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]Department of Forestry & Natural Resources and Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907, USA

[4]Department of Organismic & Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA

[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: 73 Wall Street. Seattle, WA 98121, USA

August 19, 2022

Author contributions: All authors conceived of this manuscript, which began at a Radcliffe Exploratory Seminar in 2016, and all authors contributed to manuscript revisions. AKE and EMW conceived of the idea for the literature review, database compilation, and related Radcliffe Exploratory Seminar, and wrote the manuscript. AKE compiled the datasets; AKE analyzed the data and created the figures.

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

Key words global warming, warming experiment, microclimate, phenology, bud-burst, leaf-out, flowering, fruiting, senescence

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 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). Eeffects of soil moisture were much smaller than for temperature (-7.79 versus -1.74 in standardized units), with interactive effects of temperature x moisture even smaller (inteff.bbcent). 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). One of most widespread biological responses to climate change is a shift in phenology, the timing of recurring biological events, which has occurred at a rate 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). (introduce GDD, if that part is kept in the paragraph and if we include GDD models) Recent trends of advancing 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). 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 of observational studies of soil moisture vs temperature as drivers because they are often correlated/affect one another? Or something about interactions between temperature and moisture?

Here we test how soil moisture interacts with temperature to affect plant phenology using a meta-analysis of climate change experiments. 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 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.

We expected that soil moisture may also affect phenology, with drier soils delaying budburst and leafout phenology and advancing flowering and fruiting phenology). We wanted to test interactive effects of soil moisture and temperature on phenology, as well as how shifts in soil moisture affect the cumulative growing degrees at which a phenological event occurs. We use measured microclimate and phenology data from two databases of climate change experiments to quantify effects of soil moisture and above-ground temperature on plant phenology (bud-burst, leaf-out, flowering). 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; 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 for which the database contains plot-level soil moisture and above-ground temperature data (Table S1), focusing 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, fruiting, senescence). 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 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). Models were fit using the programming language `Stan` (?) (`www.mc-stan.org`), accessed via the `brms`(?) package in R (?), 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.

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.

RESULTS

We found that soil drying delays phenology and warming temperatures advance phenology, for most phenophases. The magnitude of these effects varies across phenophases and species. We did not detect consistent differences across life forms (trees, shrubs, herbs, grasses, Fig **??**) or ecosystems (grassland versus forests).

Effects of soil moisture were strongest for budburst and leafout, and weakest for XX (Figures 1, 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).

Add a paragraph about GDD models

DISCUSSION

Altough soil moisture is expected to shift with climate change (CITE), it has not been a focus of previous meta-analyses 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 **??**), 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 (e.g., CITES). Our work here shows that soil moisture importantly affects the phenology of temperate grassland and forest systems, historically not thought to have been strongly controlled by moisture (cite).

Our finding of an overall effect delaying phenology with soil drying is consistent with **?**, who found that moisture deficit generally delays phenology, and **?**, in temperature Mongolia grasslands. Additional studies additionaly find this effect in some locations (**?**) or for some species (**?**).

Perhaps surprisingly, interactive effects of temperature and soil moisture were weak.

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 strong for flowering and senescence day of year, but were weak for budburst, leafout, and fruiting.

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

Are the temp and moisture effects synergistic or mainly acting alone? (Lizzie thinks lots of ecologists – herself included – think there will or should be a big interaction so we should test it explicitly. If we don’t see one, that's interesting.)

Conclusions

Additional Figures to make:

- Plots of (mean?) soil moisture and temperature by site
- Map of studies with symbols varying by ecosystem? (for Supp)
- Tables of models (for Supp)

References

Aronson, E. L., and S. G. McNulty. 2009. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. Agricultural and Forest Meteorology 149:1791–1799.

Berg, A., J. Sheffield, and P. C. Milly. 2017. Divergent surface and total soil moisture projections under global warming. Geophysical Research Letters 44:236–244.

Chen, I.-C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Cook, B. I., E. M. Wolkovich, T. J. Davies, T. R. Ault, J. L. Betancourt, J. M. Allen, K. Bolmgren, E. E. Cleland, T. M. Crimmins, N. J. B. Kraft, L. T. Lancaster, S. J. Mazer, G. J. McCabe, B. J. McGill, C. Parmesan, S. Pau, J. Regetz, N. Salamin, M. D. Schwartz, and S. E. Travers. 2012. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. Ecosystems 15:1283–1294.

Cui, T., L. Martz, and X. Guo. 2017. Grassland phenology response to drought in the canadian prairies. Remote Sensing 9:1258.

Delpierre, N., E. Dufrêne, K. Soudani, E. Ulrich, S. Cecchini, J. Boé, and C. François. 2009. Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in france. Agricultural and Forest Meteorology 149:938–948.

Essiamah, S., and W. Eschrich. 1986. Water uptake in deciduous trees during winter and the role of conducting tissues in spring reactivation. IAWA Journal 7:31–38.

Ettinger, A., I. Chuine, B. Cook, J. Dukes, A. Ellison, M. Johnston, A. Panetta, C. Rollinson, Y. Vitasse, and E. Wolkovich. 2019. How do climate change experiments alter plot-scale climate? Ecology Letters 22:748–763.

Ettinger, A., and E. Wolkovich. 2018. Microclimate from climate change experiments (MC3E). doi:10.5063/F1QV3JQR.

———. 2022. Phenology from warming experiments (EXPPHEN). doi TBA.

