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Forum

Drought experiments need to incorporate atmospheric drying to better simulate climate change

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Abstract

Climate models predict more frequent, prolonged, and extreme droughts in the future. Therefore, drought experiments varying in amount and duration across a range of biogeographical scenarios provide a powerful tool for estimating how drought will affect future ecosystems. Past experimental work has been focused on the manipulation of meteorological drought: Rainout shelters are used to reduce precipitation inputs into the soil. This work has been instrumental in our ability to predict the expected effects of altered rainfall. But what about the nonrainfall components of drought? We review recent literature on the co-occurring and sometimes divergent impacts of atmospheric drying and meteorological drying. We discuss how manipulating meteorological drought or rainfall alone may not predict future changes in plant productivity, composition, or species interactions that result from climate change induced droughts. We make recommendations for how to improve these experiments using manipulations of relative humidity.

Keywords: ecological drought, meteorological drought, rainout shelter, atmospheric aridity, atmospheric drying, nature-based solutions

Anthropogenic climate change is increasing the frequency and severity of drought worldwide (Masson-Delmotte et al. 2021). Understanding how future drought will affect the integrity of ecosystems and the resilience of our food system is one of the most pressing challenges of our time. Past work has shown that drought can decrease the productivity of agricultural lands by up to 45% (Ciais et al. 2005, Madadgar et al. 2017) and in the United States has cost over $2.5 billion in a single year (Wilhite et al. 2007). Severe drought can kill adult trees (Breshears et al. 2005), increase the risk of catastrophic fire, and reduce the diversity of forests (Clark et al. 2016). In drylands, drought can reduce the establishment success of seedlings, can lead to the loss of native vegetation, and can reduce overall vegetative cover in already sparsely vegetated areas (Bradford et al. 2020). In many ecosystems on Earth, water is the primary limiting resource (Seddon et al. 2016). An increased risk of drought due to climate change has the capacity to reduce productivity and ecosystem functioning at a global scale.

One tool for predicting future drought impacts is to study naturally occurring droughts across ecosystem types. For example, Knapp and colleagues (2015) assessed the impacts of a regional drought that extended across the Central United States in 2012. At six grassland sites where precipitation was approximately 40% below average during the growing season, they found that drought responses varied by more than double across the sites, with desert grasslands being far more sensitive than mesic tallgrass prairies. He and colleagues (2018) calculated that this drought resulted in significant reductions in regional carbon uptake. Using satellite data, Jiao and colleagues (2021) quantified the recovery potential of forests, grasslands, and savannas in a series of droughts during and after the Millennium drought that affected Australia from 1997 to 2009. Recovery varied on the basis of hydrological conditions, drought return interval, and drought length. These examples demonstrate how natural droughts can be used to yield valuable insights into how different ecosystems may respond to and recover from climate anomalies.

However, natural drought events may not encompass the intensity and duration of droughts that are predicted to occur more often in the future (Ault 2020). Furthermore, multiple climate variables may change simultaneously during a drought, including temperature and relative humidity. Therefore, experimental approaches are needed to assess the relative importance of different climate variables, promote cross-site comparisons, and potentially push ecosystems beyond their historical variability and extremes.

For the past 20 years, the gold standard for experimentally examining meteorological drought (defined in table 1) has been the rainout shelter (Yahdjian and Sala 2002, Hoover et al. 2017, Knapp et al. 2020). Rainout shelters allow us to remove rainfall from tractable plots of land in remote locations with very few shelter artefacts on microclimate temperature or relative humidity (Fay et al. 2000, Yahdjian and Sala 2002). Rainfall removals can be compared with unmanipulated controls or procedural controls with inverted water removal channels to test for shelter effects (e.g., Pangle et al. 2012). Because these shelters are relatively inexpensive, they have facilitated large-scale cross-site comparisons of drought, such as the International Drought Experiment (Pennisi 2022).

Rainout shelters and rainfall reduction experiments have been instrumental in our understanding of how meteorological drought will affect future ecosystems. For example, in Switzerland, a precipitation experiment reduced average rainfall inputs by 25%–56%, and this led to a 15%–56% decrease in aboveground annual net primary productivity (Stampfli et al. 2018). Stampfli and colleagues (2018) also reported altered community dynamics following strong precipitation reductions. Plant diversity declined

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Table 1. Glossary of the three different types of drought discussed in this article, as they were defined by Masson-Delmotte and colleagues (2021).

