The hydraulic limitation hypothesis revisited

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ABSTRACT

We proposed the hydraulic limitation hypothesis (HLH) as a mechanism to explain universal patterns in tree height, and tree and stand biomass growth: height growth slows down as trees grow taller, maximum height is lower for trees of the same species on resource-poor sites and annual wood production declines after canopy closure for even-aged forests. Our review of 51 studies that measured one or more of the components necessary for testing the hypothesis showed that taller trees differ physiologically from shorter, younger trees. Stomatal conductance to water vapour (g_s), photosynthesis (A) and leaf-specific hydraulic conductance (K_L) are often, but not always, lower in taller trees. Additionally, leaf mass per area is often greater in taller trees, and leaf area:sapwood area ratio changes with tree height. We conclude that hydraulic limitation of gas exchange with increasing tree size is common, but not universal. Where hydraulic limitations to A do occur, no evidence supports the original expectation that hydraulic limitation of carbon assimilation is sufficient to explain observed declines in wood production. Any limit to height or height growth does not appear to be related to the so-called age-related decline in wood production of forests after canopy closure. Future work on this problem should explicitly link leaf or canopy gas exchange with tree and stand growth, and consider a more fundamental assumption: whether tree biomass growth is limited by carbon availability.

Key-words: carbon limitation; forest production; hydraulic conductance; photosynthesis; stomatal conductance to water vapor; tree; tree height limit; turgor pressure.

INTRODUCTION

Foresters and ecologists have long recognized consistent patterns in tree and forest growth. After a brief, juvenile phase of exponentially increasing height growth, height growth slows down as trees grow taller. Trees of the same species have a lower maximum height on sites where fewer resources allow poorer growth. Annual wood production also declines after canopy closure for even-aged forests (Ryan, Binkley & Fownes 1997a; Ryan *et al.* 2004). The decline in wood production after canopy closure may or may not be mechanistically related to limits on tree height, although foresters routinely use height growth as an indicator of overall wood production in determining the harvest schedule in commercial forestry and the pattern of carbon storage with stand development. Determining the mechanism causing these patterns is a fundamental problem in forest biology and an active area of research.

Ryan & Yoder (1997) proposed the hydraulic limitation hypothesis (HLH) as a mechanism to explain these patterns, particularly the slowing of height growth with tree size and the maximum limits to tree height. HLH proposed a mechanism that would lower integrated photosynthesis (A) for a tree as it grew taller, and the lack of carbon would slow subsequent height growth as well as wood production. Furthermore, the reduced wood production in individual trees could lower the productivity of the whole forests (although stand productivity could also be influenced by changes in stand density or mortality). The HLH proposed that taller trees had greater stomatal closure as a result of three interrelated factors: (1) increased resistance with increasing length of the hydraulic path; (2) increased gravitational potential opposing the ascent of water in taller trees; and (3) maintenance of a species-specific minimum water potential in leaves. This last component was based on empirical observations that many woody species tend to regulate minimum water potentials much as thermostats maintain minimum temperatures in buildings, although Ryan & Yoder (1997) did not discuss any mechanism for this regulation.

The HLH hypothesis stimulated a great deal of criticism and new studies that compared the physiology of trees of different sizes and ages, and encouraged researchers to look more deeply into the challenges that tall trees need to overcome to move water, nutrients and sugars to where they are used. As any researcher in this area can attest, testing the hypothesis is difficult. Measurements of physiology on large trees require specialized equipment for canopy access. Because measuring the physiological response for entire, large canopies is difficult, researchers often test hypotheses by measuring small components of the whole system (e.g. a small fraction of the total canopy leaf area over a short time span), and inferring whole-canopy processes. Additional challenges come in making valid comparisons between organisms of vastly different sizes, without

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the confounding effects of differences in environment, and in evaluating age-related changes for organisms whose lifespans can be more than an order of magnitude greater than that of the investigators.

In this paper, we review progress in testing the hypothesis, examine its underlying assumptions with the benefit of hindsight and suggest how further tests of HLH or other hypotheses about limits to tree height and tree and stand growth decline might proceed. Specifically, we (1) revisit key points of the hypothesis and how they have fared in testing; (2) review new ideas for height growth limitation revealed in the past decade; and (3) discuss whether and how height growth and an 'age-related' decline in wood production may be linked.

THE HYDRAULIC LIMITATION HYPOTHESIS

Genesis of HLH

Prior to 1992, the textbook explanation for the decline in wood production after canopy closure was that increased respiratory costs of woody biomass used carbon that could have been used for wood growth. Ryan & Waring (1992) showed that woody respiration mostly declined as growth declined in a lodgepole pine (*Pinus contorta*) forest, so respiration could not account for the decreased wood growth. Ryan & Waring (1992) did find that model predictions of *A* matched the sum of carbon sinks to respiration and growth for a 40-year-old stand, but exceeded the carbon sinks for older stands. Because the sum of carbon sinks should equal canopy *A*, the discrepancy suggested that something unrelated to leaf area or photosynthetic capacity (which the model incorporated) was affecting *A*.

To explore the idea of reduced *A*, Yoder *et al.* (1994) measured diurnal patterns of stomatal conductance to water vapour (g_s) and *A* on short and tall trees of ponderosa pine (*Pinus ponderosa*) and lodgepole pine. *A* was similar for both species when vapour pressure deficit was low, but g_s and *A* were higher in the younger, shorter trees at high vapour pressure deficit. Here was a phenomenon that could explain reduced *A* for the canopy without a reduction in leaf area or photosynthetic capacity. The stomata in both species regulated leaf water potential (Ψ_{LEAF}) to maintain a species-specific midday minimum that remained similar for old and young trees. The differences in g_s and *A* seemed to derive from this regulation, and suggested that hydraulic conductance was lower in taller trees. Yoder *et al.* (1994) suggested that the lower *A* was a mechanism to explain the decline in wood growth after canopy closure and the decline in wood production:leaf area for individual trees (growth efficiency, Waring 1983). Yoder *et al.* (1994) did not discuss tree height growth or height limits.