Fujisawa, M., and K. Kobayashi. 2010. Apple (malus pumila var. domestica) phenology is advancing due to rising air temperature in northern japan. Global Change Biology 16:2651–2660.

Hamann, E., A. E. Weis, and S. J. Franks. 2018. Two decades of evolutionary changes in brassica rapa in response to fluctuations in precipitation and severe drought. Evolution 72:2682–2696.

Ibanez, I., R. B. Primack, A. J. Miller-Rushing, E. Ellwood, H. Higuchi, S. D. Lee, H. Kobori, and J. A. Silander. 2010. Forecasting phenology under global warming. Philosophical Transactions of the Royal Society B-Biological Sciences 365.

Kimball, B. 2005. Theory and performance of an infrared heater for ecosystem warming. Global Change Biology 11:2041–2056.

Kimball, B. A., M. M. Conley, S. Wang, X. Lin, C. Luo, J. Morgan, and D. Smith. 2008. Infrared heater arrays for warming ecosystem field plots. Global Change Biology 14:309–320.

McDaniel, M., R. Wagner, C. Rollinson, B. Kimball, M. Kaye, and J. Kaye. 2014. Microclimate and ecological threshold responses in a warming and wetting experiment following whole tree harvest. Theoretical and Applied Climatology 116:287–299.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637–669.

Polgar, C. A., R. B. Primack, J. S. Dukes, C. Schaaf, Z. Wang, and S. S. Hoeppner. 2014. Tree leaf out response to temperature: comparing field observations, remote sensing, and a warming experiment. International journal of biometeorology 58:1251–1257.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, et al. 2013. Global imprint of climate change on marine life. Nature Climate Change 3:919.

Reich, P. B., and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of costa rica. The Journal of Ecology pages 61–74.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60. PT: J.

Shaver, G. R., J. Canadell, F. S. Chapin, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melillo, L. Pitelka, et al. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis ecosystem responses to global warming will be complex and varied. Ecosystem warming experiments hold great potential for providing insights on ways terrestrial ecosystems will respond to upcoming decades of climate change. Documentation of initial conditions provides the context for understanding and predicting ecosystem responses. BioScience 50:871–882.

Taylor, G., M. J. Tallis, C. P. Giardina, K. E. Percy, F. Miglietta, P. S. Gupta, B. Gioli, et al. 2008. Future atmospheric CO2 leads to delayed autumnal senescence. Global Change Biology 14:264–275.

van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of ecology and Systematics 24:353–377.

Williams, J. W., S. T. Jackson, and J. E. Kutzbacht. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104:5738–5742.

Wolkovich, E. M., T. J. Davies, H. Schaefer, E. E. Cleland, B. I. Cook, S. E. Travers, C. G. Willis, and C. C. Davis. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. American Journal of Botany 100:1407–1421.

Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the tibetan plateau. Proceedings of the National Academy of Sciences 107:22151–22156.

Figures

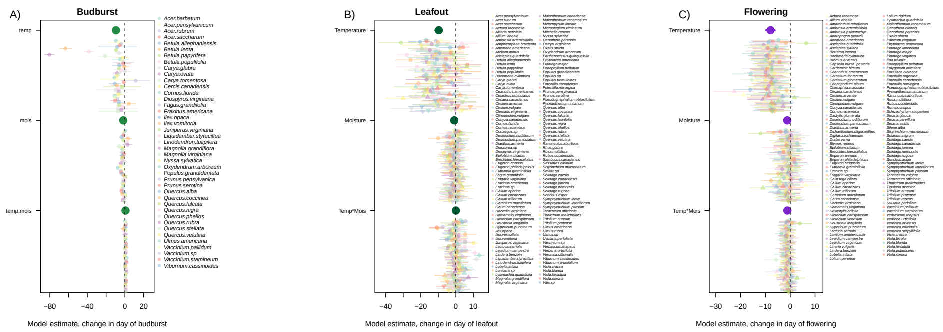

Figure 1: **Model coefficients from budburst, leafout, and flowering models (with centered predictors).**

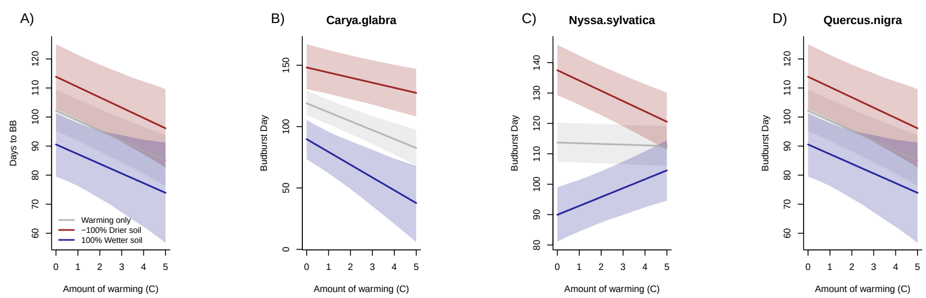

Figure 2: **Patterns of forecasted changes in budburst date with warming and shifts in soil moisture vary across species**. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and 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 changes in climate change. Budburst may occur much earlier in wetter vs drier soils with warming for species that have a super-additive interaction between soil moisture and temperature, such as *Carya glabra* (B). Whereas, other species with a sub-additive (?) interaction, such as *Nyssa sylvatica*(C), may experience delayed budburst in wet soils but advance in dry soils.