Drought Type	Definition	Outdoor approach	Known manipulations	Citations
Meteorological drought	A deficit in precipitation	Rainout shelters	At least 127 global sites	As reviewed in Yahdjian et al. 2021
Agricultural drought	Shortage of precipitation combined with excess evapotranspiration, which reduces crop production	Rainout shelters and atmospheric drying in agricultural fields	0 outdoor experiments	
Ecological drought	Shortage of precipitation combined with excess evapotranspiration, which reduces ecosystem function	Rainout shelters and atmospheric drying in natural ecosystems	1–4 experiments (only one manipulating both soil moisture and RH or VPD)	Ibe et al. 2020, Aguirre et al. 2021, as reviewed in Lopez et al. 2021

Note: On the basis of the description of each drought type, we have suggested what experimental approaches could be used to address these knowledge gaps. We have also listed known experiments that address these gaps and citations for these experiments. We restrict this list to experiments conducted outdoors.

in droughted plots, and this decline in biodiversity remained even after productivity recovered in later years. In another example, a 20% reduction in precipitation in Southern California reduced annual net primary productivity and overall ecosystem carbon storage by 40% (Potts et al. 2012). More recent examinations of meteorological drought have focused on the role of rainfall periodicity and duration. Slette and colleagues (2023) demonstrated that repeated droughts in subsequent years can reduce root production twice as much as single-year drought events. Without these manipulations of meteorological drought we would have little idea of how future precipitation may affect plant physiology, community dynamics, or whole ecosystem functioning.

A lack of alignment between experimental and natural drought results

Recent synthesis work has called for a reexamination of drought experiments because of lack of alignment between experimental drought manipulations and drought-related effects that are already taking place as a result of climate change (Korell et al. 2019, Kröel-Dulay et al. 2022). Kröel-Dulay and colleagues (2022) demonstrated that rainout shelters underpredict real-world drought impacts on aboveground biomass by an average of 50%. Other work has shown that most ecosystems on Earth respond more strongly to experimental precipitation additions than to precipitation reductions of the same magnitude (usually done using rainout shelters; Song et al. 2019). And another recent meta-analysis identified how experimental manipulations tend to manipulate precipitation too much compared with climate model predictions for a given ecosystem (Korell et al. 2019). One reason for reported discrepancies between naturally occurring drought effects and experimental drought effects may have to do with the periodicity of rainfall events: In some places, climate change may drive only slight decreases in annual rainfall, but the vast majority of the rainfall could occur in a short period of time (Hoover and Rogers 2016). However, the disparity in these results is likely also related to the differences between meteorological drought (soil moisture reductions) and the compounding influence of atmospheric drying (Ficklin and Novick 2017). When we install rainout shelters and use them to exclude rain, we are only considering one half of the ecological drought equation: precipitation inputs via meteorological drought (table 1, figure 1c). Ecosystems of the future will also be responding directly to reduced atmospheric moisture because of increased temperatures and increased vapor pressure deficit (VPD; e.g., ecological drought, table 1, figure 1d).

Defining drought for ecologists

Surprisingly, the definition of *drought* is highly inconsistent. Although the term is widely used by researchers, there appears to be no formal consensus on its definition by either climatologists or ecologists (Slette et al. 2019). In ecological contexts, *drought* is typically defined relative to some long-term measurement of precipitation or soil moisture (Smith 2011). In the present article, we consider meteorological drought (table 1) to refer to an extended period of time with below average precipitation that leads to reduced soil moisture and plant stress (as defined in Masson-Delmotte et al. 2021). The proportional reduction in precipitation below the mean would reflect the drought's severity (e.g., a 25% versus 50% reduction in average growing season rainfall) and the duration would reflect the number of consecutive days or years of lower rainfall.

Beyond meteorological drought, the majority of modern drought indices developed by climate scientists track both precipitation and evaporative demand (e.g., the Palmer Drought Severity Index, the Standardized Precipitation and Evapotranspiration Index). Warmer global temperatures can increase atmospheric water holding capacity and drive increases in the evaporative potential of the air (Yuan et al. 2019). This is often measured as the VPD, the difference between the actual vapor content in the air and the potential vapor content for a given temperature. When reduced precipitation is paired with increased VPD, this is described as *agricultural drought* when it affects crop yields and as *ecological drought* when it affects ecosystem functioning (table 1). Atmospheric drying (e.g., VPD) and soil drying can be linked via land–atmosphere feedback loops. That is, landscape-scale drier soils can drive decreases in relative humidity, and this can feed back to further drying soils (Zhou et al. 2019). However, in some ecosystems and in some circumstances, precipitation may not change even though atmospheric drying increases (e.g., Zeng et al. 2023). Even outside of a changing climate, it is important that we understand the separate and co-occurring consequences of dry soil versus dry air for plant productivity and ecosystem functioning (see figure 5a in Knapp et al. 2023).

