Soil moisture interacts with temperature to affect plant phenology

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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, 2021)

Running title Soil moisture affects phenology

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Abstract

Past studies of phenology responses to recent climate change have focused 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 to show how soil moisture interacts with temperature to affect plant phenology. We find that soil drying generally delays plant phenology, especially for budburst for which this delay occurs at a rate of 0.42 days per percent reduction in soil VWC, on average. The magnitude of effects we quantify suggest that, on average, climate change-induced shifts in soil moisture will play a small role in altering future phenology, compared to shifts in temperature, both because of the strong sensitivity of plant phenology to temperature and because of the large magnitude of projected shifts in temperature, compared to shifts in soil moisture. Nonetheless, although effects of soil moisture are comparably small on average, sensitivity to soil moisture varied dramatically by species, and soil moisture levels differed by site and among years. Thus, soil moisture is likely to play a role in phenological shifts with climate change for some species, particularly in some locations and years. Quantifying phenological sensitivity to changes in soil moisture will therefore improve forecasts of shifts in phenology with future climate change.

INTRODUCTION

Climate change is affecting organisms by altering temperature and soil moisture around the world (Parmesan, 2006; Chen et al., 2011). One of most widespread biological responses to climate change is a shift in phenology, the timing of recurring biological events, which has 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, leaf-out, 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). Recent trends of advancing phenology may be due to increases in both/either chilling and/or forcing with global warming (Fujisawa and Kobayashi, 2010; Ibanez et al., 2010; Cook et al., 2012). In places where delays in spring phenology have occurred, reductions in winter chilling are often the attributed cause (Yu et al., 2010).

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.

could add a paragraph on challenges ofobservational studies of soil moisture vs temperature as drivers because they are often correlated/affect one another?

Here we conduct a meta-analyses of climate change experiments to test whether and how soil moisture interacts with temperature to affect plant phenology. Field-based climate change experiments that warm plots to different levels offer valuable tools to study climate change impacts on plant phenology. Experiments can combine temperature and precipitation treatments to create the "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, as well as daily air and soil temperature, at the plot-level, allowing detailed quantification of how microclimate affects plant phenology.

Previous meta-analyses of phenology in climate change experiments have focused primarily on effects of temperature (e.g., Wolkovich et al., 2013). We expected that soil moisture may also affect phenology, with drier soils delaying budburst and leafout phenology and advancing flowering and fruiting phenology (add refs?). We use measured microclimate and phenology data from two databases of climate change experiments: MicroClimate from Climate Change Experiments (MC3E, Ettinger and Wolkovich, 2018)) and Experimental Phenology (ExPhen) to quantify effects of soil moisture and above-ground temperature on plant phenology (bud-burst, leaf-out, flowering, fruiting, senescence; see Materials and Methods). We also use forecasted changes in temperature and soil moisture to investigate how including soil moisture alters expected future shifts in phenology.

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). Phenology data came from a ExPhen, a new database of phenology from climate change experiments (Ettinger and Wolkovich, 2021).

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 both/either 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, which is available at KNB (Ettinger and Wolkovich, 2018). The phenology data from the same 15 experiments comprise the ExPhen database of experimental phenology, which is also available at KNB (Ettinger and Wolkovich, 2021).

Analysis– To understand how soil moisture interacts with temperature to affect phenology, we fit models with measured soil moisture, measured temperature, and their interaction to phenology response data (budburst, leafout, flowering, fruiting, senescence). Microclimate data came from the MC3E database, and phenology data came from the ExPhen database. 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 phenolophases, the response variable was day-of-year of the phenological event. Predictors for our primary models were measured air temperature, soil moisture, and their interaction. Random effects for all phenology models were species (with random slopes and intercepts), site (random intercept), and year nested within site (random intercept). Equations for these models can be found in the Supplemental Methods.

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To better understand the interactive effects of measured temperature and soil moisture, experimental treatment effects, and feedbacks between temperature and soil moisture conditions, we conducted follow-up analyses in which we fit the same phenology models to subsets of the data (controls only, low temperature treatments only, and high temperature treatments only). We also fit a model with soil temperature in place of air temperature, for the subset of sites these data were available.

