Commentary

Plant–plant interactions can mitigate (or exacerbate) hot drought impacts

Climate change will increase global surface temperatures by at least another 1.5°C in the next 50 years (IPCC, 2021). This increase in temperature is already accelerating the water cycle and shifting precipitation regimes globally, with some places receiving less precipitation while others are receiving more (IPCC, 2021). Increased global temperatures are also increasing the drying capacity of the atmosphere, measured as vapor pressure deficit (VPD; Yuan *et al.*, 2019). Elevated VPD increases the rate of water loss from soils and plants, thus exacerbating the already negative effects of reduced precipitation. Hotter droughts with elevated VPD can double productivity losses (over just precipitation reductions; Dannenberg *et al.*, 2022) and increase the risk and volatility of fires (Abatzoglou & Williams, 2016). Given the damages already seen during hotter droughts with higher VPD, it is essential that we identify how individual species and ecosystems will respond to hotter droughts in the future. In an article published in this issue of *New Phytologist*, Mas *et al.* (2024; 1021–1034) deepen our understanding of how species interactions might mitigate future hot drought effects. Mas *et al.* demonstrate how hot drought effects can be mitigated by interspecific neighbors for *Quercus pubescens* but exacerbated by interspecific neighbors for *Fagus sylvatica*. This work builds upon 30 years of biodiversity research demonstrating that higher diversity ecosystems may be better able to tolerate environmental change. This work also offers an opportunity to explore habitat-specific mechanisms that could drive how different types of ecosystems will respond to drought in the future.

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During drought, plants face multiple physiological challenges. In particular, plants must maintain water status in order to avoid dehydration and death (McDowell *et al.*, 2022). One of the most important and fast-acting mechanisms, employed during either soil water limitation or atmospheric drying, is stomatal closure (Ocheltree *et al.*, 2013). During hotter droughts, plants face contradictory stressors: while most plants close their stomata in response to drying soil conditions, some plants open their stomata to cool their leaves during hotter atmospheric conditions (Schönbeck *et al.*, 2022). Plants also vary in their stomatal sensitivity to drought and heat (Fontes *et al.*, 2018). Understanding how individual plants and whole ecosystems respond to the interaction of low soil moisture, higher temperatures, and elevated VPD is an important next step in predicting the future consequences of climate change. Mas *et al.* show that for two species with differing stomatal sensitivity to drought and temperature, prolonged hot drought (over just soil moisture limitation) leads to decreased stomatal conductance, and thinner leaf production, with a smaller evaporative surface. The authors also explore how neighbor identity, and thus community diversity, can mitigate or exacerbate these effects.

Mitigating the negative consequences of hotter droughts is a major land management priority. There is precedent in the ecological literature for focusing on plant community diversity as a management strategy during hotter and drier conditions. The vast majority of this work has focused on two possible mechanisms to understand the relationship between community biodiversity and drought. First, so-called insurance effects can occur when higher diversity communities contain species that are able to resist a given disturbance; these species can compensate for losses experienced by disturbance-sensitive species (Kreyling *et al.*, 2017; Wright *et al.*, 2021). Past work in grasslands has demonstrated that recovery of primary production increases in higher diversity communities with greater asynchrony or compensatory dynamics (Kreyling *et al.*, 2017). In forests, past work has shown how variance in hydraulic traits can moderate whole forest responses to drought (Anderegg *et al.*, 2018). In other words, forests with a greater diversity of drought strategies may include some species that maintain transpiration and photosynthesis during drought, and these species could compensate for growth and survival losses experienced by other species.

There is also precedent for a second mechanism regulating the relationship between community biodiversity and drought: higher diversity communities can cool, humidify, and reduce the VPD of the microclimate (Wright *et al.*, 2014, 2015, 2021). Past work has shown that the microclimate of higher diversity herbaceous communities can feedback and alleviate water constraints for woody seedlings (Wright *et al.*, 2014, 2015). These effects are likely also driven by some species, or combinations of species, that can maintain stomatal conductance and transpiration during drought, leading to increased evapotranspiration and humidity in the microclimate (Wright *et al.*, 2021). As plants lose water, evaporative cooling also reduces temperatures. In reality, it is likely

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a combination of insurance effects and microclimate modification in higher diversity plant communities that make diversity a potentially powerful tool in fighting the negative impacts of hotter and drier macroclimate conditions (Fig. 1).

