

Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought

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Large-scale biogeographical shifts in vegetation are predicted in response to the altered precipitation and temperature regimes associated with global climate change. Vegetation shifts have profound ecological impacts and are an important climate-ecosystem feedback through their alteration of carbon, water, and energy exchanges of the land surface. Of particular concern is the potential for warmer temperatures to compound the effects of increasingly severe droughts by triggering widespread vegetation shifts via woody plant mortality. The sensitivity of tree mortality to temperature is dependent on which of 2 non-mutually-exclusive mechanisms predominates—temperature-sensitive carbon starvation in response to a period of protracted water stress or temperature-insensitive sudden hydraulic failure under extreme water stress (cavitation). Here we show that experimentally induced warmer temperatures ($\approx 4^\circ\text{C}$) shortened the time to drought-induced mortality in *Pinus edulis* (piñon shortened pine) trees by nearly a third, with temperature-dependent differences in cumulative respiration costs implicating carbon starvation as the primary mechanism of mortality. Extrapolating this temperature effect to the historic frequency of water deficit in the southwestern United States predicts a 5-fold increase in the frequency of regional-scale tree die-off events for this species due to temperature alone. Projected increases in drought frequency due to changes in precipitation and increases in stress from biotic agents (e.g., bark beetles) would further exacerbate mortality. Our results demonstrate the mechanism by which warmer temperatures have exacerbated recent regional die-off events and background mortality rates. Because of pervasive projected increases in temperature, our results portend widespread increases in the extent and frequency of vegetation die-off.

biosphere–atmosphere feedbacks | drought impacts | global-change ecology | *Pinus edulis* | carbon starvation

Global change assessments and supporting research have largely focused on how vegetation will respond to incremental changes in the central tendency of climate variables, but the most dramatic vegetation shifts are likely to result from changes in climate extremes altering patterns of disturbance events arising from hurricanes, freezes, fires, and droughts (1, 2). The effects of drought on vegetation under warmer conditions can be severe, as highlighted by recent regional-scale woody-plant die-off across the southwestern United States (3–6) and around the globe (7–10). Worldwide, many coniferous tree species are experiencing widespread, historically unprecedented mortality, mainly as a result of drought and the eruption of tree pests, such as bark beetles (1, 3, 7–9, 11–16). Consequent impacts of regional tree die-off could include reduction in habitat for wildlife, enhanced opportunities for invasion by exotic species, formation of novel communities, alterations to the hydrologic

cycle, and temporal disruptions in ecosystem goods and services (2, 3, 17, 18). In addition, extensive tree die-off could impact regional carbon (C) budgets, reducing ecosystem potential to sequester C and increasing C losses through enhanced soil respiration rates (19–22). Drought-induced tree mortality not only alters C fluxes but also modifies water and energy fluxes between the atmosphere and land surface (3, 20, 23, 24). The consequences of potentially large releases of C from the biosphere to the atmosphere due to widespread mortality could contribute to further warming (19–21, 25). Small drought-induced increases solely in background mortality rates may even be sufficient to alter regional C budgets (13, 16, 26).

Drought-induced tree mortality is a pivotal vulnerability of vegetation to climate change, yet our understanding of, and ability to predict, tree mortality is astonishingly poor. Drought-induced tree mortality is difficult to predict because it is a nonlinear threshold process (1, 19, 27). Recent observational studies have raised concern that warmer temperatures could be amplifying the effects of drought on tree mortality both for background rates of mortality and for regional die-off events (3, 16). Yet experimental assessment of whether warmer temperatures associated with drought exacerbate tree mortality is lacking for any tree species, and therefore tree mortality has only been predicted in response to a simple metric of accumulated dry conditions (28, 29). The sensitivity of tree mortality to temperature is dependent on which of 2 non-mutually-exclusive mechanisms predominates: (i) carbon starvation, whereby trees close stomata to keep safe levels of xylem pressure, stopping most photosynthesis, and rely on stored carbohydrates to support the metabolic costs of maintaining tissue; or (ii) catastrophic hydraulic failure, whereby trees maintain stomatal conductance during drought to continue photosynthesizing, but run the risk of xylem pressures suddenly exceeding cavitation thresholds beyond which air bubbles block transport of stem water (30–32). Both hypotheses are interrelated with biotic agents, such as bark beetles and associated fungi, and carbon starvation would preclude production of the photosynthate necessary for tree defense, thereby increasing susceptibility to biotic agents (9, 33). Because respiration rates increase with temperature (34), carbon

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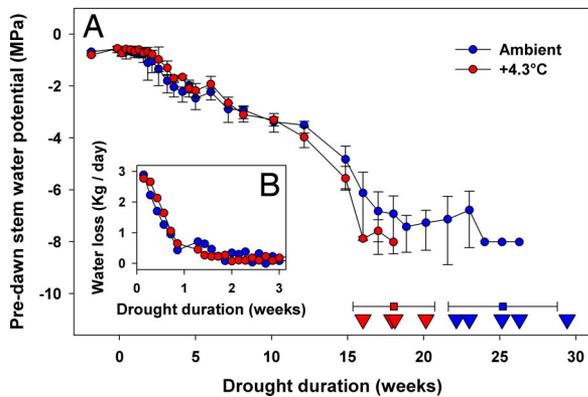


Fig. 1. Water relations progression and death dates. (A) Predawn stem water potential (circles), death dates (triangles), and death date means (squares) of piñon pines during simulated drought under ambient (blue) and elevated (red) temperatures. Error bars are standard errors. (B) Water loss from a subset of trees in A.

starvation should be highly sensitive to temperature, whereas hydraulic failure should not.