Ryan & Yoder (1997) proposed HLH as a mechanism that reduced g_s and *A* as trees grew taller. This reduction in *A* constrains the carbon available for height and other growth. They assumed that less carbon available would also reduce wood production, because other sinks would remain high. Ryan & Yoder (1997) suggested that HLH could explain maximum tree height, declining height growth, the decline in wood production for closed canopy stands after canopy closure and the differences in height growth and maximum height for the same species growing on sites with different resource availabilities.

Barnard & Ryan (2003) provided a concise statement of the hypothesis:

'The hydraulic limitation hypothesis proposes that increased path length (in roots, stems and branches) decreases leaf-specific hydraulic conductance as trees grow in height. If stomata close to regulate leaf water status to a constant mid-day minimum as trees grow taller, tall trees must close stomata at a lower leaf to air saturation deficit (*D*) than short trees. Closure of stomata will restrict the diffusion of CO_2 into the leaf and reduce net photosynthesis and tree growth and perhaps the ultimate height of the tree. We can examine the hydraulic limitation hypothesis using an Ohm's Law analogy for water flux through trees (Tyree & Ewers 1991):

$$G_C = K_L \Delta\Psi/D \qquad (1)$$

where G_C is average stomatal conductance of the tree's foliage, K_L is average hydraulic conductance of the whole tree from soil to leaf (per unit leaf area), *D* is the leaf-to-air vapour pressure deficit and $\Delta\Psi$ is the soil-to-leaf water potential difference. A reduction in K_L as trees increase in height would result in a proportional reduction in G_C if *D* and $\Delta\Psi$ remain constant'.

Barnard & Ryan (2003) suggested that three elements were necessary for the hypothesis to account for reduced height growth in taller trees (Ryan & Yoder 1997): 'First, stomata (and consequently transpiration and photosynthesis) must respond to changes in hydraulic resistance. Second, hydraulic resistance must increase with tree height or tree age. Third, photosynthesis must be lower on the foliage of older trees'. Later papers from our laboratories added that stomata on tree leaves should regulate Ψ_{LEAF} to a constant minimum with tree height, or, if minimum midday Ψ_{LEAF} declined with tree height, the lower minimum midday Ψ_{LEAF} should still lead to lower g_s (McDowell *et al.* 2002a; Barnard & Ryan 2003). Finally, Barnard & Ryan (2003) suggested the critical link that '... the reduction in photosynthesis in older, taller trees must be sufficient to account for reduced growth'. Any physiological change should be assessed within the carbon economy of the tree and be sufficient to account for reduced growth.

As of September 2005, 305 papers have cited Yoder *et al.* (1994) or Ryan & Yoder (1997) (ISI Web of Science, Thompson Scientific, Stamford, CT 06902). Fifty-one measured one or more of the traits useful for examining HLH, and these studies allow us to conduct a broad survey of HLH and its components. Barnard & Ryan (2003) reviewed studies that led to or supported the mechanistic underpinnings of HLH – the regulation of minimum midday Ψ_{LEAF}, and evidence that experimental manipulations of K_L also change g_s and *A*. We will not repeat that review here, except to note that while most trees regulate midday minimum Ψ_{LEAF} in a way

that limits g_s and water loss, some trees do not (e.g. Hinckley, Lassoie & Running 1978; Bond & Kavanagh 1999; Phillips, Bond & Ryan 2001). In addition, not all trees regulate minimum midday Ψ_{LEAF} to the same set point at all heights – many show decreases with height (Phillips *et al.* 2002; Barnard & Ryan 2003). These decreases in midday minimum Ψ_{LEAF} do not preclude hydraulically mediated reductions in g_s, but they reduce it. Finally, while many studies show that experimental manipulations of leaf-specific hydraulic conductance (K_L) can change g_s, not all do (e.g. Hubbard, Bond & Ryan 1999; Phillips *et al.* 2001).

Observations of HLH components

Almost all of the studies relevant to HLH focused on relationships amongst tree size, hydraulic resistance and leaf-level gas exchange. Only one experiment so far has linked a test of hydraulic limitation to the carbon economy and growth of trees. In this section, we will first discuss the evidence for hydraulic limitation of leaf and canopy gas exchange (components 1–4 in Barnard & Ryan 2003), followed by a brief summary of the limited evidence linking leaf or canopy gas exchange to tree or stand growth.

A summary of published research that tested one or more aspects of HLH provides broadly consistent evidence of hydraulic limitations to leaf gas exchange (Table 1, Fig. 1). For most species and studies, the stomata regulate to enforce a minimum midday Ψ_{LEAF}, and K_L, g_s and A are reduced with increasing tree height (Table 1, Fig. 1). Many studies also revealed compensations that reduce the impact of hydraulic limitations (Table 1, Fig. 1), but complete compensation was rare. Because the evidence and arguments for a hydraulic limitation of leaf gas exchange have been discussed elsewhere (Whitehead 1998; Bond 2000; Bond & Ryan 2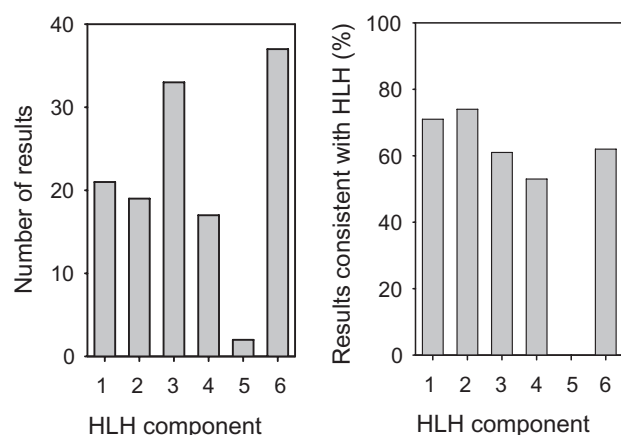000; Mencuccini & Magnani 2000; Meinzer, Clear-water & Goldstein 2001; Sperry *et al.* 2002), we will focus on those results in Table 1 that conflict with HLH predictions, as these studies may yield insight into whether hydraulic limitations to gas exchange can be considered a general feature of ageing trees.

