

Comment on 'Hydraulic limitation of tree height: a critique' by Becker, Meinzer & Wullschleger

Becker, Meinzer & Wullschleger (2000) recently presented a critique of the hypothesis that height growth in trees is limited by a hydraulic constraint determined by height itself (Ryan & Yoder 1997). In the original paper, Ryan & Yoder (1997) discussed the various hypotheses proposed to explain the decline in above-ground productivity and height growth in trees and proposed that height may reduce the ability of tall trees to transport water to the leaves at the tops of tree crowns.

In other words, there would be a negative feedback between the early increments in tree height and the subsequent increases in the resistance to water transport, which would then act to reduce further growth.

Rightly so, Becker *et al.* (2000) warn against hasty conclusions of causality and illustrate with a few examples the complexity of the factors affecting tree ecological and physiological behaviour, and particularly its water relations during growth.

Here, we would like to draw attention to some aspects, which have relevance to the arguments presented but have not been considered by Becker *et al.* (2000). For brevity, we will focus only on two aspects: (1) the proposed homeostasis of leaf-specific hydraulic conductance during a tree life cycle and (2) the role of leaf hydraulic resistance in the context of stomatal control.

HOMEOSTASIS IN HYDRAULIC SUPPLY: YES, NO, MAYBE. BUT EXACTLY HOW?

Becker *et al.* (2000) concluded that leaf-specific hydraulic conductance, i.e. the total plant hydraulic transport capacity relative to the leaf area present (units of $\text{kg MPa}^{-1} \text{m}^{-2} \text{s}^{-1}$), is unlikely to be lower in tall trees. Rather, a homeostatic mechanism would continuously maintain a constant proportion between the transpiring leaf area and the transporting tissues throughout the tree life cycle. Becker *et al.* (2000) explicitly proposed one possibility, i.e. that reductions in leaf-sapwood area ratios occur in tall trees, and apparently also suggested a second one, i.e. that xylem water transport becomes more efficient with ontogeny.

We propose that the discussion start instead from an examination of absolute values of tree hydraulic conductance without considering, for the moment, the amount of leaf area present on each tree. Introducing the relationship between hydraulic transport capacity and leaf area from the beginning only confounds the matter, because growth in diameter serves

the double purpose of supplying a larger crown and balancing the increases in path length.

We will adopt a scaling approach, i.e. we will try to interpret changes in the values of the allometric coefficients of log–log relationships between size and hydraulic properties (e.g. Niklas 1994). We will first examine the relationship between size and hydraulic properties at the scale of individual segments that compose a tree, and then we will move up to whole plants. Here, we define hydraulic conductivity (k_h , $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$) as the water transport capacity of stem segments of unitary length, whereas we define hydraulic conductance (K , $\text{kg s}^{-1} \text{MPa}^{-1}$) as the water transport capacity of whole plants of various lengths. The effect of height on the hydrostatic pressure gradient will not be considered for the time being.

In Table 1, we summarized the information for four species (two conifers and two broad-leaved), for which data are available on the allometric scaling of both stem segment k_h (part A) and above-ground K (part B). Because data are available only for the above-ground portion of the pathway, K indicates the water transport capacity from ground level to the terminal branchlets. Scaling is calculated with respect to stem segment diameter in the first case, tree breast-height diameter in the second one.

Both least square regression and reduced major axis regression show that the four regression coefficients (i.e. the slopes of the log–log regressions) of k_h against segment diameter are significantly larger than 2.0 (Table 1). If k_h scaled isometrically with the cross-sectional area (which is proportional to diameter squared), then the regression exponent will equal 2.0. These results are typical of many other studies where k_h has been scaled against segment diameter and illustrate that larger stems in fact have, as implied by Becker *et al.* (2000), a more permeable woody matrix than smaller stems. This can be caused by an increase in the number of conducting elements (tracheids or vessels) and/or an increase in their size, but this last factor is normally prevalent in trees and results from the well-known processes of cambial maturation in older trees.