We experimentally investigated the temperature sensitivity of drought-induced mortality in *Pinus edulis*, a piñon pine tree that has exhibited regional-scale die-off in response to recent drought (3, 4) and which has been evaluated in observational and modeling studies (30, 31, 35). We transplanted small, reproductively mature piñon pines into the environmentally controlled Biosphere 2 facility to grow them in either near-ambient or warmer (+4.3 °C) temperatures, and then imposed a drought treatment that completely excluded water from selected trees until all “drought” trees in both temperature treatments died.

Results and Discussion

All drought trees in the warmer treatment died before any of the drought trees in the ambient treatment (on average 18.0 vs. 25.1 weeks, $P < 0.01$; Fig. 1A). This 28% shortening in time to mortality was not reflected in a water balance difference (Fig. 1B). Indeed, predawn stem water potential measurements documented no differences in xylem pressure between drought treatments at any time during the experiment ($P = 0.88$, Fig. 1). Because water potential is highly correlated with the level of air embolism occluding water transport in the xylem (30, 32, 36), we saw no evidence of catastrophic loss of hydraulic transport as a primary driver of differences between treatments. Catastrophic loss in this species has been consistently observed at a stem water potential of -6 MPa (36). Therefore, we suggest that higher respiratory loads associated with warmer temperatures incited differences in mortality, reflecting carbon starvation, not sudden hydraulic failure as the causal mechanism required to predict tree mortality differences in a future warmer world. Such results are consistent with inferences from recent observational and modeling assessments (30, 31, 35).

During the experiment, we also measured leaf-level exchange of CO_2 before dawn to estimate respiratory load and during the middle of the day to follow photosynthetic patterns. After the start of drought treatment, photosynthesis declined rapidly and similarly in both temperature treatments, approaching zero by the third week of the experiment in drought trees (Fig. 2A). Initially, instantaneous rates of respiration were similar among drought trees in both temperature treatments, but they diverged during the third and fourth weeks of drought (Fig. 2B). An analysis of time-integrated respiration revealed that trees in the elevated-temperature drought treatment consumed C reserves faster than trees in the ambient drought treatment (Fig. 2C), reflecting the increased C cost for maintenance of tissue under

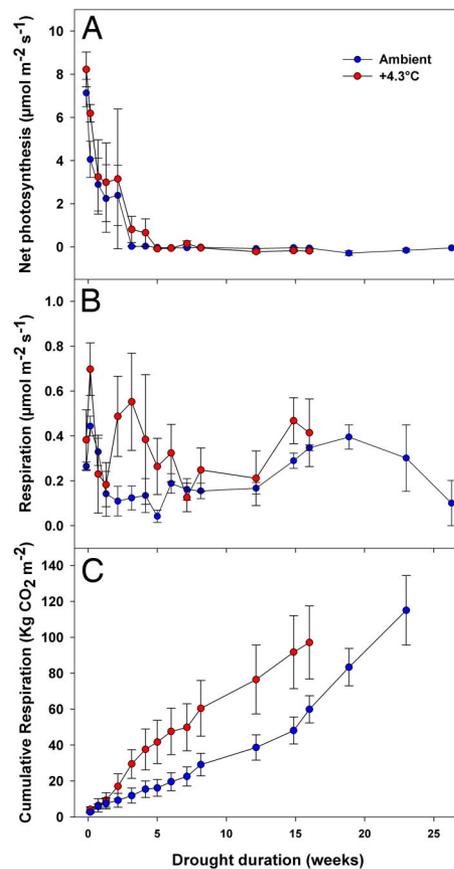


Fig. 2. Leaf carbon exchange progression. (A and B) Instantaneous midday net photosynthesis (A) and predawn respiration (B) of piñon pines during simulated drought under ambient (blue) and elevated (red) temperatures. Error bars are standard errors. (C) Cumulative time-integrated respiration costs of piñon pines during simulated drought under ambient (blue) and elevated (red) temperatures. Error bars are standard errors calculated by following standard methods for summation.

warmer temperatures (34). Mean time-integrated cumulative respiration just before mortality for drought trees did not differ significantly between temperature treatments ($P = 0.57$). Combined, our results provide experimental evidence that piñon pines attempted to avoid drought-induced mortality by regulating stomata and foregoing further photosynthesis but subsequently succumbed to drought due to carbon starvation, not sudden hydraulic failure. Importantly, we isolate the effect of temperature from other climate variables and biotic agents and show that the effect of warmer temperature in conjunction with drought can be substantial.

Our results imply that future warmer temperatures will not only increase background rates of tree mortality (13, 16), but also result in more frequent widespread vegetation die-off events (3, 35) through an exacerbation of metabolic stress associated with drought. With warmer temperatures, droughts of shorter duration—which occur more frequently—would be sufficient to cause widespread die-off. In our calculation of a 103-year record of regional drought duration for piñon, widespread mortality occurred only once, during a 6-month (26.1-week) drought in 2002 (Fig. 3A). By fitting a curve to the frequency distribution of regional drought duration, we estimated that our observed 28% acceleration in mortality with warmer temperatures indicated that a shorter, ≈ 4 -month (18.7-week) drought would cause widespread mortality. Therefore we estimated that a 4.3 °C increase in temperature corresponded to a 5-fold increase in the