Three features stand out for the results in Table 1 that were not consistent with HLH. Firstly, leaf and canopy measurements showed that integration to the canopy, differences in micro-environment and physiological differences between seedlings or saplings need to be considered when comparing trees of different sizes. Secondly, hydraulic limitations to gas exchange only appeared during portions of a growing season. Finally, several species showed structural changes with height that would tend to exacerbate hydraulic limitations to gas exchange. We discuss these features in the following subsections.

Leaf and canopy measurements

The inconsistent results for leaf and canopy gas exchange suggest that hydraulic limitation does not universally apply to taller trees. Some of these contrary results point to other factors that should be considered when comparing the physiology of large and small individuals. Seasonal, temporal or spatial variability in leaf gas exchange may obscure real differences in time-integrated crown gas exchange with height, although stable carbon isotopes demonstrate that such differences must have occurred (Bauerle *et al.* 1999; McDowell *et al.* 2002a; McDowell *et al.* 2005). Greater leaf gas exchange in mature trees compared to saplings of the same species (Thomas & Winner 2002) may indicate that changes in physiology between juvenile and mature individuals are stronger than any hydraulic changes with height (although such differences are not universal, Santiago *et al.* 2000; Niinemets 2002). Furthermore, access to soil moisture may differ between small and large trees (Grulke & Retzlaff 2001), complicating any test of HLH. Several studies using more integrated measurement methods [canopy conductance (G_s) estimated from whole tree sap flow] also failed to support hydraulic limitations to gas exchange (Phillips *et al.* 2001; Fischer *et al.* 2002; Barnard & Ryan 2003; Ewers *et al.* 2005), and results are inconsistent even within a species. For example, sap flow and G_s in ponderosa pine were lower in taller, older trees in central Oregon (Ryan *et al.* 2000), but not in northern Arizona (Fischer *et al.* 2002).

Figure 1. Summary of the results for the 51 studies that measured components of hydraulic limitation hypothesis (HLH). Components are (1) regulation of minimum midday leaf water potential (Ψ_{LEAF}), (2) reduced leaf-specific hydraulic conductance (K_L), (3) reduced stomatal conductance (g_s) or transpiration (E), (4) reduced leaf-level photosynthesis (A) or gross primary productivity (GPP), (5) reduced A sufficient to account for reduced growth and (6) compensation.

Seasonality of hydraulic limitation to gas exchange

The second feature characterizing several mixed/unclear results was the presence of hydraulic limitations to gas exchange that appeared only during some parts of the growing season (Kolb & Stone 2000; Grulke & Retzlaff 2001; Irvine *et al.* 2002, 2004; Phillips *et al.* 2002; McDowell *et al.* 2005). Seasonal variation in hydraulic limitation to gas exchange might be associated with the timing of growth processes or with changes in soil moisture. For example,

Table 1. Summary of results from 51 studies that measured components of the hydraulic limitation hypothesis (HLH)

Trait	Consistent with HLH? Yes	Consistent with HLH? No	Neutral, mixed or confusing
Minimum midday Ψ_{LEAF}			
No variation with tree height (stomata presumed to close to regulate)	K (*Populus tremuloides, Pinus banksiana*), M, Q, T, Z, AC, AH, AY	V	P
Varies with tree height, but stomata close to regulate	W, U, AM, AX		
Varies with tree height, but no reduction in stomatal conductance (g_s) (or lacking stomatal conductance data to test)	N, U	K (*Picea mariana*), Y	X
Reduced leaf-specific hydraulic conductance (K_L)	G, H, K (*P. banksiana*), P, Q, T, Y, AC (*Pinus flexilis*), AJ, AK, AL, AV, AY	K (*P. tremuloides, P. mariana*), V, Z	X
Reduced g_s or transpiration (E)			
Canopy from sap flow	A, L, Q, T, AA, AC (*P. flexilis*), AE, AS, AT, AW	G, V, AC (*Pinus ponderosa*)	X, AL
Leaf level from gas exchange	H, P, T, W, Z, AD, AI, AK, AM, AX	U, Y, AF, AH, AU	G, AJ, AR
Reduced leaf-level A or gross primary productivity			
Associated with lower g_s	P, S, W, Z, AD, AK, AP, AX	Y, AF	G, AJ, AR
Associated with other factors	AU	R, AH	E
Increased $\delta^{13}C$, reduced intercellular CO_2 concentration (indicates reduced stomatal opening)	B[d], D, G, H, O, P, Q, S, U, W, Y, AG, AO, AQ (*Pinus monticola P. ponderosa*), AR	AQ (*Pseudotsuga menziesii*)	
Reduced A sufficient to account for reduced growth?		E[e], G	
Compensation			
Increased sapwood area: leaf area	A, G, H, K (*P. tremuloides, P. banksiana*), L, T, V, X, AC (*P. ponderosa*), AN, AQ (*P. monticola, P. ponderosa*), AY	C, F, K (*P. mariana*), Q, AB, AC (*P. flexilis*), AE, AI, AN (*Picea abies, Abies balsamea*), AQ (*P. menziesii*), AS	
Reduced minimum midday Ψ_{LEAF}	G, AJ, AL		H
Increased hydraulic conductivity of sapwood	I, Q, AB		
Increased capacitance	I, J		

Studies in this table cited Yoder *et al*. (1994) or Ryan & Yoder (1997). Other relevant studies exist that did not either cite or were conducted prior to publication of these papers.[a–c] References and details for these studies are in Table 2.