Current methods to compare soil drying and atmospheric drying effects

Teasing apart the relative role of soil moisture deficit versus atmospheric drying is an active area of research at both the individual-plant and whole-ecosystem scales (although it is mostly lacking at the community scale). Recent meta-analysis and synthesis

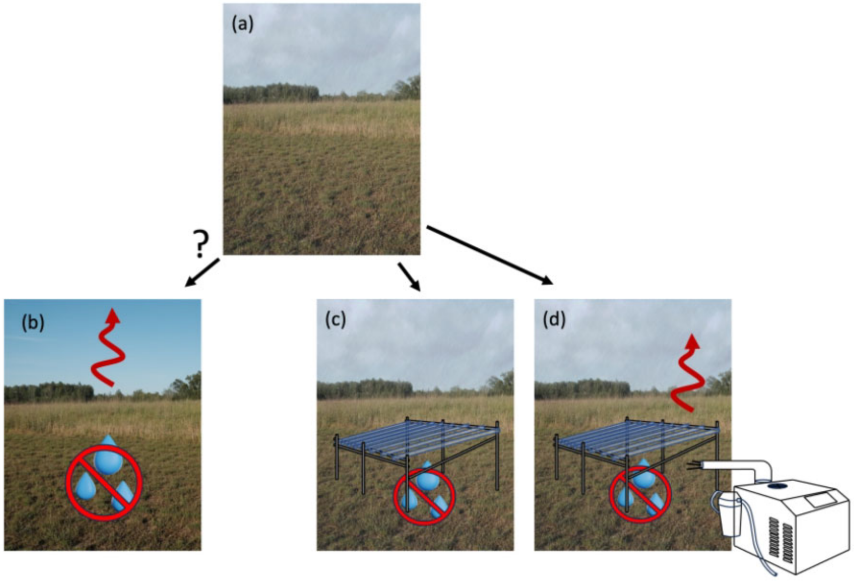

Figure 1. The goal of a drought experiment is usually to simulate future drought scenarios, given current conditions. This often involves manipulating conditions on humid or rainy days (a) to make them more like dry days (b). Ecological and agricultural drought (***sensu*** Masson-Delmotte et al. 2021) involves decreased precipitation and increased evapotranspiration. In the present figure, reduced soil moisture is indicated with rain drops with an X through them, and increased evapotranspiration is indicated with a wavy arrow coming from the land surface to the atmosphere. In the past, we have attempted to approximate these conditions by removing precipitation from hitting the soil, but this only approximates one part of future ecological drought conditions (c). In the future, we need to solve these issues with atmospheric humidity manipulations that we pair with rainout shelters (d). These manipulations would allow us to remove soil water and increase evaporative demand. These humidity manipulations could supplement our current approach and increase rates of evapotranspiration and water loss into the atmosphere (even if ambient conditions are cloudy or humid).

work indicates that drought effects on plants are sometimes more closely related to increased VPD than to decreased soil moisture (Grossiord et al. 2020, Lopez et al. 2021, Dannenberg et al. 2022, Fu et al. 2022, Lu et al. 2022, Zhong et al. 2023, but see Liu et al. 2020). The vast majority of research in this area relies on remote sensing and flux tower networks. For example, Fu and colleagues (2022) used global eddy covariance data to demonstrate that gross primary production responds more negatively to increased VPD than to decreased soil moisture in most conditions, and soil moisture effects only exceed VPD effects when the soil moisture is very low. Dannenberg and colleagues (2022) used soil moisture, temperature, and VPD data (also from flux towers) to assess the causes and consequences of the 2020 drought that occurred in the southwest of the United States. The drought caused a reduction of 122 teragrams of carbon in gross primary production below the 5-year mean. Dannenberg and colleagues (2022) found that approximately 50% of these drought impacts were driven by soil moisture deficit, whereas 40% of the impacts were driven by exceptionally high VPD. Observational work in drylands has also started to tease out the role of atmospheric moisture for plot-scale processes. For example, McHugh and colleagues (2015) documented the relationship between natural variation in atmospheric humidity and increased microbial activity in small plots. Wang and Wen (2022) correlated natural variation in soil moisture and VPD (from weather station data) and found that VPD had stronger effects on plot-level measurements of species composition (C4:C3 grass abundance) than soil moisture did.

