LETTER

Lack of direct evidence for the carbon-starvation hypothesis to explain drought-induced mortality in trees

The carbon-starvation hypothesis has been formulated to explain tree mortality due to long-term drought (1). It predicts an eventual depletion of tree carbon stores as a result of stomatal closure and insufficient carbon assimilation to meet carbon demands for tissue maintenance. Consistent with this, Adams et al. (2) show that drought-stressed *Pinus edulis* grown at experimentally induced warmer temperatures (≈4 °C) incur greater respiratory carbon loss and die earlier than drought-stressed trees grown at ambient temperature. Not surprisingly, they invoke the carbon-starvation hypothesis to explain their results. Although this hypothesis is appealing and tentatively supported by this and other research (3), direct evidence to support this hypothesis is completely lacking to date: actual depletion of carbon stored reserves prior to drought-induced mortality has never been shown. In contrast, there is evidence that mature trees store sufficient mobile carbon to meet fairly large competing carbon demands (4) and that reductions in water availability are associated with an increase rather than a decrease in stored mobile carbon (5). More importantly, potential alternative hypotheses for the carbon-starvation hypothesis have not been adequately addressed. For instance, carbon starvation need not be invoked if stress due to lack of water and exacerbated by warmer temperatures limits phloem function and long-distance carbon translocation within trees. This distinction is critical and not a matter of semantics. Testing alternative hypotheses is fundamental to advance research in tree physiology to fully understand tree, forest, and ecosystem responses to global change.

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