[a]Results in Table 1 were classified as 'consistent', 'inconsistent' or 'mixed/unclear', with respect to one or more components of HLH. We used the terms 'consistent' and 'inconsistent' if results showed variation with tree height or age in accordance with, or in opposition to, HLH, respectively. The term 'consistent' reflects the possibility that factors other than hydraulic limitation could have contributed to observed results. Results were labelled 'mixed/unclear' when results consistent with HLH were observed at some times during a season or day but not others.

[b]Fifty-one studies containing a total of 142 results populate this table; 95 results are consistent with HLH, 34 are not consistent with HLH and 13 are mixed/confusing/neutral. Of the mentioned results, 22 show 'compensation' that can be considered 'consistent' with HLH, while 12 results are inconsistent with compensation (mainly, increased leaf area/sapwood area with tree height).

[c]The following types of studies are not included in this table: modelling studies; reviews or opinion papers that did not collect original data for testing HLH (e.g. Hunt, Lavigne & Franklin 1999); studies examining *within*-tree variation in leaf or branch hydraulic/gas exchange for which shade impacts could not be independently accounted; studies considering hydraulics of leaves or branches in isolation of whole tree hydraulics; ecosystem-scale studies in which tree water/carbon fluxes could not be separated from ecosystem fluxes; studies where tree height effects on physiology could not be separated from large site effects (e.g. soil moisture, fertility); studies reporting on trees varying substantially in girth but not height (e.g. Maherali & DeLucia 2001); and studies that evaluate alternative hypotheses for growth decline without presenting data needed to evaluate HLH (e.g. Niinemets, Sparrow & Cescatti 2005).

[d]Alternative causes are cited.

[e]May partially account for reduced growth.

Ψ_{LEAF}, leaf water potential; A, photosynthesis; g_s stomatal conductance to water vapour.

Table 2. Details for studies cited in Table 1

Key	Reference	Species	Heights (m)	Ages (year)	Variables measured or calculated
A	Delzon & Loustau (2005)	*Pinus pinaster*	4–29	10–91	Sapflow, Ψ_{LEAF} (pre-dawn)
B	Davis *et al.* (2004)	*Nothofagus solandri* var. *cliffortioides*	Not reported	25, 125	$\delta^{13}C$
C	Maguire, Brissette & Gu (1998)	*Picea rubens*	9.5–24	55–160	Leaf area, sapwood area
D	Buchmann *et al.* (1998)	*Abies amabilis*	8–42	40–220	$\delta^{13}C$
E	Ryan *et al.* (2004)	*Eucalyptus saligna*	0.2–30	0–6	GPP, NPP, leaf area, A_{max}
F	Callaway, Sala & Keane (2000)	*Pinus albicaulis, Abies lasiocarpa*	?–18, ?–24	67–458	Leaf area, sapwood area
G	Barnard & Ryan (2003)	*E. saligna*	7, 26	1, 5	Sapflow, A, g_s, $\delta^{13}C$, K_L, Ψ_{LEAF}, leaf area, sapwood area
H	Delzon *et al.* (2004)	*P. pinaster*	8.5–28	10–91	Sapflow, g_s, K_L, Ψ_{LEAF}, leaf area, sapwood area, $\delta^{13}C$
I	Domec & Gartner (2003)	*Pinus ponderosa*	3–33	31–225	K_s, capacitance
J	Phillips *et al.* (2003a)	*Pseudotsuga menziesii*	15, 60	20, 450	Capacitance
K	Ewers *et al.* (2005)	*Populus tremuloides, Pinus banksiana, Picea mariana*	2.7–15, 4–7.5, 1–15	12–37, 20–37, 20–151	Sapflow, G_s, leaf area, sapwood area, Ψ_{LEAF}
L	Schäfer, Oren & Tenhunen (2000)	*Fagus sylvatica*	11–39	122	Sapflow, G_s, leaf area, sapwood area
N	Woodruff, Bond & Meinzer (2004)	*P. menziesii*	14–56	25–500	Ψ_{LEAF}
O	McDowell, Licata & Bond (2005)	*P. menziesii*	15, 60	20, 500	$\delta^{13}C$
P	Skov *et al.* (2004)	*P. ponderosa*	15–27	80–450	A, g_s, Ψ_{LEAF}, K_L, $\delta^{13}C$
Q	Phillips *et al.* (2003b)	*Quercus garryana*	10, 25	40, 250	Sapflow, K_L, Ψ_{LEAF}, $\delta^{13}C$
R	Rijkers, Pons & Bongers (2000)	*Duguetia surinamensis, Vouacapoua americana, Dicorynia guianensis, Goupia glabra*	1–20	Not reported	A_{max}
S	Koch *et al.* (2004)	*Sequoia sempervirens*	35–113	> 1000?	A, Ψ_{LEAF}, $\delta^{13}C$
T	Ryan *et al.* (2000)	*P. ponderosa*	9–41	25–302	Sapflow, K_L, G_s, g_s, Ψ_{LEAF}, leaf area, sapwood area
U	Bauerle *et al.* (1999)	*P. menziesii*	2–65	5–500	Ψ_{LEAF}, $\delta^{13}C$, g_s
V	Phillips *et al.* (2001)	*Simarouba amara, Tapirira guianensis*	18, 31; 23, 28	Not reported	Sapflow, K_L, leaf area, sapwood area, Ψ_{LEAF}, g_L
W	Matsuzaki *et al.* (2005)	*Cryptomeria japonica*	0.5, 30	Shoots grafted onto 86 years old	Ψ_{LEAF}, A, g_s, $\delta^{13}C$
X	Phillips *et al.* (2002)	*P. menziesii*	15–60	20–500	Sapflow, G_s, K_L
Y	McDowell *et al.* (2002a)	*P. menziesii*	15–60	20–500	A, g_s, $\delta^{13}C$, K_L, Ψ_{LEAF}
Z	Nabeshima & Hiura (2004)	*Acer mono*	2–23	Not reported	A, g_s, K_L