Currently, modelers and empiricists differ in their assessments regarding the relative importance of atmospheric (VPD) versus meteorological (precipitation, soil moisture) drivers of ecosystem functioning. Their models suggest that, in the future, VPD may be a more important driver of grassland production than precipitation will be (Konings et al. 2017). However, rainout shelter experiments in which VPD was not manipulated have resulted in dramatic declines in plant production (e.g., Carroll et al. 2021), highlighting the fundamental importance of precipitation and soil moisture for ecosystem functioning. Still others predict that the importance of VPD decreases and the importance of precipitation increases along a gradient of decreasing mean annual precipitation (Novick et al. 2016), whereas others highlight the importance of soil texture and type for determining soil moisture limitations (Copeland et al. 2016). In order to gain a mechanistic understanding of VPD versus soil moisture effects on ecosystem functioning, experiments are needed to assess the independent and interactive effects of these two important ecological drivers.

For at least 20 years, growth chambers and ecotrons have been employed to experimentally compare the effects of decreased humidity and increased VPD on individual plant physiology. At this stage, at least 75 species, spanning woody to herbaceous growth forms, have been examined in terms of their response to VPD in controlled growth chamber experiments (for a review, see Lopez et al. 2021). This work has illuminated some general patterns: Most plants increase transpiration rates, decrease stomatal conductance, decrease leaf area, and decrease biomass production in response to increased atmospheric drying (Lopez et al. 2021). These studies are usually constrained to single species examinations of woody species or agricultural species (not uncultivated herbaceous species or whole communities), but they have started to offer insights into how ecosystems may respond to increased VPD in the future. Only very recently have these researchers attempted to simultaneously compare atmospheric drying to soil drying. In particular, Schönbeck and colleagues (2022) demonstrated more negative leaf water potential values for three woody species growing in increased VPD conditions in an ecotron, even when soil moisture was not limiting. In other words, plants responded negatively to increased atmospheric drought even when there was no meteorological drought occurring.

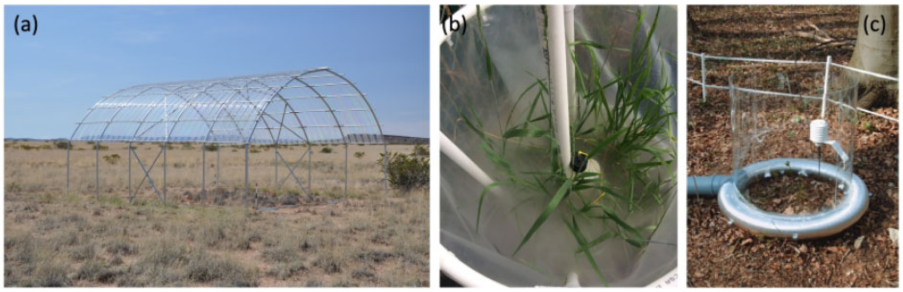

Figure 2. The vast majority of ecological drought experiments use rainout shelters to exclude some percent of rainfall and therefore manipulate meteorological drought (a). Image: Scott L. Collins, from the Extreme Drought in Grasslands Experiment in the Sevilleta National Wildlife Refuge in New Mexico, in the United States. Future experiments can pair precipitation manipulations with humidity manipulations (b–c). Panel (b) shows a humidity addition in an open-top chamber, with a fog layer visible in the cold early morning hours in Los Angeles, California, in the United States. Image: Alexandra Wright. Panel (c) shows a humidity reduction experiment using absorption air driers actively pumping dry air into chambers in Göttinger Wald beech forest, in Göttingen, Germany. Image: Cristoph Leuschner, Lendzion and Leuschner (2009).

The future: Atmospheric and soil drying experiments under field conditions

Importantly, experiments that compare atmospheric drying and soil drying for whole communities, under field conditions, are essential to validate and constrain the disparate results coming from modeling, observational, and growth chamber studies. However, outdoor experiments that manipulate relative humidity for entire plant communities are exceedingly rare: There has been a single experimental humidity reduction in a forest understory, one experimental humidity reduction in a peatland, a large experimental humidity enrichment in a canopy forest in Estonia, and a single experimental manipulation of humidity crossed with soil moisture in open-top chambers in California, in the United States (table 1). This work has started to elucidate how the combined manipulation of atmospheric moisture and soil moisture for whole communities will likely modify results from past drought experiments.

