LETTER

Reply to Leuzinger et al.: Drought-induced tree mortality temperature sensitivity requires pressing forward with best available science

Forest and woodland vulnerability to tree mortality in response to future drought and warmer temperatures is emerging as a potentially critical impact of global change (1). We directly addressed this issue experimentally in our recent study (2), on which Leuzinger et al. comment (3). Notably, we showed drought-induced tree mortality was highly temperature-sensitive, raising concern about future die-off. Other experimental studies isolating the effect of warmer temperature on drought-induced tree mortality are lacking—a major knowledge gap given how directly such a relationship underpins the potential impacts of climate change. The shorter survival period under warmer temperatures quantified in our study correspondeds to a difference in leaf-level cumulative respiration—a response consistent with the temperature sensitivity of carbon dynamics driving differences in mortality. A simple projection of this sensitivity using a 103-year historical record of drought indicated that warmer temperatures (+4.3 °C) could increase die-off frequency 5-fold. Leuzinger et al. (3) note methodological concerns regarding the study, some of which are helpful in prioritizing future research to refine insights, but nonetheless do not negate the main findings. Furthermore, these concerns should not cloud the urgency with which the research community pursues additional research to develop an improved model of plant mortality.

Our projections of increased die-off are constrained by our experimental conditions, including potential effects associated with transplanting and the relatively uniform size/age distribution that we controlled for, as Leuzinger et al. note (3). Despite these limitations, our results are the best currently available for making such a projection, and we think it would be inappropriate not to directly assess the implications of our findings.

Our finding of temperature sensitivity of carbon dynamics driving differences in mortality is consistent with two other related studies (4, 5), as we previously noted (2, 6). Leuzinger et al. (3) raise valid concerns that require additional study: an assessment of nonstructural carbohydrates through drought-induced tree death is indeed needed to confirm and refine our understanding of this mechanism (6, 7). However, the key difference in survival in our study was associated with respiration, and no component of water relations predicted this difference, a result that is most consistent with carbon starvation (6). As apparent in our results (ref. 1, Fig 3*C*), cumulative respiration was significantly higher for the warmer treatment by the fourth week (repeated measures ANOVA; P, <0.05), but final cumulative respiration just prior to death did not differ between treatments.

Interpretations of our results are of course subject to revision based on future work but, to date, are the most-direct evaluation of the sensitivity, mechanism, and implications of increased temperature on drought-induced mortality. Experimental research on drought-induced tree mortality is challenging, in part due to the large stature of trees, but needs to proceed despite limitations. Researchers should continue to advance projections based on the best currently available understanding of mechanisms and sensitivity. Welcomed discussion of mechanism specifics or projection limitations should not, however, obscure the most important finding of our research, that drought-induced tree mortality is highly sensitive to temperature.

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1. Allen CG, et al. (2009) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage*, in press.
2. 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.
3. Leuzinger S, Bigler C, Wolf A, Körner C (2009) Poor methodology for predicting large-scale tree die-off. *Proc Natl Acad Sci USA*, 10.1073/pnas.0908053106.
4. 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.
5. 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.
6. Adams HD, et al. (2009) Reply to Sala: Temperature sensitivity in drought-induced tree mortality hastens the need to further resolve a physiological model of death. *Proc Natl Acad Sci USA* 106:E69.
7. 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.

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The authors declare no conflict of interest.

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