Table 2. *Continued.*

Key	Reference	Species	Heights (m)	Ages (year)	Variables measured or calculated
AA	Moore et al. (2004)	P. menziesii	18–79	40, 450	Sapflow, leaf area index
AB	Mokany et al. (2003)	Eucalyptus delegatensis	3–42	Not reported	leaf area, sapwood area, K_S
AC	Fischer, Kolb & DeWald (2002)	Pinus flexilis, P. ponderosa	5–15, 6–17	Not reported	Sapflow, G_S, K_L, leaf area, sapwood area, Ψ_{LEAF}
AD	Niinemets (2002)	Picea abies, Pinus sylvestris	0.1–38, 0.1–25	0.1–130, 0.1–120	A, g_s
AE	Köstner, Falge & Tenhunen (2002)	P. abies	16–31	40–140	Sapflow, E, leaf area, sapwood area
AF	Thomas & Winner (2002)	P. menziesii, Tsuga heterophylla, plus meta-analysis of 33 others	0.5–61 (both species sampled)	5–500 (both species sampled)	A, g_s
AG	Fessenden & Ehleringer (2002)	P. menziesii	15, 32, 60	20, 40, 500	$\delta^{13}C$
AH	Day, Greenwood & White (2001)	P. rubens	11–21	54–117	A, g_s, Ψ_{LEAF}
AI	Santiago et al. (2000)	Metrosideros polymorpha	1–6.5	Not reported	Sapflow, g_s, leaf area, sapwood area
AJ	Kolb & Stone (2000)	P. ponderosa	2–25	22–141	A, g_s, Ψ_{LEAF}, K_L
AK	Hubbard et al. (1999)	P. ponderosa	12–33	40–230	Sapflow, Ψ_{LEAF}, g_s, A, K_L
AL	Irvine et al. (2002, 2004)	P. ponderosa	4–33	25–250	Sapflow, G_S, K_L, Ψ_{LEAF}
AM	Mediavilla & Escudero (2004)	Quercus rotundifolia, Quercus faginea	0.5–8.5	2 to >100	Ψ_{LEAF}, g_s
AN	McDowell et al. (2002b)	P. menziesii, plus meta-analysis of 12 others	15, 32, 60	20, 40, 500	Leaf area, sapwood area
AO	Samuelson, McLemore & Somers (2003)	Pinus palustris	Not reported	Sapling – 120	$\delta^{13}C$
AP	Wieser et al. (2002)	P. abies	Not reported	4–65	A
AQ	Monserud & Marshall (2001)	Pinus monticola, P. ponderosa, P. menziesii	24–39 (Combined)	60–85	$\delta^{13}C$, leaf area, sapwood area
AR	Grulke & Retzlaff (2001)	P. ponderosa	0.4 to >15	3–295	$\delta^{13}C$, g_s, A, Ψ_{LEAF}, NPP
AS	Roberts, Vertessy & Grayson (2001)	Eucalyptus sieberi	Not reported	14–160	Sapflow, leaf area, sapwood area
AT	Alsheimer et al. (1998)	P. abies	15–26	40–140	Sapflow, leaf area, sapwood area
AU	Sullivan, Bovard & Middleton (1997)	P. banksiana	4–15	11–75	A, g_s, E
AV	Mencuccini & Grace (1996a, 1996b)	P. sylvestris	2–24	7–60	leaf area, sapwood area, K_L, NPP
AW	Cienciala et al. (1997)	P. sylvestris, P. abies	23, 28	50, 100	Sapflow, G_S
AX	Fredericksen et al. (1996)	Prunus serotina	4–21	2–80	A, g_s, Ψ_{LEAF}
AY	Magnani, Mencuccini & Grace (2000)	P. sylvestris	2–24	7–59	K_L, leaf area, sapwood area

Ψ_{LEAF}, leaf water potential, generally measured at the midday minimum unless otherwise noted; $\delta^{13}C$, $^{13}C:^{12}C$ isotopic ratio, relative to standard; GPP, gross primary productivity; NPP, net primary productivity; A_{max}, maximum photosynthesis, generally measured at high light; sapflow, water flow through xylem; A, photosynthesis; g_s, stomatal conductance to water vapour; K_L, leaf-specific hydraulic conductance; K_S, sapwood conductance; G_s, canopy conductance; g_L, leaf conductance; E, transpiration.

transpiration (E) of small ponderosa pine trees exceeded that of tall trees in the early season, but became less than that of taller trees during the late season drought, as a result of less access to deep soil moisture (Irvine *et al.* 2002, 2004). By contrast, G_s was reduced in larger individuals of Douglas fir (*Pseudotsuga menziesii*) in the late growing season when soil moisture was low, but not in the mid-growing season when soil moisture was greater (Phillips *et al.* 2002). These examples represent cases in which the micro-environment of trees is not the same for trees of different sizes. These cases may be an 'unfair' test of HLH, although they highlight the importance of accounting for important confounding factors that influence the function of trees of different heights. Resolving the causes for seasonal variation in hydraulic limitation in the context of the seasonal carbon budget of trees will likely provide critical insights into the timing and degree of hydraulic limitations on gas exchange and the impact on annual carbon gain and tree growth.

