Limits to tree height: within-crown structural and physiological gradients in *Sequoiadendron giganteum*

Anthony Ambrose,[1] Steve Sillett,[2] George Koch,[3] Robert Van Pelt,[4] Chris Earle,[5] Marie Antoine,[2] Jim Spickler,[2] Cameron Williams,[2] and Todd Dawson[1]

[1] *Department of Integrative Biology, University of California, Berkeley, CA 94720*
[2] *Department of Biological Sciences, Humboldt State University, Arcata, CA 95521*
[3] *Department of Biological Sciences, Northern Arizona University , Flagstaff, AZ 86011*
[4] *College of Forest Resources, University of Washington, Seattle, WA 98195*
[5] *Jones and Stokes Associates, Bellevue, WA 98005*

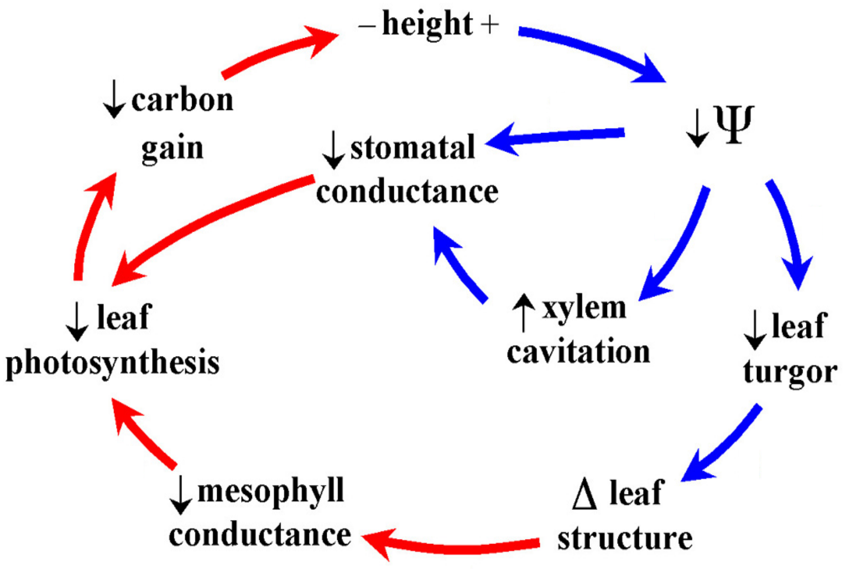
Abstract

Giant trees are treasured throughout the world for their aesthetic, ecological, and commercial values. However, knowledge of the factors regulating the physiological performance, growth, and response to environmental change of the largest and tallest tree species remains limited. In the summer of 2005, we commenced a study at the Whitaker Forest Research Station to examine how biophysical constraints influence the maximum potential height and size of giant sequoia (*Sequoiadendron giganteum*), the largest and 5th tallest tree species on Earth. Current research supports the view that constraints and trade-off's involved with water delivery to the treetop play a primary role in reducing and eventually stopping height growth as trees grow taller. The basis for the decline in height growth may be a decrease in carbon gain of leaves due to greater stomatal limitation of photosynthesis at the treetop. Altered leaf structure with increased height may also play an important role in constraining photosynthesis by limiting the supply of CO_2 to sites of carboxylation within the leaf. Finally, other components of carbon balance, most notably respiration, likely change in importance as gravitational constraints on photosynthesis increase toward the treetop. We quantified within-crown gradients of structural and physiological traits in *S. giganteum* trees of different heights and sizes in order to gain insights into the relative importance of different mechanisms likely constraining physiological performance in this species. Study trees were accessed using rope-based arborist techniques. Study tree heights ranged from 54.5 to 90.9 m, while diameters (DBH) ranged from 145 to 617 cm. Leaf water potential decreased with height, with some evidence of a mid-day depression. Leaf mass per unit area (LMA) increased with height in all trees, ranging from 326 to 943 g m^{-2}. Preliminary analyses of gas exchange data indicate that the tops of taller trees have lower mean and maximum photosynthetic rates (A), stomatal conductance (g_s), and leaf intercellular CO_2 pressure (c_i) than the tops of shorter trees. Additionally, preliminary visual assessment of treetop wood cores indicates that taller trees may experience a greater degree of inter-annual variation in tree ring growth, potentially due to higher drought sensitivity. Preliminary results generally support the hypothesis that decreased water potential at the tops of tall trees directly and indirectly reduces carbon gain and height growth. Detailed analyses of leaf morphology, gas exchange, stable carbon isotopes, and tree rings are on-going. Additional structural and physiological measurements and analyses are scheduled for the summer of 2006.

