

COMMENTARY

A RESPONSE TO: LIMITATIONS WITHIN “THE LIMITS TO TREE HEIGHT”¹

GEORGE W. KOCH^{2,4} AND STEPHEN C. SILLETT³

²Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA; and ³Department of Forestry and Wildland Resources, Humboldt State University, Arcata, California 95521 USA

Here we respond to the communication in *American Journal of Botany* (96: 542–544 in this issue) by Netting, who proposes several ways in which our paper “The Limits to Tree Height” (*Nature* 428: 851–854) may have erred in estimating the biophysical limits to height growth in *Sequoia sempervirens*. We first explain that because embolism repair requires long time periods and is generally incomplete, xylem vulnerability characteristics offer a sound basis for estimating performance limits in woody plants. We reaffirm our earlier use of vertical gradients of foliar carbon isotope composition with new data for *S. sempervirens*. We support these arguments with reference to studies in other tree species. We take exception with Netting’s view that the turgor pressure–cell expansion relationship for *Zea mays* is applicable to *S. sempervirens*. Finally, we second Netting’s call for more work on carbon allocation vis a vis height growth limits.

In the Brief Communication in this issue, Netting (2009, pp. 542–544 in this issue) discusses potential flaws in our approach to estimating the limits to height growth in *Sequoia sempervirens* (Lamb. ex D. Don) Endl. (redwood; Cupressaceae) (Koch et al., 2004). We appreciate the interest in our work and the opportunity to respond as a means to further the discussion of biophysical constraints on tree height and size growth. Netting’s analysis of our study makes four main points:

(1) The use of xylem vulnerability to cavitation for estimating height limits is problematic if embolism repair occurs.

(2) Foliar morphology (leaf mass/area ratio) may be a response to, rather than a determinant of, the large differential between cellular turgor and the xylem pressure.

(3) The regression model we used for describing trends in foliar $\delta^{13}\text{C}$ with height may have been flawed.

(4) Our use of light-saturated photosynthesis per unit leaf mass as a measure of biomass investment in leaf expansion excludes investment in branch and trunk wood.

Here we examine each of these criticisms in turn and provide some additional comments regarding the status of efforts to understand tree height limits.

Netting’s first point is that the use of xylem vulnerability characteristics for estimating height limits may be inappropriate if embolism repair occurs in redwood. Partial recovery of lost hydraulic conductivity has been observed in stems, petioles, and leaves of other conifers as well as angiosperms during periods when xylem pressure was substantially more negative than that required for bubble dissolution (e.g., Sperry et al., 1994; Tyree et al., 1999; Hacke and Sperry, 2003; Bucci et al., 2003; Woodruff et al., 2007). The mechanism of such “novel refilling” (sensu Hacke and Sperry, 2003) remains unclear. In the case of redwood, foliar uptake of fog water and reverse flow of xylem sap during periods of heavy fog (Burgess and

Dawson, 2004) allow for the possibility of passive refilling of embolized tracheids during transient periods when water potentials might rise above the hydrostatic tension.

So, we recognize the possibility of embolism reversal in redwood, but we doubt that it invalidates the use of xylem vulnerability characteristics as one of several tools for estimating maximum height. Hacke and Sperry (2003), in the study of embolism reversal that Netting cites, found that one angiosperm species (*Laurus nobilis*) but not another (*Acer negundo*) was able to recover about half (from 80% to 40%) of the conductivity lost in previous exposure to a water potential of -2.7 MPa. Thus, despite the apparent recovery of significant fraction of embolized vessels, after “recovery” these plants were still 40% below full hydraulic capacity. Similarly, other studies of embolism repair have shown only partial recovery of hydraulic conductivity (e.g., Sperry et al., 1994). In a situation of daily evaporative stress, such as in the early fall along the northern California coast when the summer drought reaches its greatest expression, trees do not have the 24 h of well-watered, low light conditions required by *Laurus nobilis* to recover half of its lost hydraulic capacity. Moreover, even if a redwood recovered as described for *L. nobilis*, it would still begin each subsequent day with less hydraulic capacity, seemingly placing the remaining “vulnerable pipelines” at greater risk. Pending more research in this important area, our general view of embolism repair is that it does not negate the ecological significance of xylem vulnerability characteristics. More directly pertinent to Netting’s discussion, we see no reason why the water stress (-2.7 MPa) from which *L. nobilis* partially recovered hydraulic conductivity should be used as the limit value in our regression-based approach.