However, when above-ground K is scaled against tree diameter at 1.3 m height (part B of Table 1), regression coefficients significantly lower than two are obtained (at least $P < 0.05$), irrespective of the particular methods used for estimating above-ground conductance. If trees were perfectly capable of hydraulically compensating for their height solely by the production of a more efficient xylem, then the scaling coefficient of above-ground hydraulic conductance K with stem diameter should equal 2.0. In other words, above-ground hydraulic conductance K should increase in exact proportion to the square of

Table 1. Allometric scaling of hydraulic conductivity k_h of stem segments (A) and of hydraulic conductance K of trees (B) with their respective diameters. Conductivity of stem segments and hydraulic conductance of whole trees are defined in the text: b^{LS} , regression coefficient based on least square regression; b^{RMA} , regression coefficient based on reduced major axis regression; SE_b , standard error of the regression coefficient; R^2 , percentage of variance explained by least square regression. The regression for whole *Pinus banksiana* trees is based on resistances from ground level to the upper third of the crown only

Species	A Regression coefficients for k_h				B Regression coefficients for K				Authors
	b^{LS}	b^{RMA}	(SE_b)	R^2	b^{LS}	b^{RMA}	(SE_b)	R^2	
<i>Acer rubrum</i>	2.63	2.72	(0.05)	0.94	1.66	1.73	(0.08)	0.92	Yang & Tyree (1994)
<i>Acer saccharum</i>	2.64	2.67	(0.05)	0.98	1.62	1.64	(0.14)	0.97	Tyree & Sperry (1988), Yang & Tyree (1994)
<i>Pinus sylvestris</i>	2.55	2.63	(0.08)	0.94	0.97	1.22	(0.14)	0.63	Mencuccini & Grace (1996)
<i>Pinus banksiana</i>	2.42	2.52	(0.24)	0.92	1.14	1.34	(0.31)	0.72	Pothier <i>et al.</i> (1989)

diameter, irrespective of total height. However, despite cambial maturation, K scales allometrically with respect to the cross-sectional area.

What is the cause for the reduced scaling of the above-ground water transport capacity despite production of a more efficient xylem? We propose that tree height was a major factor in all four cases of Table 1. Height can be involved directly in more than one way but we present only one argument here: in tall trees the proportion of total hydraulic resistance accounted for by the central stem increases, while the importance of small branchlets declines as trees grow in height (Yang & Tyree 1994; Mencuccini & Grace 1996). Height is also involved indirectly, because taller trees will also tend to have longer branches.

Trade-offs

Clearly, from the perspective of leaf gas exchange, what is relevant is not the absolute value of plant hydraulic conductance but the relationship between this property and the leaf area supported. This underscores the importance of considering how leaf area changes with functional sapwood as trees grow taller. From what has been said above, it is obvious that reductions in leaf-sapwood (A_L/A_{SW}) area ratios are a necessity, if one postulates that a homeostasis in the above-ground leaf-specific hydraulic conductance is maintained during growth.

The available data support the hypothesis that A_L/A_{SW} frequently decline with age. However, in three of the four studies of Table 1, despite changes in A_L/A_{SW} , the above-ground leaf-specific hydraulic conductance declined during growth. Even for *Acer saccharum* (Yang & Tyree 1994) a re-analysis of the published data set indicates that the reduction with size was highly significant ($y = 5.308 + 0.084/x$, adjusted $R^2 = 0.38$, $F = 20.4$, $P < 0.0001$). For the second species, *Acer rubrum*, the sample size was too limited to draw any significant conclusion. The published evidence does not unequivocally suggest that above-ground leaf-specific hydraulic conductance is independent of height. In fact, it is quite the contrary.

Costs

Also, the question must be raised whether the decreases in A_L/A_{SW} are mediated by increases in A_{SW} or, vice versa, decreases in A_L . In either case, the carbon costs and gains to the plant are affected and, one would think, growth would be negatively affected as well. Is increased allocation to sapwood production obtained at the expense of further leaf area growth? If so, from an evolutionary perspective, would it be selectively advantageous for a tree to maintain more leaves even though the hydraulic transport capacity is less than optimal?

An alternative

In an alternative treatment of the concept of hydraulic limitations to growth, Magnani *et al.* (2000) proposed that allocation to fine roots compensate for increased hydraulic resistance above-ground, so that a constant level of hydraulic supply to the leaves is maintained at the whole-plant (not the shoot) scale during tree growth. The carbon cost of maintaining and replacing fine roots was very large in mature trees, and enough to reduce the forest net primary productivity (see Magnani *et al.* 2000). The suggestion here is that the hydraulic limitation hypothesis should be reformulated considering partitioning of dry matter above and below ground and the consequent carbon gains and costs in addition to considering structural changes and leaf area-sapwood area changes with increasing tree height.

LEAF HYDRAULIC RESISTANCE. ARE WE INTERPRETING THE DATA CORRECTLY

One argument that Becker *et al.* (2000) put forward to discount the role of path length was that axial resistance only accounts for a minor fraction of the total soil-to-leaf resistance, the major components of which are located elsewhere.

While it is difficult to disagree with the statement that it is the total soil-to-leaf resistance that it is of relevance in this context, it is also necessary to

clarify some confusion in relation to the magnitude and role played by leaf hydraulic resistance.

