Koch et al. (Nature 428: 851–854) measured various parameters that were thought to limit the height of *Sequoia sempervirens* from northern California and concluded that the maximum height for this species is 122–130 m because within this range: (1) Irreversible embolism formation was proposed to occur when the xylem pressure was less than −1.9 MPa. (2) The leaf mass to area ratio exponentially approached 833 g m⁻². (3) The discrimination against ¹³CO₂ exponentially approached −20. (4) Light-saturated photosynthesis per unit leaf mass decreased to zero, indicating no net gain in leaf biomass. These conclusions are questioned here by reassessing the assumed limits to the biophysical parameters and by reexamining the proposed linear and exponential relationships between these parameters and tree height. It is concluded that: (1) Embolism repair mechanisms could have occurred at −2.7 MPa. (2) The leaf mass to area ratio could be a result of, rather than a determinant of, the large differential between cellular turgor and the xylem pressure. (3) The discrimination against ¹³CO₂ may show two populations of foliage with apparent linear relationships with height rather than one exponential relationship. (4) The light-saturated photosynthesis per unit leaf mass as a measure of biomass investment in leaf expansion excludes investment in branch and trunk wood. As a result, tree height may be limited by a long-term balance between dieback and continued growth.

“Limitations” in the title here is an attempt to convey the sense that the major conclusion in the *Nature* article (Koch et al., 2004) entitled “The Limits to Tree Height” is not necessarily valid. Their conclusion was that the maximum height that the coast redwood, *Sequoia sempervirens*, from the Humboldt Redwoods State Park, California, could reach is 122–130 meters. Due to the increased negative pressure on the water column with height, embolisms tend to form, and hydraulic conductivity is lost; this loss was shown to be zero at a pressure of −1.9 MPa, which corresponded to a height of 122 m. However, the angiosperm *Laurus nobilis* has been shown (Hacke and Sperry, 2003) to be able to remove embolisms and partially restore hydraulic conductivity even though the water column remains under considerable negative pressures. Thus, we need to show that an embolism repair mechanism is lacking in tall conifers (Burgess and Dawson, 2007) if the maximum tree height for *S. sempervirens* (Koch et al., 2004) is to remain undisputed. Such an embolism repair mechanism is of some significance in that if we accept the height limit of 122 m for *S. sempervirens* we may well be turning a blind eye to the importance of embolism repair under considerable negative pressures because we believe that we understand the parameters that limit tree height. It is also important in that tree heights over 150 m were reported for *Eucalyptus regnans* from eastern Victoria, Australia, at the end of the 19th century (Carder, 1995) so that an implication that embolism repair cannot occur at considerable negative pressures tends to render these extraordinary heights inexplicable. So, my aim in this paper is to discuss the implication for the maximum tree height of *S. sempervirens* of assuming that embolism repair can occur at negative pressures and to also offer some alternative explanations for other parameters that were thought to limit tree height (Koch et al., 2004). I do wish to make clear that I am in no way criticizing the data of Koch et al. (2004) or the almost heroic means of collecting it; I am offering some different interpretations.

In *S. sempervirens* from northern California, the percentage loss of hydraulic conductivity was measured (Koch et al., 2004, supplemental online material) for branches from 109 ± 1 m and from 57 ± 5 m. There was a sharp increase in the rate of loss of hydraulic conductivity at xylem pressures of less than −3.0 MPa, and the results obtained for −1.0 MPa to −3.0 MPa gave a linear relationship with zero loss of hydraulic conductivity at −1.9 MPa. This value was substituted into a linear equation for xylem pressure, measured in small foliated branches collected at midday during the dry season, against height to give an estimate that the maximum tree height is 122 m, as mentioned. However, the novel embolism repair mechanism of *L. nobilis* reduced the percentage loss in hydraulic conductivity over 24 h from 80% at an initial negative pressure of −2.7 MPa to about 45% with light watering to give a final stem water potential of about −0.6 MPa (Hacke and Sperry, 2003). Thus, if *S. sempervirens* has a similar embolism repair mechanism, we should perhaps substitute −2.7 MPa into the linear equation for xylem pressure against height, giving a maximum height of 204 m for *S. sempervirens*. A case might also be made that we should substitute a value of −3.0 MPa because the rate of loss of hydraulic conductance commenced to increase more sharply at this value and because this is the pressure at which the “seals” on bordered pits of conifers appear to fail (Zimmermann, 1983). Substituting −3.0 MPa into the linear equation gives a maximum height of 235 m.