Comparing diversity-drought responses in grasslands and forests also offers us an opportunity to think about whether different diversity mechanisms might prevail in different types of ecosystems. While this area of research is mostly unexplored, there are some hints from flux tower networks. Forest leaves tend to have a lower albedo than herbaceous species (Jackson *et al*., 2008). Forests have thicker and rougher boundary layers than grasslands and this can increase convection and sensible heat flux between the microclimate (under vegetation) and the macroclimate (Muller *et al*., 2021). Some past work has shown that grasslands can respond to heat waves with greater latent heat flux than forests due to maintenance of high stomatal conductance and higher rates of evapotranspiration, at least as long as soil moisture is not limiting (Teuling *et al*., 2010). Heat exchange between the microclimate and the macroclimate (due to either latent or sensible heat flux) could have important implications for the species growing in these systems. It is thus possible that the mechanisms underlying diversity-drought

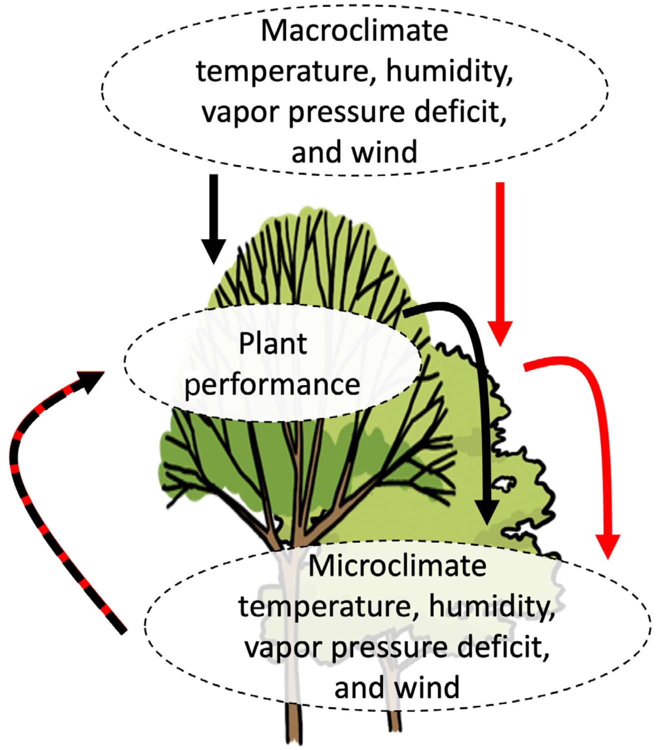

Fig. 1 Macroclimate drought conditions will affect each species in a forest differently (represented by the black line leading straight down to one tree species and the red line leading straight down to a second tree species). These species will respond directly to drying or heating pressures. However, these species will also affect the microclimate in unique ways (red and black feedback arrows pointing to microclimate conditions). Due to the additive or emergent effects of these two species on the microclimate, plant performance will also respond indirectly to drought and heating through these feedbacks.

relationships (insurance effects vs microclimate amelioration) shift and operate differently depending on the physical and biological properties of the plant community.

Mas *et al.* deepen our understanding of the physiological mechanisms underlying plant diversity effects during drought. By growing tree species in interspecific and intraspecific mixtures, and measuring detailed stem and leaf physiology, these authors show how community interactions modulate individual plant responses to hotter droughts. Specifically, *Q. pubescens* was able to maintain stomatal conductance for longer periods during hot droughts, particularly when it was grown in two-species mixtures. *Quercus pubescens* may have reduced stomatal sensitivity to soil moisture or atmospheric drought. In this way, *Q. pubescens* could act as 'insurance' against losses experienced by the other species (e.g. Anderegg *et al*., 2018). Conversely, the two-species mixtures could potentially mitigate the microclimate: increasing humidity or decreasing microclimate VPD. In this scenario, the oak species could be responding positively to the microclimate of its neighbors, though this was not measured in the present study. Conversely, *F. sylvatica* did not experience this same change in stomatal conductance, and in fact experienced more negative midday leaf water potential when growing in the two-species mixtures. The authors point to this as an indication of increased soil moisture impacts experienced by the beech species compared with the oak. While this study focuses on two species, this is a test case for how species interactions modulate drought responses in a broader sense.

These results are a valuable next step in hot drought research. While the specific community mechanisms underlying interactions between diversity and drought are still unresolved, this study helps move us forward. As stated by Mas *et al*., microclimate measurements, feedbacks on constituent species, and inclusion of microclimate facilitation in process models (or Earth Systems Models), is still understudied in drought research. While some species may respond strongly to competition for soil water, others could benefit from lower microclimate VPD near interspecific neighbors (Wright *et al*., 2014). Inclusion of the species with greater cuticular conductance or the maintenance of greater stomatal conductance may have humidified and/or cooled the microclimate (Wright *et al*., 2021). The study by Mas *et al.* was conducted in shallow soils, and soil depth likely also interacts strongly with microclimate modifications. Understanding the feedbacks between macroclimate, diversity, and microclimate will help inform models and specific management decisions in a hotter and drier world (Fig. 1). While vegetative feedbacks likely cannot mitigate the most negative consequences of long-term warming and drying (IPCC, 2021), studies like this help pave the way for understanding how to best manage these ecosystems in the future.

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ORCID

Alexandra J. Wright https://orcid.org/0000-0002-5205-8576

Alexandra J. Wright

Department of Biological Sciences, California State University, 5151 State University Dr., Los Angeles, CA 90032, USA
(email: awrigh20@calstatela.edu)

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