To quantify how climate manipulations affect temperature and soil moisture, we used microclimate data from the 4 sites in the MC3E database that manipulated both precipitation and temperature, and measured both above-ground temperature and soil moisture (exp01,exp05,exp07,exp12). We then fit two groups of hierarchical models to microclimate data from these sites: one group with temperature response variables (including mean annual, and mean seasonal temperatures), and the other group with soil moisture as response variables (including mean annual, and mean seasonal soil moisture). For both groups of models, explanatory variables were temperature treatment, precipitation treatment, and their interaction. The models included a random effect of site, with a random slope and intercept structure, to allow effects of experimental treatments to vary across sites. Models also included random effects of day-of-year, nested within year, on the intercept only, to account for non-independence of measurements taken on the same day within the same year. 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 most phenophases. The magnitude of these effects varies across phenophases, species, and sites.

Effects of soil moisture were strongest for budburst and leafout, and affected all phenophases except fruiting (Figures **??**, 1S). 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.

Increasing air temperature advanced phenology for all phenophases except senescence (Figure 1S). Our models estimate that warming advances budburst phenology at a rate of 3.42 days per ˚C, advances leafout at a rate of XX, advances flowering a rate of XX, and advances fruiting at a rate of XX These estimates are consistent with estimates from previous meta-analyses (Wolkovich et al., 2013).

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- **Soil moisture effect size is bigger in full dataset than in controls only, for BB.** Mean and range of SM is similar (though max is a bit higher in full dataset; min is similar).

- **Effects of climate manipulations on temperature and soil moisture**

Mean annual soil moisture is negatively affected by target temperature treatment, and positively affected by precipitation treatment. (Figure **??**). These effects varied by site; for example, at exp07 soil moisture was positively affected by temperature treatment. Air temperature is positively affected by target temperature treatment, and negatively affected by precipitation treatment. (Figure **??**).

DISCUSSION

Across the ecosystems included in the ExPhen database (Table **??**), soil moisture affects phenology of budburst, and leaf-out. Soil moisture had previously been investigated primarily in grassland ecosystems (e.g. XXX), and has not been a focus of experiments and meta-analyses (e.g. Wolkovich). We quantify effects of soil moisture across forest, grassland, other ecosystems. -Show estimated effects by manipulating posteriors by biome? -group species by biome and show -3 biomes- histograms of effects of soil moisture across species of different

Species differences.- people may ask about phylogeny. why to think about this? functional groups- trees, shrubs, grasses, forbs. This may be confounded with biome and that's ok. -Make histogram for each biome with stacked bars or transparent for each functional group. For soil moisture and temperature effects.

global change factors interact- we know it for CO2, no matter biome you're in, can't just analyze this in a vaccuum; limiting resources

microclimate- how temp is affected by soil moisture, and how soil moisture is affected by tmperature treatments include datapoints,

Phenophases

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.

Conclusions

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Figures

map of studies with symbols varying by ecosystem

Figure 1: **Model coefficients from budburst and leafout models (with centered predictors).**

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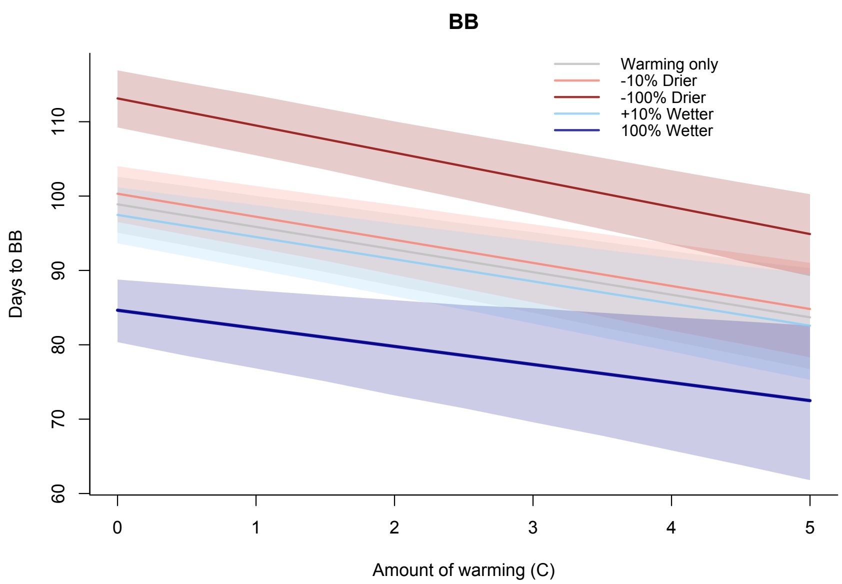

Figure 2: **Forecasting changes in soil moisture with warming.** instead of showing the mean choose 1-2 or more common species from each biome and show their differences.