Different approaches to establishing estimates for the limits to tree height have been taken by Niklas and Spatz (2004) and by Du et al. (2008). Niklas and Spatz proposed a linear equation that related plant height to the basal stem diameter to the 2/3rds power, but as far as I am aware, the numerical values for the two allometric constants in this equation are not available for

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**Key words:** carbon isotope discrimination; hydraulic failure; limits to tree height; photosynthesis per unit leaf area; predawn turgor.
the population of *S. sempervirens* studied by Koch et al. (2004). Thus the predictions of Niklas and Spatz (2004) cannot be compared with the data of Koch et al. at present. Du et al. (2008) presented a biophysical model based on the principle that trees develop physiological compensations to, first, resist increasing water stress with height (presumably embolism repair could be one such compensation) and, second, to overcome the biochemical limitation on photosynthesis. Their model agreed well with the experimental data of Koch et al. (2004) except for the predicted relationship between light-saturated photosynthesis per unit leaf mass and height. They also predicted, utilizing the apparently unjustified assumption that the tallest *S. sempervirens* at 112.7 m is over 2200 yr old, that these trees approached a maximum height of 139 m asymptotically over some 30,000 yr. It is of interest in attempting to assess this model that Koch et al. (2004) stated that their results indicate that the uppermost branches of the tallest redwoods are growing by up to 0.25 m yr⁻¹ (more than the maximum of about 0.24 m yr⁻¹ for very young trees in the model), but the graph of tree height against growth time (Fig. 9 in Du et al. [2008]) suggests that, at 112 m, the growth rate should be as little as 0.014 m yr⁻¹.

Koch et al. (2004) found a negative linear relationship for predawn turgor against height such that the turgor at 120 m was 0.86 MPa and the predawn turgor was always greater than 0.8 MPa. Such a turgor would seem adequate given that the maximum turgor in maize was slightly less than 0.8 MPa at the completion of elongation (Boyer, 1995): substituting 0.8 MPa into the equation for the predawn turgor against height gives a maximum height of 134.1 m for *S. sempervirens*. The predawn xylem pressure at 120 m was −1.34 MPa (estimated from Fig. 1a in Koch et al. [2004] in the absence of an equation), and most of the cellular expansion is likely to occur at night. At this time, the cellular turgor is maximal (Koch et al., 2004) so that the cells in the leaves of *S. sempervirens* are apparently able to maintain their integrity in the face of this large height-dependent pressure differential (−2.2 MPa at 120 m). Perhaps this differential is responsible for the thickened cell walls rather than there being a direct relationship between the leaf mass-to-area ratio (LMA) (Koch et al., 2004) and the proposed maximum height of 122 m for *S. sempervirens* (Koch et al., 2004).

Thus the LMA is a result of this large pressure differential rather than a measure of the possibility of continued growth, and this might, in turn, imply that continued growth could occur as long as there is a large pressure differential between the cells and the xylem, with the final result being smaller cells and smaller leaves.

A diminution of the enzymatic discrimination against ¹³CO₂ (δ¹³C) in 2-year-old internodes was used as an integrated measure of stress, including the height component, in these trees. When the exponential regression line for the within-crown data against height was extrapolated (Koch et al., 2004) to a δ¹³C value of −20, the apparent limit for C₃ plants from arid environments, an estimate of a maximum height for *S. sempervirens* of 130 m was obtained. Yet, in the graph of δ¹³C against height (Fig. 1c in Koch et al., 2004), there are two distinct populations. One of these contains data points mostly from the tops of trees from 85 m to 113 m tall, and the other is mostly from within the crowns of five trees over 110 m tall. If one includes the measurements made at some 112 m from trees with a maximum height of 112.7 m, because these would be exposed to sun (Koch et al., 2004), wind, and possibly snow like most of the tree tops, this population appears to have a linear relationship between foliage δ¹³C and height; δ¹³C would approach a value of −20 at 140 m to 150 m. Similarly, the remaining population containing data almost entirely from within-crown measurements also appears to have a linear relationship. In this case, δ¹³C approaches −20 at about 180 m. Could this mean that the more exposed tree tops grow at a slower rate so that the somewhat less exposed within-crown foliage tends to catch up? Could the faster growing within-crown foliage leap-frog past the slower growing tree-top foliage and then become slower growing so that the roles of providing protection and providing vigorous growth are reversed?