It has been shown a number of times that leaf hydraulic resistance can play a significant role in plant water relations. However, we urge caution in the interpretation of recent measurements (e.g. Yang & Tyree 1994; Cochard *et al.* 1997), for two main reasons. The method used (perfusion of individual leaves and subsequent measurement of liquid water flow under a known pressure gradient, ΔP) does not give comparable results with alternative approaches (water potential Ψ of bagged vs non-bagged leaves; kinetics of water loss during pressure-bomb experiments – see discussion in Yang & Tyree 1994). The discrepancy among methods is large: the estimate of $\Delta\Psi$ within a leaf varied from 0.15 to 0.25 MPa for one method to 0.4–1.0 MPa for another. Until such discrepancies are solved, conclusions about the role of leaf resistance are not well rested (see discussion in Yang & Tyree 1994).

More important, the method yields a measurement of hydraulic resistance, and consequently of water potential Ψ , referred to the ultimate sites of evaporation within the leaf (cf. Yang & Tyree 1994). In the context of stomatal responses to changes in axial resistances, however, the relevant parameter is the hydraulic resistance, and the consequent Ψ , of the putative controlling sites where the hydraulic/metabolic signals for stomatal responses are produced.

It is not presently clear whether these putative sites are physically within the bulk of the transpiration stream and how close they are to the final sites of bulk evaporation. It may also be that they are located fairly closely to the central leaf bundle sheaths and xylem vessels, so that the relevant hydraulic resistance would only be slightly larger than the resistance from the petiole to the veins.

Because it is very unlikely that these signals are produced *right at the sites* of evaporation, it can be concluded that the values reported for leaf resistance, although correct, may not bear much relevance to the problem in question.

CONCLUDING REMARKS

Path length is a fundamental component of the plant hydraulic system (Table 1). Ontogenetic changes in leaf-sapwood area ratios cannot be considered separately from the simultaneous changes in height and branch length that occur during growth. Increased allocation to sapwood volume (above and below ground) must occur at the expense of further leaf area production, with likely costs for plant growth.

There is a contradiction in arguing that homeostasis exists in leaf-specific hydraulic conductance and that old trees have a larger capacitance volume. If that were the case, large trees would have higher per-unit-leaf gas-exchange rates or less negative water potentials, and homeostasis would not really

be present. It is instead more likely that increased reliance on capacitance water is accompanied by a reduced carbon investment in transport tissues.

The hypothesis of hydraulic limitations to tree height growth is likely to be a simplistic approximation of a much more complex phenomenon, but it may be useful in highlighting the areas in which further investigations and experiments are necessary.

We propose here that future studies of tree hydraulics should concentrate on determining the ontogenetic changes in (1) root hydraulic resistance and (2) whole-plant hydraulic capacitance.

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In our paper in *BioScience* (Ryan & Yoder 1997), we noted that there are striking similarities in growth patterns of woody plants. For example, height growth, maximum height and stem growth tend to be closely correlated for even-age stands or open-grown trees,

and all are highly predictable for a particular species on a particular site. We reviewed several hypotheses to explain these patterns and concluded that one of them, which we termed the 'hydraulic limitation hypothesis', was especially attractive. The hydraulic limitation hypothesis predicts that the hydraulic resistance of the soil-to-leaf pathway will increase as trees grow in size and that this increased resistance will reduce stomatal opening, photosynthesis and growth as trees approach maximum height. The hypothesis provides a functional linkage among height growth, photosynthesis and productivity, and there is experimental evidence supporting underlying mechanisms. For the alternative hypotheses we considered, either there is experimental disproof (for the respiration hypothesis) or limited information available (for the maturation hypothesis).

In their critique, Becker, Meinzer & Wullschlegel (2000) offer interpretations that they believe contradict the hydraulic limitation hypothesis. They discuss ways that woody plants may 'compensate' for the effects of size on hydraulic resistance and they offer several alternate mechanisms for height limitation: competition, genetics, reproduction and environmental damage. We welcome their criticism and the discussion it provokes, for, as Wilson (1998) stated:

'there (are) two kinds of original thinkers, those who upon viewing disorder try to create order, and those who upon encountering order try to protest it by creating disorder. The tension between the two is what drives learning forward.'