Hydraulic compensation versus exacerbation

In its original development, the HLH focused on the impacts of hydraulic path length and gravitational potential on leaf gas exchange, but did not emphasize any role for structural or anatomical changes with tree size. Several studies presented evidence of compensations that reduce the impact of tree height on the conducting system, including decreased leaf area:sapwood area, reduced minimum midday Ψ_{LEAF}, increased sapwood conductivity and increased capacitance (Table 1). All of these are consistent with an increased hydraulic limitation with tree height, but work against a hydraulically driven reduction in total tree A. The impacts of these structural changes on the carbon balance of the tree, if any, remain unknown.

The ratio of leaf area:sapwood area frequently increased with tree height (Table 1), exacerbating the hydraulic changes that occur with tree height. This increase in leaf area to sapwood area is a strong counter-argument to hydraulic limitation, because no advantage of reducing leaf-specific hydraulic conductivity has been found. A recent model of optimal tree carbon gain and allocation (Buckley & Roberts 2005) suggests that trade-offs between water transport, leaf gas exchange and nutrient and light capture might explain why some trees show increased leaf area to sapwood area with height.

Even the studies that failed to support HLH generally showed a coordination of structural (leaf area to sapwood area) and physiological regulations of tree water flux (Whitehead, Edwards & Jarvis 1984; Andrade *et al.* 1998). In the tropical tree species *Simarouba amara* and *Tapirira guianensis* (Phillips *et al.* 2001), g_s increased with tree size, which was inconsistent with the predictions of HLH. However, leaf area to sapwood area of branches decreased dramatically with tree size, confering greater hydraulic sufficiency and allowing for greater g_s in taller trees. Similarly, height-related variations in minimum midday Ψ_{LEAF}, G_s, K_L and leaf area to sapwood area ratio in aspen (*Populus tremuloides*) and black spruce (*Picea mariana*) (Ewers

et al. 2005) were inconsistent with HLH, but in combination, these variables conformed to a model linking G_s to hydraulic properties of trees.

Linking hydraulic limitation of leaf gas exchange with tree growth

Only one experiment (Barnard & Ryan 2003; Ryan *et al.* 2004) explicitly linked physiological tests of HLH with tree or stand growth. This study showed that HLH was not responsible for the decline in canopy A and annual wood production. G_s remained similar for *Eucalyptus saligna* trees 7 and 26 m tall in adjacent experimental plots, because decreased leaf area to sapwood area ratio and minimum midday Ψ_{LEAF} compensated for the increased path length and influence of gravity in taller trees.

Although other studies are clearly needed, we found no evidence to support the idea that reductions in A seen at the leaf level would account for reductions in stand wood production (see Ryan *et al.* 1997a). Differences in A or conductance with tree height are generally measured under conditions ideal for discerning differences – high light and low humidity, and at the top of trees. Differences for A integrated over the canopy for a season would likely be lower given less light in the lower canopy and periods of clouds and high humidity. Furthermore, reductions are much greater for wood production (30–90%) (Ryan *et al.* 1997a) after canopy closure than those measured for hydraulic limitation of A where it occurs [e.g. 21% (Hubbard *et al.* 1999), 28% (Skov *et al.* 2004), 27% (Niinemets 2002)]. Substantially larger reductions in A on a weight basis have been reported (Niinemets 2002; Nabeshima & Hiura 2004), for example, from 40 to 10 nmol g^{-1} s^{-1} for 30–110 m trees (Koch *et al.* 2004), but unless accompanied by a reduction in leaf area, these lower weight-based rates cannot explain lower biomass production. Finally, the lack of a universal response to hydraulic limitation of gas exchange argues against HLH being the explanation for 'age-related' decline in wood production.

Additional features of literature summary

Several additional features of our literature summary are notable. Firstly, few studies have investigated multiple components of HLH. None of the 51 studies tested all six of the components of HLH listed in Table 1; three studies tested five of the six (McDowell *et al.* 2002b; Barnard & Ryan 2003; Skov *et al.* 2004); three studies tested four of six; 13 studies tested three of six; six studies tested two of six; 19 studies tested one of six; and four additional studies reported only on hydraulic compensation. Secondly, the distribution of findings amongst components of HLH is highly uneven. For example, 17 results of carbon isotope discrimination were relevant to HLH, but only two studies (in a single experiment) evaluated whether a decline in A was sufficient to account for a decline in growth. Thirdly, a large number of results come from relatively few, temperate conifer species (ponderosa pine, Douglas fir, Scots pine

(*Pinus sylvestris*) and Norway spruce (*Picea abies*), although the total number of species studied was evenly distributed amongst conifer (16) and deciduous (18) species.

LINKS BETWEEN REDUCED HEIGHT GROWTH, 'AGE-RELATED' PRODUCTION DECLINE AND MAXIMUM HEIGHT?

Yoder *et al.* (1994) and Ryan & Yoder (1997) suggested the link between declining height growth and declining tree and stand biomass growth, but these papers did not demonstrate that link. The link seemed plausible because the 'age-related decline' in wood productivity occurs in even-aged stands after canopy closure (Ryan *et al.* 1997a), and stands are composed of trees of the same age. In this section, we will explore the links between tree height or height growth, and tree and stand biomass growth, using the *E. saligna* data set from Ryan *et al.* (2004).