Our general approach of using vertical gradients in hydraulic features to understand height limits in trees is supported by the elegant recent work with *Pseudotsuga menziesii* (Douglas-fir) by Domec et al. (2008). That study documented a reduction in tracheid pit aperture conductance with height and used a regression-based extrapolation to conclude that conductance would fall to zero in branch pits at a height of 138 m. The xylem pressure threshold for runaway embolism (i.e., rapid increase with further pressure drop) was about -3.2 MPa in that study, cor-

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⁴ Author for correspondence (e-mail: george.koch@nau.edu)

responding to a height of 110 m to 136 m based on observations of minimum dry season xylem pressure in twigs. Obviously, the lower the “critical” xylem pressure chosen, the greater the corresponding maximum tree height estimate. In our study, we used the xylem pressure at which embolism initiates (c. -1.9 MPa) because we assumed that any significant amount of embolism would place further stress on the hydraulic system and should correspond to the point at which stomatal regulation acts to prevent further decrease in xylem pressure. Interestingly, in a study of the coordination of hydraulic architecture and stomatal regulation in Douglas-fir (Woodruff et al., 2007), the diurnal xylem pressure at which stomatal conductance began to decrease at the tops of the tallest trees was -1.86 MPa, quite similar to the limit value we used.

Because experiments to manipulate xylem tension in the field and to evaluate consequences for stomatal control or runaway embolism are lacking, choices of “critical” xylem pressures will remain somewhat subjective. That said, we completely agree with Netting that more study is needed of the xylem pressure at which permanent hydraulic failure occurs and results in branch death. As we expressed previously (Koch et al., 2004), occasional severe dry periods are likely responsible for the top dieback that is evident in most tall redwoods. We plan to test this idea by dating these dieback events and relating them to historical and surrogate climate records.

For his second major point, Netting discusses our estimates for leaf turgor pressure in relationship to variation in foliar morphology (mass/area) with height. He points out that the minimum turgor we estimated at the tops of the tallest trees was similar to the maximum turgor in *Zea mays* (maize) (Boyer, 1995) and implies that turgor at the tops of redwoods is therefore “adequate.”

We do not know the yield threshold or the relationship of turgor pressure to cell expansion rate for redwood, but we think they could differ substantially from maize. Lacking data, we intentionally avoided estimates of maximum height based on extrapolations of turgor pressure gradients. We are intrigued by Netting’s secondary message in this section: that the increasing pressure gradient between xylem and mesophyll cells with height may underlie a thickening of cell walls in foliage at the tops of the tallest trees. This hypothesis is certainly worth testing and is amenable to experimental manipulation of drought stress in small plants. This idea does not appear to be mutually exclusive with our interpretation that reduced turgor pressure may drive slower cell expansion.

We should clarify that our use of the term LMA (leaf mass : area) (Koch et al., 2004) was in error. For that study, we did not separate the scale-like upper crown leaves from the stems to which they were tightly appressed. Rather, we measured the entire shoot mass and projected area, and so the values we reported are properly termed SMA (shoot mass : area). By carefully removing leaves from annual shoots, we now have a conversion of SMA to true LMA for redwood. The equation is $LMA = 15.568(SMA)^{0.41377}$ ($N = 86$, $R^2 = 0.81$). A detailed examination of the role of light and water relations in influencing LMA in *S. sempervirens* is provided by Ishii et al. (2008).

Netting’s third point concerns the curve-fitting approach we used in analyzing height trends in foliar $\delta^{13}C$. He notes that we presented two populations of foliar $\delta^{13}C$ values, one for within-crown variation and one for variation among treetops. The exponential equation we used for estimating the height (130 m) at which the proposed limit value of -20% would be reached was based on the within-crown (including tree top) $\delta^{13}C$ data for the

five tallest trees. As we noted (Koch et al., 2004), the sensitivity of that estimate to the limiting value of $\delta^{13}C$ is not high; choosing limit values of -19% and -21% leads to maximum height estimates of 134 m and 125 m, respectively. The exponential equation fit to the treetop-only data estimated a height of 133 m for a $\delta^{13}C = -20\%$.

If we understand correctly, Netting proposes to include data for near-treetop foliage in the overall relationship of $\delta^{13}C$ vs. treetop height, from which he then estimates, based on a linear relationship, a height of 180 m for $\delta^{13}C = -20\%$. We disagree with this approach because we have observed morphological differences between the true treetop foliage and foliage just a meter below, or on a nearby nonleader shoot. We believe this is related to a distinct hydraulic architecture of leader shoots and invalidates use of sub-treetop foliage in treetop based regressions. Additional support of our $\delta^{13}C$ regression approach: when applied to the treetop $\delta^{13}C$ vs. height data for Douglas-fir from McDowell et al. (2002), our regression estimated a height of 125 m for $\delta^{13}C = -20\%$. Interestingly, this falls within the range of maximum heights for Douglas-fir recently estimated from the extrapolation of the vertical trend of main trunk and branch pit aperture conductance (Domec et al., 2008). Moreover, both these foliar $\delta^{13}C$ -based height maxima for Douglas-fir, as well as our previous maximum height estimate for *S. sempervirens* (Koch et al., 2004) are very similar to a revised value (-20% reached at 123.7 m) we recently obtained by regressing year 2006 foliar $\delta^{13}C$ data from the crowns of seven redwoods 108.5–115.6 m tall.

