger and Wolkovich, 2018; Ettinger et al., 2019). The phenology data from these 14 experiments comprise the ExPhen database of experimental phenology, which is also available at KNB (Ettinger and Wolkovich, 2022).

Here, we analyze phenology data from the eight experiments in ExPhen, which contain plot-level soil moisture and above-ground temperature data (Table S1). We focus on the most common three phenophases monitored: 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, and spanning grasses (XX species), forbs (xx species), woody taxa (i.e., trees and shrubs, XX 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)

To better understand how shifts in soil moisture may alter phenology under climate change, we additionally fit phenology models in which the response variable was cumulative growing degree days at the time of the phenological event and the predictor variable was measured soil moisture.

For both model structures, we used herarchical 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 XXX. For each model fit, we ran two chains simultaneously, each with 4 000 sampling iterations (2 000 of which were used for warm-up). Equations for these models can be found in the Supplemental Methods.

RESULTS

We found that soil drying delays phenology and warming temperatures advance phenology. For budburst, the soil moisture effect was -1.7 standardized units (or -51.5 natural units) and the temperature effect was-7.8 standardized units (-3.4 natural units), with interactive effects of 0.5 standardized units (3.5 natural units). The magnitude of soil moisture effects varied across phenophases, with effects on budburst being stronger than those on leafout (-0.9 standardized units) and flowering (-1.2 standardized units). Similar to budburst, temperature effects were stronger than soil moisture for leafout (for which the temperature effect was -9.7 standardized units) and flowering (for which it was -7.9 standardized units), across all species (Fig 2).

These overall effects varied widely across species, however (Fig 2). Species-level variance for the effect of moisture was 2.74 standardized units for budburst, 4.48 for leafout, and 4.30 for flowering. Species level variance was even greater for temperature effects: 16.32 for budburst, 10.66 for leafout, and 5.94 for flowering. We did not detect consistent differences across life forms (trees, shrubs, herbs, grasses, Fig **??**) or ecosystems (grassland versus forests) Fig **??**).

Soil drying delays spring budburst at a rate of 0.42 days per percent reduction in soil VWC. Thus, if soil moisture is reduced by 10% of its current state (mean across all sites for which budburst was monitored= XX), as is expected over the next 50 years in the northeastern US (Berg et al., 2017) budburst would be delayed by approximately XX days on average, due to changes in soil moisture alone (Fig 3).

DISCUSSION

1. Some opening paragraph that just reviews our findings – soil moisture strongly affected phenology in temperature systems. Soil moisture is and will continue to shift with climate change. While we found sm had smaller than temperature it could have a big impact, especially for some species. We might reference back to a point in the intro about what this means – plants need water to advance and dry soils seem to delay – moisture as kind of a hidden but potentially limiting factor in temperate systems.

2. I would then have a section (couple paragraphs, could have subheading but I don't think you need it) comparing these results to other systems and putting it in context – this would cover much of your first

two paragraphs below

3. Species and phenophase variance in soil moisture (subsection I think)
   (a) If you add a plot of the posteriors of your moisture and temperature sigmas (I would overlay density plots quickly and see how it looks) you could review those results and discuss here
   (b) Our findings of variance across species and phenophase may explain discrepancies in previous studies
   (c) It's interesting (to me at least) that this variance was lowest for budburst – suggesting across species, species need moisture for budburst? In contrast to temperature where it's high – and this jives with species using forcing cues to spread out and temporally assemble in the spring ... would like to see the plots though first.
   (d) Here you can also mention the lack of findings across functional types
   (e) Some of your text on native/invasive add here (and other stuff in that section)
4. Forecasting effects of soil moisture with warming (subsection I think)
   (a) Open and remind people that moisture is really changing – NE USA is getting wetter, other places are getting longer dry spells and bigger rains ...
   (b) Some of your multiple global changes factors paragraph would fit here
   (c) Real work (last paragraph you have) may fit here too.

Altough soil moisture is expected to shift with climate change (CITE), it has not been a focus of previous meta-analyses (e.g., Wolkovich et al., 2013). Thus, our finding that soil moisture affects phenology, across the experiments in commmonly studied temperate forest and grassland ecosystems (i.e., those included the ExPhen database, Table **??**, Fig. 1), may surprise some. Soil moisture has been investigated frequently in arid or semi-arid ecosystems (e.g. CITE), including experiments that find either no effects (cites) or contrasting results across species (cites). Effects of moisture or precipitation on phenology have been extensively studied in alpine systems dominated by snowpack, as well, where less snow generally advances phenology (e.g., Dunne et al., 2004; Sherwood et al., 2017).

Our work here shows that soil moisture affects the phenology of temperate grassland and forest systems, historically not thought to have been strongly controlled by moisture (cite). Our finding that soil drying has an overall delaying effect on phenology is consistent with Seyednasrollah et al. (2018), who found that moisture deficit generally delays phenology, and Tao et al. (2020), in temperate Mongolia grasslands. Other studies additionaly find this effect in some locations (Wang et al., 2022) or for some species (Tao et al., 2019). Note that our study differs from some (e.g., XX) because we used field-measured soil moisture, which is hard to get – most studies use precipitation (REF) or gridded moisture products (REF). The problems with these proxies are widely known (REF). However, our use of measured soil moisture was also a limitation as we were able to use only a subset of all the climate change experiments included in the ExPhen and E3 databases.