Aguirre and colleagues (2021) manipulated soil moisture in line with 50-year averages and compared with expected meteorological drought conditions. They simultaneously manipulated atmospheric humidity at two levels: ambient and humid (figure 2). The experiment was conducted in Southern California; therefore, the ambient conditions were in line with expected atmospheric drying in this region. Commercial humidifiers were used to increase humidity to approximately 11% above ambient (a decrease of 0.5 kilopascals [kPa] VPD). Aguirre and colleagues (2021) worked with native perennial grass species and demonstrated a loss of approximately 50% of annual net primary productivity, but only when dry soils were combined with dry air. Plant communities grown in dry soils and humidified air were as productive as communities grown in wet soils. Similarly, in a deciduous forest understory, European beech seedling biomass declined by 30% when relative humidity was reduced by 15%, even when soil moisture was not limiting (Lendzion and Leuschner 2008). Watson and colleagues (2023) demonstrated how energy allocation of a model grass species growing in these communities differed depending on whether the individuals were grown in dry soils (reflecting meteorological drought) or dry soils combined with dry air (reflecting ecological drought). Watson and colleagues (2023) found a strong shift in energy allocation during ecological drought: The model species shifted to more belowground growth, decreased leaf area, and smaller individuals than those individuals grown in meteorological drought conditions. All of this evidence points in the same direction: Soil moisture manipulations associated with rainout shelters alone may not accurately predict the future consequences of drought associated with climate change.

Researchers have also indirectly manipulated VPD under field conditions using experimental warming of the air. These experiments have the capacity to increase evaporative demand indirectly via warmer temperatures (Cowles et al. 2016). Mas and colleagues (2023) highlighted how increased VPD, driven by experimentally higher temperatures, can modify species interactions during hotter droughts. Unfortunately, this approach does not allow us to directly tease out soil moisture effects from atmospheric aridity effects, or to assess direct temperature effects versus indirect atmospheric aridity effects. For example, Schönbeck and colleagues (2022) describe how increased temperatures can lead to induced stomatal opening, presumably as a mechanism to evaporatively cool leaves and maintain temperature optima. This would be the exact opposite prediction for leaves growing in dry air (with a high VPD): Most leaves respond to increased VPD (and constant temperature) by closing stomates (Ocheltree et al. 2013). Future work to address these contradictory hypotheses will need to include direct manipulation of atmospheric aridity.

Moving forward, atmospheric drying experiments can be done in at least two ways outside of temperature manipulations. First, atmospheric aridity can be reduced via humidity additions (Kupper et al. 2011, Rosenvald et al. 2020, Aguirre et al. 2021, Lopez et al. 2021, Watson et al. 2023). This allows for comparisons between arid ambient conditions and humid experimental conditions (of the past or future). This approach is similar to drought studies that examine rainfall *additions* to compare with dry ambient soil conditions in drylands (e.g., Plaut et al. 2012). This approach has now been piloted in deciduous forests and perennial grasslands, indicating that there may be potential for broad applications. In fact, rainout shelters are often limited in terms of their use in large stature vegetation (e.g., forests). In some of these systems, large-scale misting systems may have more success (e.g., Kupper et al. 2011). Conversely, large scale humidification or misting systems also require a power source and this can limit their use in remote locations.

Second, atmospheric aridity can be increased using commercial dehumidification systems in open-top chambers (e.g., Lendzion and Leuschner 2008, Ibe et al. 2020) or by using passive silica desiccant (Aguirre et al. 2021, Varghese et al. 2023).

Silica desiccation packets can be suspended in open-top chambers and used to reduce humidity by up to 4% in humid environments (the equivalent to up to 0.5 kPa VPD, depending on ambient temperatures). High temperatures and high humidity could lead to increased silica packet moisture uptake in passive dehumidification systems, but the exact environmental conditions that allow for low-tech passive humidity reductions of this kind requires more research (Varghese et al. 2023). We should be considering this an opportunity for creative problem solving given the benefits that this work can provide.

Conclusions

Rainout shelters are an important tool in a toolbox intended to help us predict the future consequences of drought. Until we can calibrate drought experiments to align with results from observational drought data collected over time, rainout shelters may lack the predictive power needed to understand the multiple factors that change during drought. Designing experiments that are capable of simulating both soil moisture deficits and increased VPD will likely help us use data from rainout shelters to better calibrate Earth system models (Fisher et al. 2018) and therefore refine global climate models (e.g., Masson-Delmotte et al. 2021). These types of biosphere–atmosphere feedback loops have long been identified as one of the primary remaining areas of uncertainty in future climate projections. Although some dynamic global vegetation models consider humidity, evapotranspiration, soil moisture, and plant water balance (e.g., Xu et al. 2016), there are no models that calibrate on the basis of results from rainout shelter experiments. There is still massive uncertainty in terms of the strength of land–atmosphere feedback loops and how plants respond to soil moisture versus VPD. The next generation of rainout shelters should integrate manipulations of atmospheric drying to better resolve these issues and therefore have the capacity to further inform decision-making.