We will limit our response to three points. First, Becker *et al.* (2000) misinterpret the hypothesis and most of the counter examples they offer are not valid tests of the hydraulic limitation hypothesis. We also discuss studies not completed when the original article was published. Second, Becker *et al.* (2000) suggest that there are compensatory mechanisms that allow trees to maintain 'homeostatic' balance of water supply and demand as they grow. We agree that compensation occurs [Mencuccini & Magnani (2000) have written an excellent summary of these adjustments] but offer counter-examples that suggest that these compensations do not entirely offset hydraulic limitation. Third, we argue that the alternatives offered by Becker *et al.* (2000) for height limitation either are not satisfactory or do not exclude the role of hydraulics in limiting tree height and tree growth.

Becker *et al.* (2000) use two inappropriate comparisons when attempting to examine the hydraulic limitation hypothesis. First, they compare hydraulic characteristics for trees not only of different size but also of different species and, second, they compare trees of the same species and different size, but growing in different environments. Neither of these is a valid test of the hydraulic limitation hypothesis. The hydraulic limitation hypothesis predicts that whole-

tree hydraulic conductance, normalized by leaf area (which we term leaf-specific conductance, or K_L) of genetically identical trees in identical environments should decrease as they approach their maximum height. The hypothesis does not predict that K_L should always decrease with increasing height. Species differ in maximum height, hydraulic architecture, xylem anatomy and vulnerability to xylem cavitation, and it would be quite surprising if K_L increased with height for any combination of species.

Even within a species, there are many situations in which K_L may be unrelated or even positively correlated to tree height without contradicting the hypothesis of hydraulic limitation to maximum height. As we explained in Ryan & Yoder (1997), trees growing on nutrient-poor sites are expected to have low K_L compared to larger trees of the same species on better sites because of changes in carbon allocation and wood structure, such as an increase in the proportion of latewood to earlywood. This may explain why maximum height varies with site fertility for genetically identical trees. Likewise, a small tree in a forest understorey with suppressed growth rates owing to shading or limited space for root exploration will not necessarily have greater K_L than a non-suppressed, larger tree of the same species.

Becker *et al.* (2000) cited several studies that found little or no relationship between K_L and tree height. None of these studies is a reasonable test of the hypothesis that height and productivity are ultimately constrained by tree hydraulics. In three of the studies (Andrade *et al.* 1998; Goldstein *et al.* 1998; Becker, Tyree & Tsuda 1999), different species were compared, with one case (Becker *et al.* 1999) even comparing tropical and temperate species. Dawson (1996) reported lower sapflow (per unit leaf area) for small *Acer saccharum* compared with large trees, but the roots of the large trees grew through cracks in a soil hard pan, allowing them access to ground water that was not available to the smaller trees. The critical question in reference to hydraulic limitation is whether K_L and transpiration decline *after* the trees gain access to ground water and approach their maximum height for that site. In another study (Saliendra, Sperry & Comstock 1995) cited by Becker *et al.* (2000), K_L decreased with increasing size of *Betula occidentalis* (juveniles > saplings > adults). However, the trees were growing in a riparian community and it is not clear whether small and large trees were growing in equivalent environments; small trees may have been in the understorey. So even though this study conforms to expectations of hydraulic limitation to height, it is not a good test of the hydraulic limitation hypothesis.

To avoid these problems in interpretation, we have limited most of our comparisons to individual, open-grown trees of different sizes in the same environment or to chronosequences of even-age stands in similar environments. Furthermore, we have sought experimental situations where we know that height growth

and volume growth efficiency decreased with size. Since our 1997 paper, several new studies have demonstrated a decrease in K_L with increasing size in such situations. K_L was lower in 12–15 m *Nothofagus solandrii* compared to adjacent 3–4 m trees (M. G. Ryan and D. Whitehead, unpublished data). Also, for five paired old and young *N. solandrii* stands along an elevation gradient, $\delta^{13}\text{C}$ was 1.5‰ greater in the older stands, indicating a consistent pattern of lower canopy stomatal conductance in the older trees (M. G. Ryan and D. Whitehead, unpublished data). In wet soil conditions in Wind River, WA, K_L of 400+ year-old Douglas-fir trees was significantly lower than that of 20 and 40 year-old trees (Phillips *et al.* 1999). When gravitational resistance was subtracted, the 40 year-old trees had higher K_L than either of the other two age classes. Growth and yield data for the area show that productivity peaks at about 35–45 years. In another recent study, mean stomatal conductance of *Fagus sylvatica* was 60% less in trees 30 m taller when soil moisture was high (Schafer, Tenhunen & Oren 1999).