Conceptual Framework

The effect of height on tree physiological performance is thought to be primarily due to the increasing influence of gravity and friction on xylem water potential (Ψ) towards the tops of trees. Vertical climatic gradients within tall, closed canopies also result in greater evaporative demand and subsequent water stress with increasing height. The idea that biophysical constraints due to increased water stress at the tops of tall trees might explain the slowing and eventual cessation of height and size growth was formally developed by Ryan and Yoder (1997) as the "hydraulic limitation hypothesis." A recent analysis of height limitation for coast redwood (*Sequoia sempervirens*), including 5 of the 8 tallest known trees (Koch et al. 2004), builds on this hypothesis and provides a conceptual model for the present study (Figure 1) . The central hypotheses of this model is that the reduction in water potential as trees grow taller increasingly reduces photosynthesis and carbon gain via both direct impacts to stomatal conductance and indirect effects mediated by altered leaf structure.

Figure 1. Conceptual model depicting hypothesized feedback relationships among tree height, water potential, leaf structure, and photosynthesis that affect further height growth. Effects due to altered water potential are depicted by **blue** arrows, and pathways leading to altered carbon balance are depicted by **red** arrows.



Research Objectives

The primary objective of this research is to characterize structural and physiological traits influencing tree performance and growth along vertical and horizontal gradients within the crowns of *S. giganteum* trees of different heights and sizes. By characterizing within-crown structural and physiological gradients in mature *S. giganteum* tree crowns, we hope to assess the effects of height-related variation in water stress on photosynthetic carbon gain in this species.

Materials and Methods

- ***Tree Crown Structure*** – mapping of the three-dimensional crown architecture to provide estimates of trunk and branch wood volume, height growth, and foliage mass/area.
- ***Xylem Water Potential*** – measurement of vertical gradients and daily patterns in treetop xylem water potential.
- ***Leaf Gas Exchange*** – measurement of daily patterns in gas exchange parameters (photosynthesis (A), stomatal conductance (g_s), and intercellular CO_2 concentration) of treetop *in situ* and cut and re-hydrated ("cut-hydro") foliage samples.
- ***Leaf Structure*** – measurement of within-crown gradients in leaf mass per unit area (LMA) as an index of leaf structure potentially influencing carbon gain.
- ***Stable Carbon Isotope Composition*** - measurement of within-crown gradients in leaf stable carbon isotope composition ($\delta^{13}C$) as an index of integrated leaf-level water stress.
- ***Dendrochronology*** – examination of interannual patterns of $\delta^{13}C$ and growth evident in the annual rings of wood cores along the vertical gradient of the main trunk as measures of sensitivity to long-term drought.