Finally, most drought mitigation strategies are focused on reducing water consumption or managing water supply infrastructure (UNDRR 2021). Using next generation rainout shelters to refine biosphere–atmosphere feedback loops may even have the capacity to reveal new nature-based solutions to drought mitigation. For example, although meteorological drought may drive decreased soil water availability and although this could be exacerbated by vegetation, atmospheric drought can be alleviated by vegetation, because the presence of plants with deep roots can move water from deep soil water reserves and humidify the air (Wright et al. 2021). Higher diversity plant communities may be more effective at this process than lower diversity plant communities (Wright et al. 2014). In a more general sense, humidity can be higher under the canopy of plants with higher evaporation rates (Bruner et al. 2023). Increased humidity can also cool the microclimate in the lower canopy layers, and this can reduce evaporative drying (Richter et al. 2022). Plant functional traits and community properties that increase the boundary layer thickness of the vegetation or that decrease turbulent air flow between the vegetative air mass and bulk atmospheric air can ensure that this humidity is kept in place (Meinzer 1993). This may also be an important component of guarding against soil drying. These types of insights are impossible without careful experimentation and isolation of belowground drought (soil moisture) and aboveground drought (VPD). For the future of drought research, it is essential that we refine our experimental methods for manipulating atmospheric drying and integrate them into experimental drought research.

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Author contributions

A. J. Wright (Conceptualization, Funding acquisition, Visualization, Writing – original draft, Writing – review & editing), and S. L. Collins (Funding acquisition, Supervision, Writing – original draft, Writing – review & editing)

References cited

Aguirre B, et al. 2021. The experimental manipulation of atmospheric drought: Teasing out the role of microclimate in biodiversity experiments. *Journal of Ecology* 109: 1986–1999.

Ault TR. 2020. On the essentials of drought in a changing climate. *Science* 368: 256–260.

Bradford JB, Schlaepfer DR, Lauenroth WK, Palmquist KA. 2020. Robust ecological drought projections for drylands in the 21st century. *Global Change Biology* 26: 3906–3919.

Breshears DD, et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences* 102: 15144–15148.

Bruner SG, Palmer MI, Griffin KL, Naeem S. 2023. Planting design influences green infrastructure performance: plant species identity and complementarity in rain gardens. *Ecological Applications* 33: e2902.

Carroll CJW, et al. 2021. Is a drought a drought in grasslands? Productivity responses to different types of drought. *Oecologia* 197: 1017–1026.

Ciais P, et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437: 529–533.

Clark JS, et al. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology* 22: 2329–2352.

Copeland SM, Harrison SP, Latimer AM, Damschen EI, Eskelinen AM, Fernandez-Going B, Spasojevic MJ, Anacker BL, Thorne JH. 2016. Ecological effects of extreme drought on Californian herbaceous plant communities. *Ecological Monographs* 86: 295–311.

Cowles JM, Wragg PD, Wright AJ, Powers JS, Tilman D. 2016. Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology* 22: 741–749.

Dannenberg MP, et al. 2022. Exceptional heat and atmospheric dryness amplified losses of primary production during the 2020 US Southwest hot drought. *Global Change Biology* 28: 4794–4806.

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL. 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. *Ecosystems* 3: 308–319.

Ficklin DL, Novick KA. 2017. Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere. *Journal of Geophysical Research Atmospheres* 122: 2061–2079.

Fisher RA, et al. 2018. Vegetation demographics in Earth system models: A review of progress and priorities. *Global Change Biology* 24: 35–54.

Fu Z, et al. 2022. Atmospheric dryness reduces photosynthesis along a large range of soil water deficits. *Nature Communications* 13: 989.

Grossiord C, et al. 2020. Plant responses to rising vapor pressure deficit. *New Phytologist* 226: 1550–1566.

He B, Liu J, Guo L, Wu X, Xie X, Zhang Y, Chen C, Zhong Z, Chen Z. 2018. Recovery of ecosystem carbon and energy fluxes from the 2003 drought in Europe and the 2012 drought in the United States. *Geophysical Research Letters* 45:4879–4888.

Hoover DL, Duniway MC, Belnap J. 2017. Testing the apparent resistance of three dominant plants to chronic drought on the Colorado Plateau. *Journal of Ecology* 105: 152–162. https://doi.org/10.1111/1365-2745.12647

Hoover DL, Rogers BM. 2016. Not all droughts are created equal: The impacts of interannual drought pattern and magnitude on grassland carbon cycling. *Global Change Biology* 22: 1809–1820.

