LETTER

Poor methodology for predicting large-scale tree die-off

In a recent issue of PNAS, Adams et al. (1) project a 5-fold increase in the frequency of tree die-off in piñon (*Pinus edulis*) under drought in the southwestern United States due to elevated temperature alone. Their study is based on 10 excavated individuals grown in containers and exposed to complete drought under either ambient or elevated temperature (+4.3 °C, 5 replicates). Trees experiencing higher temperatures died 7 weeks earlier than control trees. The authors explain this by a trend to increased respiration under warmer conditions resulting in earlier carbon starvation. In addition to the recent letter by Sala (2) pointing out that there is no direct evidence for carbon starvation as a cause of tree death to date, we are concerned with (*i*) the methods used to arrive at Adams et al.'s (1) interpretation and (*ii*) the way tree die-off is extrapolated to large spatio-temporal scales from their small sample size.

The authors' interpretation of carbon starvation hinges on a short period (weeks 3 and 4) of the experiment, when leaf respiration rates "diverged" between the treatments, though no statistical test is provided. In any case, this divergence does not constitute evidence for carbon starvation because enhanced leaf respiration is no proof of carbon reserve exhaustion at tree level; such evidence could only rest on measures of mobile carbon reserves (nonstructural carbohydrates). Drought might actually enhance carbon reserves, driven by continuing though low rates of photosynthesis at otherwise blocked meristematic (sink) activity (3).

In an attempt at looking at temperature alone, relative air humidity was kept constant in both treatments. However, higher temperature alone increases evaporative demand and thus water loss at any given relative air humidity, making desiccation more likely for purely physical reasons. Also, the definition of death at 90% needle browning is problematic, given that −6 MPa suffices to interrupt hydraulic conductivity in piñon (4). This value was reached for both treatments at the same time (around week 15). Because needle browning is not the cause but a symptom of the death process, mortality may have occurred at any point after week 15, such that needle browning, which is temperature-dependent, may have masked the true time of death.

The upscaling of results based on the response of only five small trees, which do not represent the size and age distribution of any actual tree population, implies overly high confidence in the results. The transplantation of naturally grown trees into 100-L containers (pot depth, 50 cm) must have resulted in severe damage to their root system. *P. edulis* may root 6 m (5), with deep roots ensuring survival during drought under natural conditions (6). We therefore suggest that the future drought-induced mortality rate is strongly overestimated.

In conclusion, we do not perceive sufficient evidence for the claim of carbon starvation as a significant cause of tree death for *P. edulis* in a warmer world. An upscaling to ecosystem level without accounting for rooting depth in situ and true tree-size distribution is not warranted.

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1. Adams HD, et al. (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global change-type drought. *Proc Natl Acad Sci USA* 106:7063–7066.
2. Sala A (2009) Lack of direct evidence for the carbon starvation hypothesis to explain drought-induced mortality in trees. *Proc Natl Acad Sci USA* 106:E68.
3. Körner C (2003) Carbon limitation in trees. *J Ecol* 91:4–17.
4. Linton MJ, Sperry JS, Williams, DG (1998) Limits to water transport in Juniperus osteosperma and *Pinus edulis*: Implications for drought tolerance and regulation of transpiration. *Funct Ecol* 12:906–911.
5. Foxx TS, Tierney GD (1987) Rooting patterns in the pinyon-juniper woodland. *Proceedings Pinyon-Juniper Conference, USDA Forest Service, General Technical Report INT-215*, Richard L. Everett, ed. (Intermountain Forest and Range Experiment Station, Ogden, UT).
6. West AG, Hultine KR, Burtch KG, Ehleringer JR (2007) Seasonal variations in moisture use in a piñon-juniper woodland. *Oecologia* 153:787–798.

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