We proposed that hydraulic limitations to height and productivity are universal, so it is important to test the hypothesis in a variety of ecosystems and situations. In measurements of two tropical hardwood species (*Tapirira guianensis* and *Simarouba amara*) in Panama, we found no evidence of lower K_L in larger trees compared with smaller trees (N. Phillips *et al.*, unpublished). We also discovered that it is very difficult to design a good test of the hydraulic limitation hypothesis in mixed-age, mixed-size tropical forests. For small trees in gaps, the light and humidity environment is distinctly different from the overstorey trees, and their growth may be suppressed by competition from neighbouring trees. In this mixed-age and mixed environment stand, we were not comparing trees of different size growing under identical conditions. In fact, it is quite possible that the smaller trees were growing *less* per unit leaf area than the larger trees.

We realized that to test the hydraulic limitation hypothesis, experiments must be designed carefully to avoid misinterpretations owing to possible change in environmental conditions as trees grow. One approach might be to remove competing vegetation around trees of different sizes (but with the same species) and examine their growth and water relations over several years. Alternatively, a very long-term study could follow growth and water relations of individual trees as they emerge from the subcanopy to the overstorey and achieve their maximum height. We suspect that the choice of experimental locations may underlie the different interpretations between us and Becker *et al.* (2000). Most of the studies cited in Becker *et al.* (2000) are mixed-age stands, where environment almost certainly differs with tree size, and where tall trees are in an environment with greater evaporative demand.

Becker *et al.* (2000) discussed three mechanisms that could compensate for hydraulic resistance owing to increased size: decreased leaf area:sapwood area ratio

(A_L/A_S), increased wood permeability and increased water storage (capacitance) in larger trees. There is good experimental evidence for all three mechanisms. Magnani, Mencuccini & Grace (1999) proposed a fourth possibility: increased allocation to fine roots may compensate for increased hydraulic resistance above ground (thus decreasing the relative importance of below-ground resistance in larger trees). But do these mechanisms allow trees to maintain a homeostatic balance between water supply and demand as they approach maximum height? We know that they do not in the *Pinus ponderosa* system we have studied intensively. Three independent measurements, including leaf-level gas exchange (Yoder *et al.* 1994; Hubbard, Bond & Ryan 1999), stable carbon isotopes in foliage and stemwood (Yoder *et al.* 1994) and whole-tree sapflow (M. G. Ryan *et al.* unpubl. data) all indicate that larger trees have lower stomatal or canopy conductance than small trees in the same environment. Mencuccini & Magnani's (2000) analysis of published data showed that changes in sapwood permeability and A_L/A_S were not sufficient to compensate for total above-ground resistance with increasing tree size.

If trees adjust their carbon allocation or xylem anatomy to compensate for potential increases in hydraulic resistance owing to size, then this resistance must be an important factor in both evolutionary adaptation and acclimation through the life of the individual. In our view, the fact that these compensations occur is evidence that hydraulic limitations *must* be important to overall fitness of woody plants. As Mencuccini & Magnani (2000) point out, these compensations are likely to incur 'costs'. For example, increased vulnerability to xylem cavitation is associated with increases in permeability, and allocation to fine roots would reduce above-ground growth. A more sophisticated and comprehensive view of hydraulic limitations to tree height and tree growth should take into consideration these costs in addition to the direct effects of decreased K_L on leaf gas exchange.

We conclude with a brief discussion of genetic vs physical limitations of height growth. The form and functions of all living things are constrained by genetic factors, *operating interactively with environmental factors*. This is not incompatible with the idea of hydraulic limitation. Genetic factors could determine differences among species in hydraulic architecture, vulnerability to xylem cavitation, and stomatal sensitivity to water stress. According to the hydraulic limitation hypothesis, these genetic differences should result in different maximum heights for different species growing in the same conditions. The hypothesis also accounts for why an individual might achieve a different maximum height in different environmental conditions. There is no doubt that reproductive efforts also have a large impact on productivity and probably height growth. But again, this is not incompatible with the idea that maximum height is ultimately constrained by hydraulics.

It is true, as Becker *et al.* (2000) point out, that grafting experiments have demonstrated a 'memory' effect. Tissues from older plants grafted onto younger rootstock maintain growth characteristics of the older plant. We discussed this in our *BioScience* article and will not repeat the arguments here except to point out that very little is known about internal, or genetic, regulation of maturation and senescence processes in perennial plants. However, if a genetic change has occurred with age, there would need to be some measurable characteristic (such as a decrease in photosynthetic capacity) to cause a reduced growth at the same leaf area. Currently, the evidence for such a characteristic is mixed (Ryan, Binkley & Fownes 1997). For genetic differences to explain observed patterns of height and volume growth as woody plants age, it will be necessary to demonstrate how endogenous controls interact with environmental cues such that genetically identical individuals achieve different maximum heights and sizes in different environmental conditions.

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