Ibe K, Walmsley D, Fichtner A, Coners H, Leuschner C, Härdtle W. 2020. Provenance- and life-history stage-specific responses of the dwarf shrub *Calluna vulgaris* to elevated vapour pressure deficit. *Plant Ecology* 221: 1219–1232.

Jiao T, Williams CA, Kauwe MGD, Schwalm CR, Medlyn BE. 2021. Patterns of post-drought recovery are strongly influenced by drought duration, frequency, post-drought wetness, and bioclimatic setting. *Global Change Biology* 27: 4630–4643.

Knapp AK, Carroll CJW, Denton EM, Pierre KJL, Collins SL, Smith MD. 2015. Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* 177: 949–957.

Knapp AK, et al. 2020. Resolving the Dust Bowl paradox of grassland responses to extreme drought. *Proceedings of the National Academy of Sciences* 117: 22249–22255

Knapp AK, Condon KV, Folks CC, Sturchio MA, Griffin-Nolan RJ, Kannenberg SA, Gill AS, Hajek OL, Siggers JA, Smith MD. 2023. Field experiments have enhanced our understanding of drought impacts on terrestrial ecosystems: But where do we go from here? *Functional Ecology* https://doi.org/10.1111/1365-2435.14460

Konings AG, Williams AP, Gentine P. 2017. Sensitivity of grassland productivity to aridity controlled by stomatal and xylem regulation. *Nature Geoscience* 10: 284–288.

Korell L, Auge H, Chase JM, Harpole S, Knight TM. 2019. We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology* 26: 325–327.

Kröel-Dulay G, et al. 2022. Field experiments underestimate aboveground biomass response to drought. *Nature Ecology and Evolution* 6: 540–545.

Kupper P, et al. 2011. An experimental facility for free air humidity manipulation (FAHM) can alter water flux through deciduous tree canopy. *Environmental and Experimental Botany* 72: 432–438.

Lendzion J, Leuschner C. 2008. Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. *Forest Ecology and Management* 256: 648–655.

Lendzion J, Leuschner C. 2009. Temperate forest herbs are adapted to high air humidity evidence from climate chamber and humidity manipulation experiments in the field. *Canadian Journal of Forest Research* 39: 2332–2342.

Liu L, Gudmundsson L, Hauser M, Qin D, Li S, Seneviratne SI. 2020. Soil moisture dominates dryness stress on ecosystem production globally. *Nature Communications* 11: 4892.

López J, Way DA, Sadok W. 2021. Systemic effects of rising atmospheric vapor pressure deficit on plant physiology and productivity. *Global Change Biology* 27: 1704–1720.

Lu H, Qin Z, Lin S, Chen X, Chen B, He B, Wei J, Yuan W. 2022. Large influence of atmospheric vapor pressure deficit on ecosystem production efficiency. *Nature Communications* 13: 1653.

Madadgar S, AghaKouchak A, Farahmand A, Davis SJ. 2017. Probabilistic estimates of drought impacts on agricultural production. *Geophysical Research Letters* 44: 7799–7807.

Más E, Cochard H, Deluigi J, Didion-Gency M, Martin-StPaul N, Morcillo L, Valladares F, Vilagrosa A, Grossiord C. 2023. Interactions between beech and oak seedlings can modify the effects of hotter droughts on the onset of hydraulic failure. *New Phytologist* https://doi.org/10.1111/nph.19358

Masson-Delmotte V, et al. (eds). 2021. *Climate Change 2021: The Physical Science Basis*. Cambridge University Press.

McHugh TA, Morrissey EM, Reed SC, Hungate BA, Schwartz E. 2015. Water from air: An overlooked source of moisture in arid and semiarid regions. *Scientific Reports* 5: 13767.

Meinzer FC. 1993. Stomatal control of transpiration. *Trends in Ecology and Evolution* 8: 289–294.

Novick KA, et al. 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nature Climate Change* 6: 1023–1027.

Ocheltree TW, Nippert JB, Prasad PVV. 2013. Stomatal responses to changes in vapor pressure deficit reflect tissue-specific differences in hydraulic conductance. *Plant Cell and Environment* 37: 132–139.

Pangle RE, Hill JP, Plaut JA, Yepez EA, Elliot JR, Gehres N, McDowell NG, Pockman WT. 2012. Methodology and performance of a rainfall manipulation experiment in a piñon–juniper woodland. *Ecosphere* 3: 1–20.

Pennisi E. 2022. Global drought experiment reveals the toll on plant growth. *Science* 377: 909–910.

