



Commentary

The bigger they are, the harder they fall: CO₂ concentration and tree size affect drought tolerance

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A major concern in recent years has been the widespread tree mortality seen in many parts of the world associated with droughts and heat waves (Hartmann 2011). Although rising temperatures and shifting precipitation regimes are expected to cause more of these mortality events, the associated rise in atmospheric CO₂ concentrations could improve tree water use efficiency, thus mitigating the effect of heat and drought on trees. In this issue, Warren et al. (2011) report the opposite—elevated CO₂ concentrations promoted greater senescence in temperate trees (*Liquidambar styraciflua*, sweetgum) experiencing a severe summer drought when compared with ambient CO₂ conditions. Stands exposed to elevated CO₂ had greater root standing biomass and lower stomatal conductance (g_s) than ambient stands, which should increase water uptake ability and soil moisture, respectively, thereby improving drought tolerance. However, trees in high-CO₂ plots were hit harder by the drought: they shed more foliage and had lower modeled net photosynthetic rates during the drought than trees from ambient CO₂. The paper synthesizes a wide range of data across a number of scales, including leaf-level gas exchange, branch hydraulics, stem sap flow, fine root dynamics and stand-level biomass estimates, to provide a multi-faceted picture of how carbon and water fluxes were affected by this climatic event. The results also concur with another recent report, where *Populus deltoides* grown at elevated CO₂ for 3 years were more susceptible to water stress, and shed more total leaf area during a drought, than trees from ambient CO₂ (Bobich et al. 2010).

Could rising CO₂ actually increase the susceptibility of forests to droughts? A reduction in g_s at elevated CO₂ is a common response across many species, with an average decrease of 22% (Ainsworth and Rogers 2007), leading to the expectation that plants will use less water in a high-CO₂ world and be less

susceptible to drought. On a larger scale, this direct stomatal effect has been incorporated into global models—for example, to predict increased water run-off at the continental scale (Betts et al. 2007). However, this leaf-level effect can disappear at the canopy level if leaf area increases at high CO₂ (Field et al. 1995). At the Oak Ridge Free Air CO₂ Enrichment (FACE) site, where Warren et al. (2011) worked, elevated CO₂ led to a 22–24% decrease in leaf-level g_s over the growing season, which scaled to a more modest 14% decrease in canopy conductance (g_c) over the same period (Wullschleger et al. 2002). Across FACE experiments, leaf area index is usually greater in high-CO₂ plots than in ambient plots, a shift that can offset leaf-level g_s -based water savings or even increase water use at the stand and global scales (Kergoat et al. 2002, Bobich et al. 2010, Warren et al. in press).

As Warren et al. (2011) point out, lower g_s also reduces the capacity of leaves to dissipate heat through latent heat loss (i.e., evaporative cooling). While canopy temperatures were not directly measured by Warren et al. (2011), modeled leaf temperature differences between CO₂ treatments showed that elevated CO₂ should have increased leaf temperatures by 1–2 °C over ambient CO₂ leaves. Warmer leaves have been found in other CO₂ enrichment experiments, with canopy temperatures up to 2 °C warmer on days with bright sunshine (Kimball and Bernacchi 2006, Bernacchi et al. 2007). This rise in leaf temperature can directly increase the leaf-to-air vapor pressure deficit, thus increasing transpiration rates and offsetting the effect of lower g_s on transpiration. Indirectly, lower g_s at elevated CO₂ can decrease the humidity within the canopy, again increasing the vapor pressure deficit and transpiration rates (Wullschleger et al. 2002).

While increases in leaf temperature can affect plant water loss, they also impact carbon fluxes. Plants across a diversity

of environments regulate leaf temperature within a range that is conducive for photosynthesis (Helliker and Richter 2008). While a 1–2 °C warming may stimulate photosynthesis at low air temperatures, a high-CO₂ environment is more likely to coincide with increases in the frequency of heat waves and droughts than of suboptimal temperatures. During heat events, such as the one documented in Warren et al. (2011), warming of leaves above the photosynthetic thermal optimum will reduce carbon gain, while short-term temperature increases will also stimulate respiration, both reducing tree carbon balance. Rising CO₂ is often thought to mitigate heat-induced carbon balance decline, since elevated CO₂ stimulates photosynthetic rates and increases the thermal optimum for photosynthesis (Sage and Kubien 2007). However, in the system studied by Warren et al. (2011), nitrogen limitations have caused acclimation of photosynthesis to high CO₂. When measured at treatment CO₂ and optimum leaf temperatures, there was only a 6% enhancement of photosynthesis in elevated CO₂ leaves compared with ambient CO₂ leaves and net photosynthetic rates in both CO₂ treatments had similar temperature responses, especially at high leaf temperatures (Warren et al. 2011). With similar photosynthetic rates in ambient and elevated CO₂ sites, the 1–2 °C leaf warming modeled for high-CO₂ conditions should have reduced carbon gain in elevated CO₂ stands during heat events, while the cooler ambient stands would be less affected. Warren et al. (2011) postulate that a decline in carbon balance in elevated CO₂ stands during the heat and drought event led to greater leaf abscission and fine root mortality in high-CO₂ sites than in ambient CO₂ stands.

So should we expect rising CO₂ to mitigate or exacerbate heat and drought stress in forests? Part of the answer may lie in differences between stand characteristics. In Warren et al. (2011), large trees in both CO₂ treatments had bigger drops in g_c than small trees in response to drought, so the CO₂ effect of suppressing g_s was greatest in big trees. If this decrease in g_s , with associated increased leaf temperatures and reduced carbon balance, underlies the results in Warren et al. (2011), high CO₂ may exacerbate heat and drought stress more in older forests with larger individuals. Responses between species will also be important: while sap flow, and measures of g_c , declined in sweetgum exposed to elevated CO₂ relative to ambient CO₂ at the Duke FACE site, *Pinus taeda* (loblolly pine) showed an increase in sap flow (Schäfer et al. 2002). Similarly, water stress led to reductions in a standardized measure of g_s at the canopy level in sweetgum and *Ulmus alata* (winged elm), but not loblolly pine or *Cornus florida* (flowering dogwood), in high-CO₂ plots relative to ambient CO₂ conditions (Domec et al. 2010). The reasons underpinning these differences in drought response across species are not yet understood, but would prove informative for making predictions about future forest responses. Lastly, decreased carbon balance under severe droughts may be more prevalent in stands where nitrogen limi-

tations prevent photosynthetic stimulation by high CO₂. However, since nitrogen limitations are common in forest ecosystems, size class and species differences may be more important factors in governing tree responses to drought under rising CO₂ than nutrient availability.

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