Does a decline in tree or stand biomass growth occur at the same time as a decline in height growth? For individual *E. saligna* trees, height growth declines with tree height (Fig. 2a), but the amount of decline and the height at which it occurs varied with tree density, fertilization treatment and position within the stand. The rate of decline in height growth appears to be similar for all trees in all treatments, because the slopes are similar. The biomass growth for individual trees decreases with tree height (Fig. 2b), but the relationship with tree height differs with tree density and fertility. The biomass growth of individuals is poorly related to tree height growth (Fig. 2c), and the relationship of height growth and biomass growth differs with tree density, fertility and stand age. The tallest trees (6-year-old trees in 2000) increase biomass much more relative to height growth than do younger trees. For example, 1 m of height growth for a 30-m-tall tree in 2000 relates to 20 kg biomass growth per year, compared to <1 kg biomass growth per year for an 8-m-tall tree in 1995. A potential explanation for this pattern is that the mass needed to support wind loads on the canopy scales exponentially with diameter (Long, Smith & Scott 1981; King 2005). Because of these structural needs to prevent buckling or snapping, maintaining a constant height growth as trees grow taller would require exponentially increasing biomass growth.

At the stand level, biomass production was weakly related to average tree height for the *E. saligna* trees, probably because biomass production *is* slowing as the trees become larger (Fig. 3a). Stand biomass production does appear to be positively related to average tree height growth, but the pattern differs with tree density (Fig. 3b). Because of this complicated pattern and the change in the relationship between tree biomass production and tree height growth as trees grow taller (Fig. 2c), inferences of tree or stand biomass production based on tree height growth are likely to be poor.

Do individual trees show the same pattern for growth as do stands? This question relates to the ability to make inferences about a decline in stand wood production from
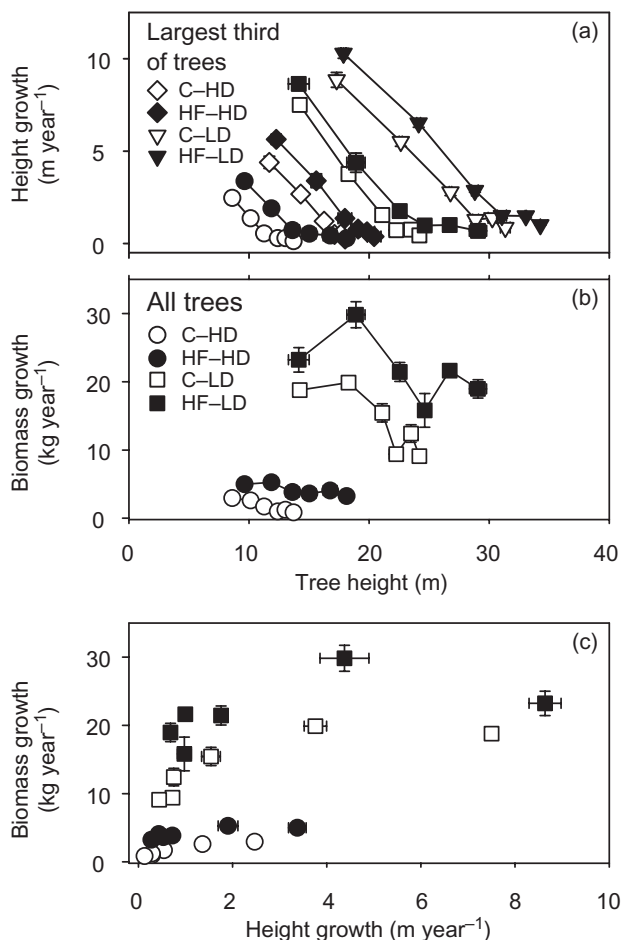

Figure 2. Patterns of biomass growth, tree height and height growth for individual trees in *Eucalyptus saligna* plantations of Ryan *et al.* (2004) for their 12 'control' (C) and 'high-fertility' (HF) plots. (a) Height growth decreases with tree height, but the relationship differs with fertility, tree density [low density (LD) = 3 × 3 m spacing, 1111 trees ha^{-1}; high density (HD) = 1 × 1 m spacing, 10^4 trees ha^{-1}] and size of tree within the stand. (b) Tree biomass growth decreases with tree height, and the relationship differs with tree density and fertility. (c) Biomass growth of individuals is poorly related to tree height growth ($R^2 = 0.33$), and the relationship of height growth and biomass growth differs with tree density, fertility and stand age. Tree height was estimated from an allometric relationship developed from diameters and heights measured for 36 trees (5–55 m heights) harvested on site or at a nearby site. Height (m) = [diameter at breast height (d.b.h) × 77.763]/(d.b.h. + 32.29), $R^2 = 0.95$.

measurements on individuals. Stand biomass growth is the sum of the biomass growth of all individuals in the stand, but not all individuals grow at the same rate. Biomass growth may differ for trees of different sizes, which an arithmetic average may obscure. In addition, once canopy closure occurs, the population of trees segregates into different competitive classes (dominants, co-dominants, suppressed), and trees in these different competitive positions may grow and use resources differently (Binkley *et al.* 2002).