Plaut JA, et al. 2012. Hydraulic limits preceding mortality in a piñon–juniper woodland under experimental drought. *Plant, Cell, and Environment* 35: 1601–1617.

Potts DL, Suding KN, Winston GC, Rocha AV, Goulden ML. 2012. Ecological effects of experimental drought and prescribed fire in a southern California coastal grassland. *Journal of Arid Environments* 81: 59–66.

Richter R, Ballasus H, Engelmann RA, Zielhofer C, Sanaei A, Wirth C. 2022. Tree species matter for forest microclimate regulation during the drought year 2018: Disentangling environmental drivers and biotic drivers. *Scientific Reports* 12: 17559.

Rosenvald K, et al. 2020. Elevated atmospheric humidity prolongs active growth period and increases leaf nitrogen resorption efficiency of silver birch. *Oecologia* 193: 449–460.

Schönbeck LC, Schuler P, Lehmann MM, Mas E, Mekarni L, Pivovaroff AL, Turberg P, Grossiord C. 2022. Increasing temperature and vapor pressure deficit lead to hydraulic damages in the absence of soil drought. *Plant, Cell and Environment* 45: 3275–289.

Seddon AWR, Macias-Fauria M, Long PR, Benz D, Willis KJ. 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531: 229–232.

Slette IJ, Post AK, Awad M, Even T, Punzalan A, Williams S, Smith MD, Knapp AK. 2019. How ecologists define drought, and why we should do better. *Global Change Biology* 25: 3193–3200.

Slette IJ, Hoover DL, Smith MD, Knapp AK. 2023. Repeated extreme droughts decrease root production, but not the potential for post-drought recovery of root production, in a mesic grassland. *Oikos* 2023: e08899.

Smith MD. 2011. An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology* 99: 656–663.

Song J, et al. 2019. A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nature Ecology and Evolution* 3: 1309–1320.

Stampfli A, Bloor JMG, Fischer M, Zeiter M. 2018. High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. *Global Change Biology* 24: 2021–2034.

[UNDRR] United Nations Office for Disaster Risk Reduction. 2021. Global Assessment Report on Disaster Risk Reduction 2021. UNDRR.

Varghese S, Aguirre BA, Isbell F, Wright AJ. 2023. Simulating atmospheric drought: Silica gel packets dehumidify mesocosm microclimates. bioRxiv Preprint. https://doi.org/10.1101/2023.10.06.561294.

Wang J, Wen X. 2022. Increasing relative abundance of C4 plants mitigates a dryness-stress effect on gross primary productivity along an aridity gradient in grassland ecosystems. *Plant and Soil* 479: 371–387.

Watson SJ, Aguirre BA, Wright AJ. 2023. Soil versus atmospheric drought: A test case of plant functional trait responses. *Ecology* 104: e4109. 10.1002/ecy.4109.

Wilhite DA, Svoboda MD, Hayes MJ. 2007. Understanding the complex impacts of drought: A key to enhancing drought mitigation and preparedness. *Water Resources Management* 21: 763–774.

Wright A, Schnitzer SA, Reich PB. 2014. Living close to your neighbors: The importance of both competition and facilitation in plant communities. *Ecology* 95: 2213–2223.

Wright AJ, Barry KE, Lortie CJ, Callaway RM. 2021. Biodiversity and ecosystem functioning: Have our experiments and indices been underestimating the role of facilitation? *Journal of Ecology* 109: 1962–1968.

Xu X, Medvigy D, Powers JS, Becknell JM, Guan K. 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* 212: 80–95.

Yahdjian L, Sala OE. 2002. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* 133: 95–101.

Yahdjian L, Sala OE, Piñeiro-Guerra JM, Knapp AK, Collins SL, Phillips RP, Smith MD. 2021. Why coordinated distributed experiments should go global. *BioScience* 71: 918–927.

Yuan W, et al. 2019. Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Science Advances* 5: eaax1396.

Zeng Z, Wu W, Peñuelas J, Li Y, Zhou Y, Li Z, Ren X, Huang H, Ge Q. 2023. Anthropogenic forcing decreased concurrent soil drought and atmospheric aridity in the historical period 1850–2013. *Earth's Future* 11: e2022EF003349.

Zhong Z, et al. 2023. Disentangling the effects of vapor pressure deficit on northern terrestrial vegetation productivity. *Science Advances* 9: eadf3166.

Zhou S, et al. 2019. Land–atmosphere feedbacks exacerbate concurrent soil drought and atmospheric aridity. *Proceedings of the National Academy of Sciences* 116: 18848–18853.

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