Functional traits of Giant Sequoia crown leaves respond to environmental threats

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The *Sequoiadendron* canopy, from the *American Journal of Botany* article "Phenotypic plasticity of leaves enhances water-stress tolerance and promotes hydraulic conductivity in a tall conifer" by Alana R. O. Chin and Stephen C. Sillett. Credit: Stephen C. Sillett and Marie E. Antoine

Hundreds of feet above the ground, atop a giant sequoia tree, as many as 2 billion leaves vie for resources. Twigs teem with leaves growing long and splayed or short and tight, depending on their placement in the crown. Leaves that establish live for up to 20 years, drawing water up the tree's trunk and sending nutrients down, while the trunk amasses wood and survives for thousands of years. The giant sequoia's size—-it's the most massive non-fungal organism on Earth—-is possible in part because its leaves are responsive to environmental changes. "In terms of both carbon acquisition and water-stress risk, the buck stops at the leaf-level," explains researcher Alana R. O. Chin, of American River College and Humboldt State University. Chin and co-author Stephen C. Sillett, also of Humboldt State University, wanted to know precisely how the leaves respond to the environment to facilitate the trees' impressive growth.

Under changing conditions, if the leaves can't change too, will giant sequoia groves and other old-growth conifer forests be at heightened risk of degradation? If the leaves do change, how will that impact the trees and the larger ecosystem? To address these questions, they published "Phenotypic plasticity of leaves enhances water-stress tolerance and promotes hydraulic conductivity in a tall conifer," in a recent issue of the *American Journal of Botany*.

"Leaf anatomy is often viewed as an old-fashioned thing to study," Chin acknowledges, "but modern analytical tools are letting anatomists scale up our observations." Such analyses enable researchers to use data from leaf variation to predict whole-tree and ecosystem responses to ecological changes.

Chin and Sillett roped up to climb and gather samples from across the crowns of five giant sequoia trees. The five stand in a montane forest within Sequoia National Park and are part of ongoing studies by this team and others. Like all giant sequoias, these five have a short growing season and depend on melting snowpack from the Sierra Nevada mountains for many months of the year. Low snowpack creates drought conditions for the trees. Even in wet years, giant sequoia trees have the challenging task of conducting water up hundreds of feet, against gravity, to carry through processes for photosynthesis. Drought could make their job even more difficult.

Can they cope? What traits make the leaves function while water-stressed? Chin and Sillett suspected several traits, from stem diameter to succulence to fiber count, may play a hand. From their samples, the researchers measured 18 structural traits of shoots and leaves. They also manipulated some samples for an induced-drought experiment, pioneering a new "sealed-end" method of dipping the cut ends of samples into wax to more realistically provoke physiological responses.

Their analyses reveal that giant sequoia leaves do respond in patterned ways to environmental conditions and changes. Overall, leaf anatomy varies more due to the availability of water than to the availability of light. The leaves growing in the "toughest," most exposed places at the top of the crown grow better suited to withstand water stress than leaves in the lower crown do. Structures within leaves called transfusion tissue are surprisingly large in giant sequoia leaves and seem to promote water flow through the leaf. All of these traits enhance the giant sequoia's ability to grow large and tall through targeted investments to meet water-stress challenges.

From this study, we now know that leaves from the upper crown and lower crown in giant sequoia trees differ in toughness and succulence. Leaves in the upper crown have more fibers, which provide structural support and enable the leaf to enter its 20th or 21st year. Once the leaves do die, their toughness should cause them to decompose more slowly than leaves from the lower crown. In these ways, they slow the carbon cycle—-the storage and release of carbon—-for the system. Leaves in the upper crown are more succulent than leaves in the lower crown in part because they contain more transfusion tissue. These tissues store water and, during water stress, promote resilience from cell collapse. While it's common for tall conifers to have transfusion tissue in upper crown leaves, the cross-sections of upper crown giant sequoia leaves measured in this study have three times more transfusion tissue than the leaves of the giant sequoia's super-tall relative, *Sequoia sempervirens*, the coast redwood. The giant sequoia's transfusion tissue effectively "stretches across" most of a leaf's width.

What's more, according to Chin and Sillett, the transfusion tissue also accumulates heat and drives transpiration. It does this by intercepting radiation from the leaf's interior and evaporating water—-not unlike the cooling systems in our everyday electronics. The giant sequoia's leaf pores, or stomata, on the surface and undersides of upper crown leaves provide ample opportunity for the vapor to diffuse. Harnessing heat to boost the rate of water movement allows these trees to take advantage of "narrow daily windows" for photosynthesis during the short Sierra summer. Chin says that the adaptations for "radiation-driven transpiration may help these massive trees 'make hay while the sun shines' through rapid hydraulic throughput."

The co-authors were "amazed" at this anatomy of the giant sequoia leaf that "indicates an ability to respond to local environmental signals" and furthers inquiry into the effects of climate change on forest ecosystems. In addition, Chin says the new sealed-end method is useful for myriad applications, including side-by-side drought response comparisons. Perhaps most promising is an agricultural application: "If a farmer wanted to choose which of her trees to propagate," Chin posits, "she could determine their relative tolerance of acute water-stress without needing anything fancier than pruning shears and a tub of melted wax."

More information: A. R. O. Chin et al, Phenotypic plasticity of leaves enhances water-stress tolerance and promotes hydraulic conductivity in a tall conifer, *American Journal of Botany* (2016). DOI: 10.3732/ajb.1600110

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