Reply to Sala: Temperature sensitivity in drought-induced tree mortality hastens the need to further resolve a physiological model of death

Our recent study (1) of piñon pine (*Pinus edulis*) response to change in climate, on which Sala (2) comments, documented that drought-induced mortality was temperature-sensitive. In addition, we showed that time to tree mortality was predicted by leaf-level cumulative respiration for ambient and warmer treatments. Notably, our study experimentally assessed temperature sensitivity of drought mortality by tracking individual physiological responses throughout the death process. Ambient and warmer treatments did not differ in water balance in such a manner as to drive differences in mortality, yet higher respiration rates under warmer temperatures were associated with earlier death of individual trees. Two related studies provide additional support implicating carbon starvation via respiration during protracted water stress. First, modeling of physiological responses indicated that even short droughts drove leaf water potential of piñon pine—a drought-avoiding, isohydric species—quickly below its zero-carbon assimilation point (3). Second, long-term observational measurements of predawn water potential of piñon pine documented that trees could survive shorter but not longer periods of water stress below their zero-carbon assimilation point (4).

To further refine our understanding of variation in mortality responses among systems and species, more detailed, specific physiological insights are now needed, as Sala suggests (2). For piñon pine, a species that cannot resprout foliage after its loss, carbon metabolism at the leaves—the location of growth and tissue maintenance—is associated with mortality (1). Starvation could occur through a reduction in local pools and/or a breakdown in the tree's ability to translocate resources from distant pools to the site of metabolism, as Sala notes (2). Resolving tensions and dynamics between these carbon pools is indeed key to refining our understanding of how mortality occurs (2). If carbon translocation limitation is an important part of this process, then resources stored prior to drought would have a reduced influence on survival if they were inaccessible. Carbon starvation and hydraulic failure certainly are interrelated (3), as noted previously (1). When the trees died in our experiment, water potentials indicated complete xylem embolism had occurred, which would interfere with phloem function following the pressure-flow model (5), but low water potentials alone did not predict time to mortality. Although no study has yet shown depletion of tree carbon resources prior to drought-induced death, some studies do indeed indicate that carbon resources can decrease during drought stress. For example, reductions in nonstructural carbohydrates are evident with seasonal drought in the leaves of 3 Mediterranean sclerophyllous shrubs (6) and during severe drought in the roots of *Pinus palustris* (7). Independent of this point, our results indicate that the physiological component of drought-induced tree mortality that is highly sensitive to temperature is associated with respiration. Such a finding provides a mechanistic foundation for predicting patterns of mortality in the future. All else remaining equal, warming temperatures will sharply increase the frequency of regional tree die-off under warmer climate. Development of an improved physiological model of how trees die from drought and warmer temperature is now a common challenge for the research community.

Henry D. Adams[a,b,1]***, Maite Guardiola-Claramonte***[a,c]***, Greg A. Barron-Gafford***[a,b]***, Juan Camilo Villegas***[a,d,e]***, David D. Breshears***[a,b,d,f]***, Chris B. Zou***[g]***, Peter A. Troch***[a,c]***, and Travis E. Huxman***[a,b,f]
[a]*B2 EarthScience/Biosphere 2, P.O. Box 210158-B, University of Arizona, Tucson, AZ 85721;* [b]*Ecology and Evolutionary Biology, P.O. Box 210088, University of Arizona, Tucson, AZ 85721;* [c]*Hydrology and Water Resources, 1133 East James E. Rogers Way, University of Arizona, Tucson, AZ 85721;* [d]*School of Natural Resources, University of Arizona, Tucson, AZ 85721;* [e]*Facultad de Ingeniería, Calle 67 Nro. 53 108, Universidad de Antioquia, Medellín, Colombia 050010;* [f]*Institute for the Environment, 715 North Park Avenue, University of Arizona, Tucson, AZ 85721; and* [g]*Natural Resource Ecology and Management, 008C Ag Hall, Oklahoma State University, Stillwater, OK 74078*

1. Adams HD, et al. (2009) Temperature sensitivity of drought-induced tree mortality: Implications for 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* 10.1073/pnas.0904580106.
3. McDowell N, et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:719–739.
4. Breshears DD, et al. (2009) Tree die-off in response to global change-type drought: Mortality insights from a decade of plant water potential measurements. *Front Ecol Environ* 7:185–189.
5. Cernusak LA, Arthur DJ, Pate JS, Farquhar GD (2003) Water relations link carbon and oxygen isotope discrimination to phloem sap sugar concentration in *Eucalyptus globulus*. *Plant Physiol* 131:1544–1554.
6. Korner C (2003) Carbon limitation in trees. *J Ecol* 91:4–17.
7. Sayer MAS, Haywood JD (2006) Fine root production and carbohydrate concentrations of mature longleaf pine (*Pinus palustris* P. Mill.) as affected by season of prescribed fire and drought. *Trees-Struct Funct* 20:165–175.

Author contributions: H.D.A., M.G.-C., G.B.-G., J.C.V., D.D.B., C.B.Z., P.A.T., and T.E.H. designed research; H.D.A., M.G.-C., G.B.-G., J.C.V., D.D.B., and C.B.Z. performed research; H.D.A., M.G.-C., G.B.-G., J.C.V., and T.E.H. analyzed data; and H.D.A., M.G.-C., G.B.-G., J.C.V., D.D.B., C.B.Z., P.A.T., and T.E.H. wrote the paper.

The authors declare no conflict of interest.

[1]To whom correspondence should be addressed. E-mail: henry@email.arizona.edu.