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TREE MORTALITY

Large trees losing out to drought

Large trees deliver many benefits to forest ecosystems, including the provision of habitats for other species and the storage of carbon. A synthesis of tree growth and mortality data from around the globe now suggests that under drought large trees are dying in higher numbers than smaller trees.

Michael G. Ryan

Large trees provide many ecological services in forests. They provide seeds for reproduction and food, habitat for plants and animals, and shade for understory vegetation. Older trees and forests store large quantities of carbon, tend to release more water to streams than their more rapidly growing younger counterparts, and provide wood for human use. Mature trees of many species also record past climate in their rings, providing clues about how plants have endured enormous climate variability over the ages. Finally, large trees inspire and comfort many, helping to connect us with the natural world. Writing in *Nature Plants*, Bennett and colleagues[1] synthesize studies of drought effects on tree growth and mortality from around the globe, and show that tree size matters: drought susceptibility — decreased growth and increased mortality — increases with tree diameter.

Understanding the influence of drought on tree mortality and growth has been hampered by inconsistent and often inadequate sampling procedures. Tree mortality data from different studies are difficult to synthesize because there are no standard methods for measuring the prevalence and cause of mortality, the area surveyed varies among studies, and tree size and stand characteristics are not always measured. Parameters such as the length and intensity of the drought, and plant and soil water status, are either undetermined or only estimated regionally and not for measurement plots. However, drought-induced mortality and reductions in growth can be concentrated in locations where soils have a low water-holding capacity, at low elevations where water availability is reduced, or in stands with higher tree numbers and water use, and can therefore be missed in large-scale inventory surveys. Drought-induced mortality and growth reductions can also be widespread when drought weakens trees and triggers bark beetle epidemics, or when soil water status is similar across a landscape, as in portions of the Amazon.

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Dead piñon pines (*Pinus edulis*) in the Jemez mountains of New Mexico, USA.

Despite the shortcomings of many of the drought mortality surveys conducted to date, Bennett and colleagues[1] find a clear influence of tree size on susceptibility to drought that holds across biomes. They compile data from 40 studies that compared trees under drought and non-drought conditions at locations around the globe, and use a mixed effects model to examine the influence of tree size on sensitivity to drought. Studies in this synthesis measured tree size as diameter or diameter class, and relative or absolute mortality; a subset also measured diameter growth. Compiling the data they find that relative growth decreases with tree size, and relative mortality increases with tree size. Because tree mass, height and age are all strongly correlated with tree diameter, their findings suggest that the oldest, tallest and largest trees have died in greater numbers than smaller trees in recent droughts.

They also show that this size-dependent susceptibility to drought generally holds in broadleaf temperate and tropical forests, in ecosystems with and without seasonal precipitation patterns, and in forests where bark beetle mortality is not apparent. A broader survey of studies that measured absolute mortality after drought (and included many sites where bark beetle mortality was the final cause of mortality) showed a more mixed, but broadly similar pattern, with the effect of tree size more pronounced when community or stand mortality was higher.

The link between tree mortality and tree size under droughts is disturbing, given that climate models project more frequent, and potentially more intense, droughts in the future[2,3]. Future droughts could also impact trees more because they are expected to be accompanied by higher temperatures, causing increased water loss and physiological stress for trees near their thermal limit. Large trees provide many more ecological benefits than small trees, and their regrowth takes substantially longer. Forests that continually lose the largest trees to drought would provide less habitat and structural diversity, release carbon to the atmosphere, and possibly have lower water output to streams.

The potential impact of drought-induced mortality on forest carbon balance should be set in the context of other historical trends in forest growth and mortality. Large-scale, intense and long-lasting dry periods have occurred in many ecosystems in past centuries[4], so drought mortality is a component of most forest ecosystems. In recent decades, forests of Europe and North America have soaked up significant quantities of carbon as they have developed from past harvesting and agricultural clearing, in the relative absence of fire, and under increased atmospheric carbon dioxide concentrations and nitrogen deposition[5]. However, recent increases in fire, drought, and drought-induced bark beetle outbreaks have increased tree mortality in western North America, and this may reduce or eliminate this carbon sink[6]. Clearing for agriculture is rendering tropical forests a carbon source[5], but the impact of

drought-induced mortality in tropical forests is as yet poorly assessed.

We do not yet understand the mechanisms that make older, larger trees more susceptible to drought. Despite the potential for large trees to access deeper water[7] and buffer droughts, data on tree size and root depth are sparse. Large trees differ in structure and function from small trees[8], and maintenance of stomatal conductance for photosynthesis and the integrity of the water column becomes more difficult as trees grow taller[9,10]. As such, taller trees may be more prone to hydraulic failure and tree death under drought. To further understand the patterns and mechanisms of drought-induced mortality, future studies should incorporate measurements of tree growth prior to mortality, tree size, competition for resources from neighbouring trees, local drought conditions, and precipitation manipulation experiments.

Bennett and colleagues[1] show that size is a key determinant of tree susceptibility to drought. If droughts become more frequent and intense in the future, forests will likely lose a greater number of large trees, changing forest structure and releasing forest carbon to the atmosphere. Predicting the ultimate impact of these drought-related changes is difficult considering the concurrent enormous changes in forest land use and fire, rising atmospheric carbon dioxide concentrations, and nitrogen deposition. ❐

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References

1. Bennett, A. C., McDowell, N. G., Allen, C. D. & Anderson-Teixeira, K. J. *Nature Plants* **1,** 15139 (2015).
2. IPCC *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) (Cambridge Univ. Press, 2013).
3. Settele, J. *et al.* in *Climate Change 2014: Impacts, Adaptation and Vulnerability* (eds Stocker, T. F. *et al.*) Ch. 4 (IPCC, Cambridge Univ. Press, 2014).
4. George, S. S. *Quat. Sci. Rev.* **95,** 132–150 (2014).
5. Le Quere, C. *et al. Nature Geosci.* **2,** 831–836 (2009).
6. Canadell, J. G. *et al.* in *Terrestrial Ecosystems in a Changing World* (eds Canadell, J. G., Pataki, D. E. & Pitelka, L. F.) 59–78 (Springer, 2007).
7. Christina, M. *et al. Ecosphere* **2,** art27 (2011).
8. Meinzer, F. C., Lachenbruch, B. & Dawson, T. E. (eds) *Size- and Age-related Changes in Tree Structure and Function* (Springer, 2011).
9. Ryan, M. G., Phillips, N. & Bond, B. J. *Plant Cell Environ.* **29,** 367–381 (2006).
10. McDowell, N. G. & Allen, C. D. *Nature Clim. Change* **5,** 669–672 (2015).

Erratum: Tree mortality: Large trees losing out to drought

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In the original version of this News and Views, the caption of the photograph was incorrect. The trees shown are piñon pines (*Pinus edulis*) in the Jemez Mountains of New Mexico, USA. This has been corrected.