These authors also measured the light-saturated photosynthesis per unit leaf area in foliage cut at different heights at a uniformly high laboratory water potential (−0.6 ± 0.3 MPa) and found that this parameter did not vary with height. However, when they converted this measurement to photosynthesis per unit leaf mass, they found a decrease with height indicative of an increasing investment in biomass, presumably cell wall material, as mentioned. As photosynthesis per unit leaf mass reached zero at 125 m, they concluded that a lack of a net increase in biomass from photosynthesis also imposed a limit to tree height. It is of interest here that the coast redwood can apparently live for ~2500 yr but that their vertical growth rate tends to decline after about 500 yr (Carder, 1995). As the bole diameter increases with age, it follows that the biomass that is not invested in increasing the height, perhaps because the uppermost foliage is too exposed, tends to be used to increase the diameter of the trunk and branches. Thus a crown results that is more likely to be able to withstand strong winds and storms with its uppermost buds ready to take advantage of any lull in the severity of adverse conditions. It should also be noted that the investment in cell wall material would occur essentially after cell expansion is complete so that photosynthesis per unit leaf mass would only influence growth to the extent that smaller cells, and therefore smaller leaves, as observed (Koch et al., 2004), would be obtained to give a reduced annual growth rate. One approach to determine if this parameter does indeed affect tree height might be to measure the growth rates of shoots near the tops of redwoods of various heights, taking into account the possibility that there may be two populations. If a plot of growth rate against height approaches zero between about 122 m and 130 m, it would indeed support the claim that there is an absolute limit on tree height, and this estimate would be independent of our assumptions regarding limiting factors and the periods of time for which they are relevant. Another approach might be to determine if the number of leaf cells is essentially independent of height, a result that would imply that the amount of cell wall material was dependent on the number of cells rather than on their size. If this did turn out to be true, it would imply that these small cells in this uppermost foliage did indeed achieve sufficient turgor for significant growth. Achieving this turgor could be assisted by the dry season fogs that would allow the uppermost foliage to take up some water even though ground water may be limiting; clearly, water was available because a 2 m tall epiphytic redwood was found growing in a pocket of soil at a height of 95 m (Koch et al., 2004).

Four hypotheses have been put forward to explain limitations in tree height (Ryan and Yoder, 1997). These are: (1) “Dominating respiration”—respiration, presumably to synthesize ATP, is so important that it consumes as much carbohydrate as is photosynthesized and has been considered in the section on light-saturated photosynthesis per unit leaf area and per unit leaf mass. (2) “Nutrient limitation”—insufficient nutrients are available in the uppermost branches to support protein...
synthesis and other essential metabolic activity. (3) “Matura-
tion”—cells at the top of tall trees have undergone hundreds,
if not thousands, of divisions under UV light and other poten-
tially damaging environmental factors. (4) “Hydraulic limita-
tion” (as considered earlier). To these might be added: (5)
“Repeated dieback—the crown dies back, presumably from one
of the other four causes, and has to recommence growth from
the surviving bole.

Because the tallest redwoods are growing by up to 0.25
m yr\(^{-1}\) (Koch et al., 2004) the first two hypotheses are unlikely
here. Perhaps “maturation” is a possibility although, if these
trees have grown at this rate since seed germination, they may
only be about 450 yr old, while the proposals presented (Koch
et al., 2004) imply that 0.25 m yr\(^{-1}\) is toward the lower end of
the overall probable range. However, trunk diameter is a better
indicator of the age of living trees than is height (Carder, 1995)
so that “maturation” cannot be ruled out. If, as proposed here,
embolism formation does not impose a limit of 122 m on the
height of \(S. \text{ sempervirens}\), it is critical to understand how embo-
lisms could be removed when the xylem is under negative pres-
sure. Hacke and Sperry (2003) found that the solute concentra-
tion in the xylem increases when refilling occurs under consider-
able negative pressures and, because two mechanisms have been put
forward (Netting, 2000; Zwieniecki et al., 2001) for embolism
repair utilizing an increased solute concentration in the xylem,
these and any other possible mechanisms should be investi-
gated. Finally, the parameters responsible for repeated dieback
should be examined because, if the average dieback rate over
decades is equal to the average growth rate, there will be no net
increase in height. It seems most likely that hydraulic failure
due to some environmental factor such as severe drought (Koch
et al., 2004) would be responsible for dieback as the other pa-
rameters would tend to limit growth rather than kill the crown.
As a first step, we should be able to estimate the negative xylem
pressure at which permanent hydraulic failure occurs using
published techniques (Hacke and Sperry, 2003) so that we can
begin to understand the complexities underlying the limitations
to tree height.

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\textbf{Note:} A response to this article can be found in this issue at Koch, G. W., and S. C. Sillett. 2009. A response to: Limitations within “The Limits to Tree
Height” \textit{American Journal of Botany} 96: 545–547.