Vertical gradients in foliar $\delta^{13}C$, and our height estimates based on them, relate to xylem vulnerability characteristics to the extent that stomatal control of leaf gas exchange regulates both cavitation and carbon isotope discrimination. While we have evidence that some portion of the variation in treetop $\delta^{13}C$ in redwood is attributable to variation in internal conductance (L. Mullin, Northern Arizona University, unpublished data), our direct measurements of leaf conductance and upper crown sapflow (A. Ambrose, University of California–Berkeley, unpublished data) indicate increasing stomatal regulation of gas exchange with height in redwood. In this respect, we believe the description for Douglas-fir provided by Domec et al. (2008, p. 12072) applies equally well to redwood: “This highly conservative behavior of stomata suggests that tension-induced embolism may not be readily reversible in the xylem of Douglas-fir branches and that cumulative increases in the number embolized tracheids must be avoided if branch xylem is to remain conductive for many years.” The clear implication here is that the increase in $\delta^{13}C$ with tree height in redwood (Koch et al., 2004) and Douglas-fir (McDowell et al., 2002) is a result of the increasing requirement for stomatal regulation to avoid hydraulic dysfunction.

We were most interested in Netting’s fourth major point, which relates to our measurements of vertical gradients of light-saturated photosynthesis and involves broader considerations of carbon allocation in giant trees. Netting’s suggestion that carbon balance must be considered beyond the leaf level is well taken, and we agree that more work is needed to understand how photosynthate produced at any position in a tree crown is distributed to above- and belowground structures and functions necessary to support that foliage. Netting also suggests that measurements of growth rates of shoots near the tops of redwoods of various heights might be a useful direct assessment of height growth limitation. In fact, we have data on annual height growth rates of the main stem of 15 redwoods from 68 m to 113

m tall. These do indeed show a reduction in height growth with height, with an extrapolation to zero height growth at a height of 128.7 m (S. Sillett et al., unpublished data). We can also refine our statement from Koch et al., (2004) that the tallest redwoods are growing at up to $25 \text{ cm} \times \text{yr}^{-1}$. While this is true, we now have analyzed annual height growth records since 2000 for 11 trees over 110 m in height. The average annual height growth is $10.3 \text{ cm} \times \text{yr}^{-1}$, with a range among trees of $0.5\text{--}20.9 \text{ cm} \times \text{yr}^{-1}$.

We thank Professor Netting for his insightful analysis of our work. Although we are taught to avoid extrapolations beyond the range of variables that produce regression equations, we believe this can be a useful basis for pondering what might be, developing new hypotheses, and provoking discussion!

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Note from Netting: In recent experiments with tomato plants it has been shown (Netting et al., unpublished) that two sequential precursors of abscisic acid (ABA) that occur in the xylem consume at least one and probably two molecules of oxygen in their catabolism to release ABA. If a similar metabolic sequence occurs in gymnosperms, it seems clear to me that the release of ABA and, therefore, stomatal closure and the transition from active growth to a stress-tolerant quiescent state (Netting, 2000) could be intimately associated with the consumption of dissolved oxygen and, therefore, potentially, with the removal of embolisms. In a recent paper (Brodribb and Cochard, 2009), it was shown that the “minimum reversible water potential” (i.e., the minimum water potential from which four gymnosperm species could refill embolisms over up to 100 days) was -2.4 and -3.8 MPa for two temperate rainforest species and -10.4 and -11.4 MPa for two dry woodland species. Thus a case can still be made that *S. sempervirens* could recover from a water potential of less than -1.9 MPa, the figure used by Koch et al. (2004). Using the assumptions and data of these authors, a water potential of less than -1.9 MPa would predict a maximum height for *S. sempervirens* of greater than 122 m. However, the regression equations developed by Koch et al. (2004) imply a theoretical limit to tree height based on the contribution of height to the tension in the uppermost xylem vessels, but in many years, if drought is prevalent, a lack of water will also contribute to a loss of hydraulic conductivity (Brodribb and Cochard, 2009). The inference is that there is a practical limit to tree height that is a long-term balance between loss of hydraulic conductivity from height and drought, on the one hand, and continued growth when water supply is adequate, on the other.

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