Despite these overall effects of delays in phenology with soil drying, our analyses estimate wide variation across species in phenological responses to soil moisture. This variation is consistent with previous studies finding inconsistent effects of moistre. For example, Wolkovich et al. (2013) found that exotic species advance with precipitation, whereas native species delay at one site (Fargo) and suggest that drought avoidance strategies at Konza Praire (where results are less strong) may explain divergent responses to precipation across species. (... connect to observational studies finding differences among ecoregions where species also differ (see end of doc, where I added some notes). Could stress our results mean we need to understand the drivers of these species-level differences better...

Multiple global change factors affect phenology (temperature and soil moisture here, also CO2?, nitrogen?, photoperiod) -limiting resources: Variable responses to moisture (and precip) may be caused by temporal and spatial variation in the most limiting resource (e.g., temperature vs moisture). As global warming reduces temperature limitation, importance of moisture limitation in plant phenology may increase.

Although multiple environmental conditions affect phenology, interactive effects of soil moisture and temperature were weak for most phenophases. Interactions were weak for budburst and leafout, and stronger for flowering (Fig. 2).

Relating experiments to ”real world: -Moving beyond treatments levels to analyze plot-level microclimate- closer to how plants may be experiencing treatments -how temperature is affected by soil moisture, and how soil moisture is affected by temperature treatments

Conclusions

Additional Figures to make for supp:

- Plots of (distribution of) soil moisture and temperature by site
- Tables of models (for Supp)

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Figures

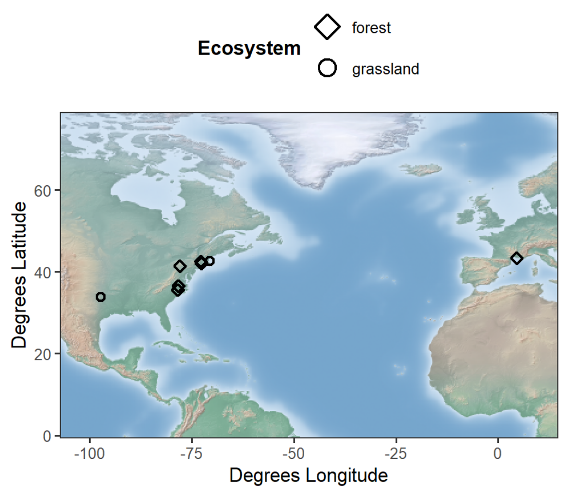

Figure 1: **Map of locations of experiments included in this meta-analysis.Add phenophases to this- perhaps fill shapes by coloirs associated with phenophase**

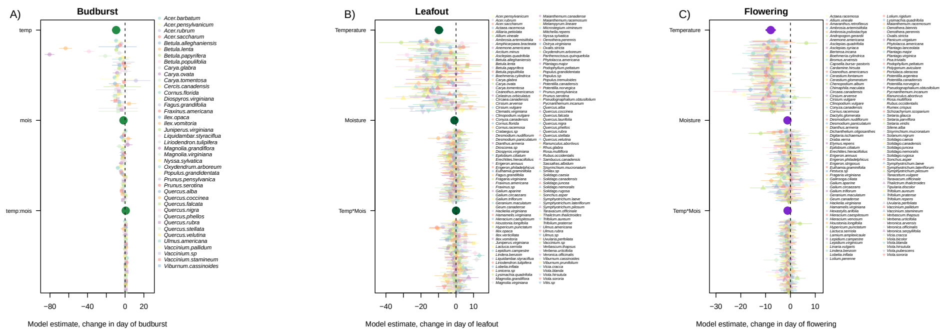

Figure 2: **Model coefficients from budburst, leafout, and flowering models (with centered predictors).**

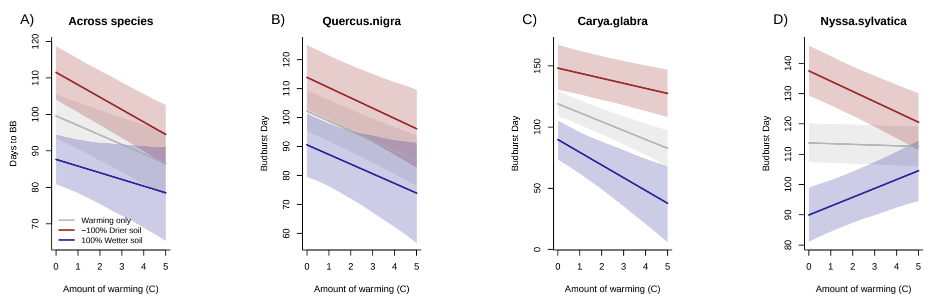

Figure 3: **Patterns of forecasted changes in budburst date with warming and shifts in soil moisture vary across species**. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and 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 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 a antagonistic interaction, such as *Nyssa sylvatica*(D), may experience delayed budburst in wet soils but advance in dry soils.