Preliminary Results

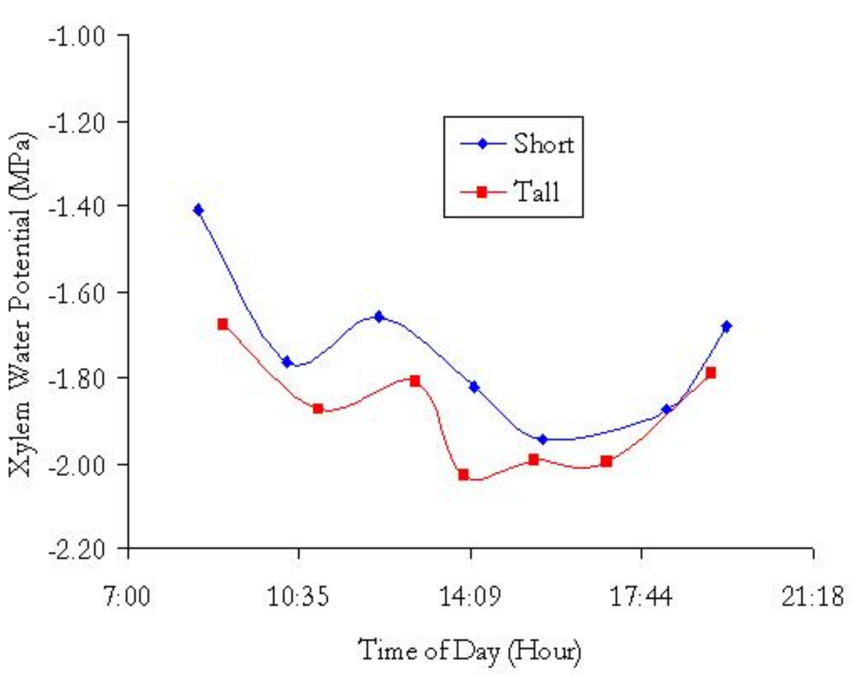


Figure 2. Comparison of daily time course of treetop xylem water potential in a tall (~90 m) versus short (~60 m) *S. giganteum* tree. Note that both trees experience a mid-day depression in water potential, with the taller tree exhibiting more negative values throughout the day.

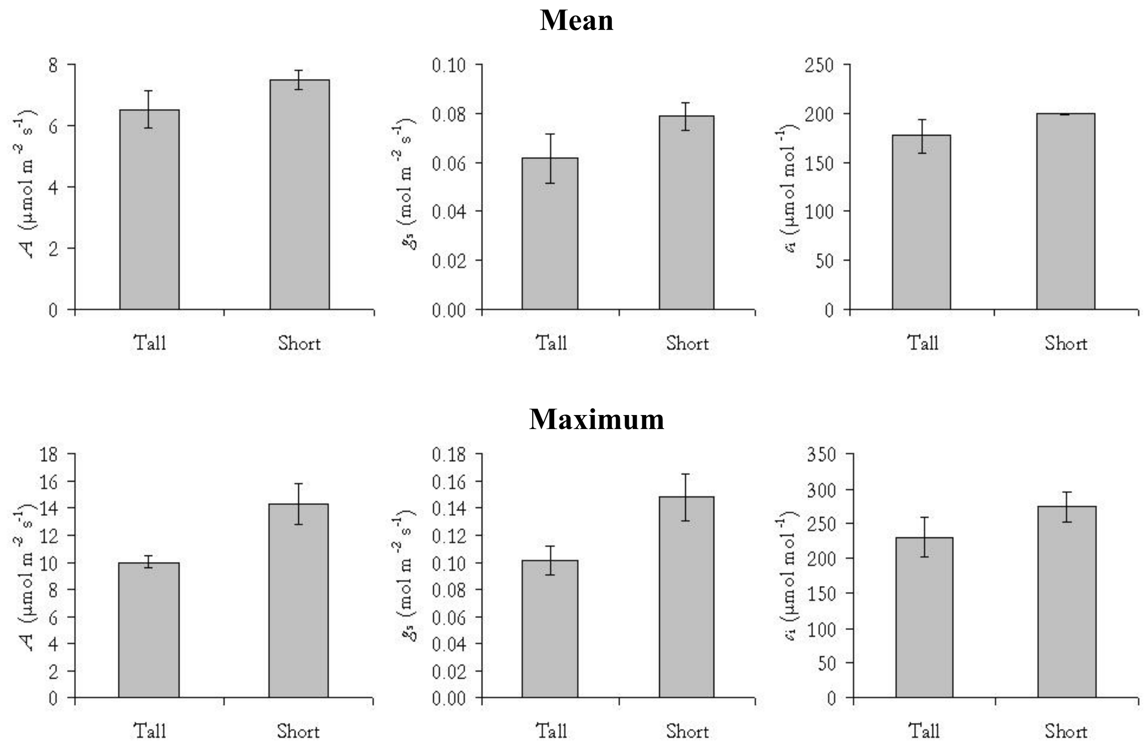


Figure 3. Comparison of mean and maximum leaf-level gas exchange parameters [photosynthesis per unit leaf area (A), stomatal conductance (g_s), and leaf intercellular CO_2 concentration (c_i)] in tall (~90 m) versus short (~60 m) *S. giganteum* trees (values are daily means ± one standard error, n = 3 trees per height class).

Literature Cited

Koch, G.W., S.C. Sillett, G.M. Jennings and S.D. Davis. 2004. The limits to tree height. *Nature* 428: 851-854.
Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. *Bioscience* 47(4): 235-242.

Acknowledgements

Financial support for this research is generously provided by Save-the-Redwoods League, Global Forest Society, and the National Science Foundation. The authors wish to thank the UC Berkeley Center for Forestry for permission to use the Whitaker Forest Research Station for this research.