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Going out on a (redwood tree) limb

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As the morning fog lifts above the redwood canopy at Bull Creek (Humboldt Redwoods State Park, California, USA) a morphological mystery is revealed. Here at over 100 m above the ground, the small awl-like leaves (foreground) are half as wide as and four times shorter than the flat, expanded leaves growing more than 50 m below. As the plant species with the tallest individuals, redwood provides an unparalleled opportunity to examine the external factors controlling within-plant variation in foliar structure. To separate the effects of light availability on leaf morphology and anatomy from the effects of gravity-induced water stress we used arborist style climbing techniques to collect height-paired foliar samples from both the dark inner and bright outer crowns. We found that the hydrostatic gradient in water potential drives the observed reduction in leaf expansion with height as well as inducing investments in functional traits that promote water-stress tolerance in the upper crown, all with no detectable influence from light availability. Credit: Alana Oldham

How tall can a tree grow? Does sunlight or water limit the size and photosynthetic capacity of a leaf? Could constraints on leaf growth really determine the height of a tree? These are all questions that Alana Oldham of Humboldt State University, CA, was eager to answer as she and her colleagues dangled from an ancient redwood tree well over a football field's length in height above the ground.

Most trees, and many other plants, have thicker leaves on the top of their canopies with wider, more expanded leaves below. This difference in "sun" vs "shade" leaves is usually explained as an adaptation to different levels of light availability within the plants' crown. However, Oldham and her collaborators set out to investigate whether water stress might play an equal or more important role than light availability on the variation in top to bottom leaf anatomy in one of the tallest plants on earth, the redwood tree (*Sequoia sempervirens*). They published their novel findings in the July issue of the American Journal of Botany.

In order to separate the effects of light from water potential the authors collected data on a range of morphological and anatomical variables in leaves using a paired design, sampling from the inner and outer crown of each of five redwood trees at increasing height positions.

"This is the first time plant anatomists have collected height-paired leaf samples from both the inner and outer crowns of trees of significant height," Oldham notes. "Accessing the outermost branch tips in trees of this size requires risky techniques that have taken many years for more experienced canopy researchers than I to learn and develop. Only by obtaining leaves that grew at the same height in the tree but in different light environments could we separate the effects of light availability from those of hydrostatic tension."

"Some data are worth going out on a limb for," Oldham jokes.

Water stress increases with height in a tree's canopy—gravity pulls down on the water column, which in turn decreases water pressure as you move up the tree. To compensate for this decreased water pressure with increasing height, trees make anatomical changes in leaves which can lead to a reduction in photosynthesis in the upper canopy. Of the variables the authors measured—leaf length, leaf width, and the amount of air space (or mesoporosity) in a leaf—all decreased with height (explaining decreasing photosynthesis with height) while leaf thickness and transfusion tissue (which improve water-stress tolerance) increased with height. In contrast, none of the 15 anatomical traits measured differed between the inner and outer crown positions, where light availability differed.

"In tall redwoods its not light that drives leaf anatomy and morphology, but rather a height-associated increase in water stress due to the force of gravity pulling down on the water column as it rises over 110 m from the roots to the tree top," Oldham explains. "This gravitational pressure, known as hydrostatic tension, decreases water availability with height and so directly reduces leaf expansion which in turn lowers photosynthetic capacity in the tree tops. At the same time, hydrostatic tension puts tall trees at increased risk during drought events thus driving investments in functional anatomical traits that may allow redwoods to reach such great heights, but are costly in terms of lost opportunity for growth."

Oldham notes that "For Earth's tallest trees the force of gravity may be the biggest obstacle to further increases in height." With increasing height, the increasing effects of gravity drive tissue investments toward water stress tolerance, resulting in tradeoffs with carbon gain per unit leaf mass in the upper crown. This could result in diminishing rates of height growth with increasing height in redwoods.

Do other tall tree species also experience these tradeoffs? "Our current endeavor is to explore foliar anatomy across the height gradient in the three next tallest conifer species" Oldham said. "We plan to compare and contrast the impacts of hydrostatic tension on leaf development as well as uncover any species-specific traits that may help explain why some species have taller individuals than others."

More information: http://www.amjbot.org/cgi/reprint/ajb.0900214v1

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