Finally, mortality, recruitment and the size of the initial population can alter the number of trees and the leaf area
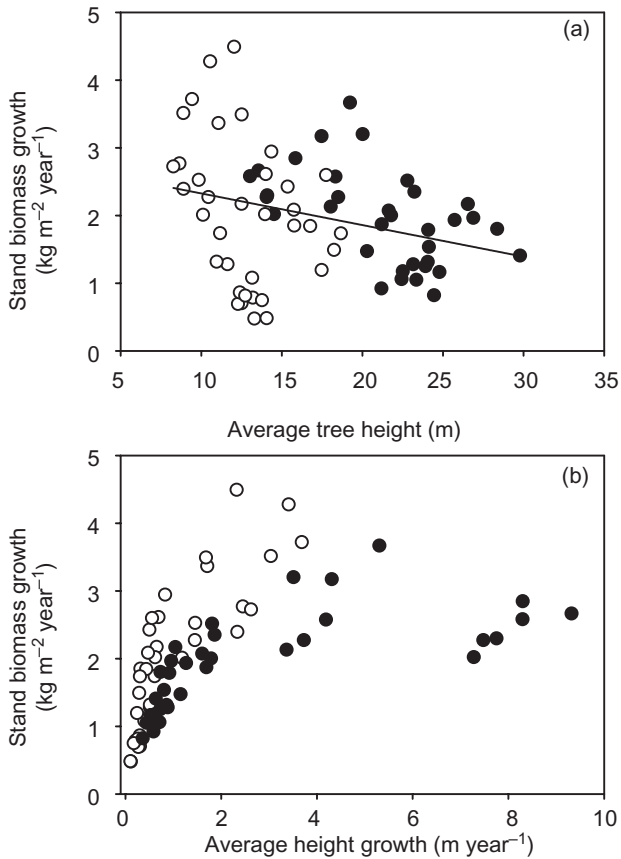
Figure 3. (a) Stand growth declines with average tree height ($R^2 = 0.08$), and (b) increases with average tree height growth. Date from trees in *Eucalyptus saligna* plantations of Ryan *et al.* (2004) for their 12 'control' and 'high-fertility' plots. Open symbols are plots with trees planted at 1×1 m spacing (10^4 trees ha^{-1}), closed symbols are plots with trees planted at 3×3 m spacing (1111 trees ha^{-1}).

of the stand, and these differences in population size amongst stands can alter the overall biomass production.

Figure 4 shows that for the *Eucalyptus* example, growth for trees of different sizes differed from that of the stand average (which, when multiplied by the number of trees would yield the stand growth). For example, the average tree growth at age 6 was 46% of that at age 2 (when canopy closure occurred), and 54, 18 and 5% for the largest, middle and lowest third, respectively (Fig. 4a). The rate of decline in biomass growth for the largest trees was less than that of the smaller trees, so the stand growth reflected the combination. The rate of decline in biomass growth in Fig. 4a and b does reflect a large influence of largest trees, because these will have the most growth (in Fig. 4, the largest third of the trees in the stand was responsible for 65–85% of the biomass growth). In this *Eucalyptus* study, the stand and tree growth peaked and declined at the same time. Another study showed that stand biomass growth peaked and started to decline about 40 years earlier than the largest trees did (Binkley 2004).

These examples provide several lessons for evaluating HLH or any hypothesis about why tree and stand biomass production declines with tree size: (1) In an even-aged stand, patterns in tree biomass growth may not reflect those of the stand, because trees of different sizes grow differently and contribute to stand biomass growth differently. (2) Slowing the biomass growth of the larger trees in the stand likely yields slowing stand biomass growth, but the peak and decline for individuals may not coincide with that of the stand. (3) Height growth does decline with tree size and age. (4) The link between tree height growth and tree or stand biomass production is tenuous and varies with tree size (and, in the *Eucalyptus* data, with stand density and fertility).

OTHER EXPLANATIONS FOR AGE-RELATED DECLINE IN NET PRIMARY PRODUCTIVITY (NPP)

Other explanations have been offered to explain age-related decline in NPP (Gower, McMurtrie & Murty 1996;
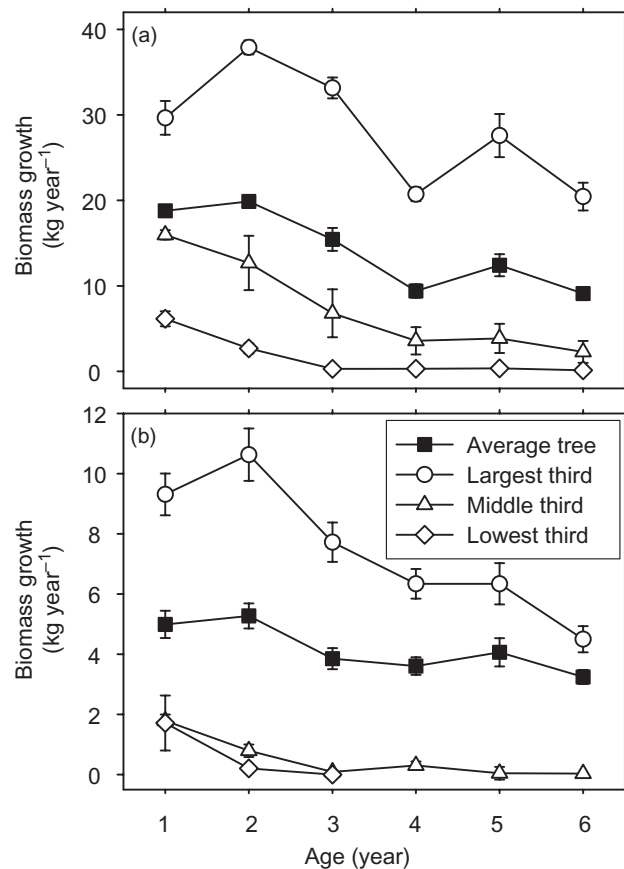

Figure 4. Biomass growth and the rate of decline in biomass growth of the average tree differed from that of trees in different size classes (largest, middle, lowest third). Data are from *Eucalyptus saligna* plantations described in Ryan *et al.* (2004). (a) 'Control' treatment planted at 3×3 m spacing (1111 trees ha^{-1}). (b) 'High-fertility' treatment planted at 1×1 m spacing (10^4 trees ha^{-1}).

Ryan *et al*. 1997a), such as declining nutrition (nutrients become locked in biomass, lowering leaf area and *A* and increasing below-ground allocation) and respiration (allocation to wood respiration lowers wood growth). The *Eucalyptus* forest development study (Ryan *et al*. 2004) tested these ideas, and found that sustained nutrition slowed down but did not stop the decline in wood growth, and wood respiration was unrelated to the decline. The *Eucalyptus* study also found no support for the hypothesis that an increased allocation to fine roots will offset any decrease in leaf-specific hydraulic conductivity (Magnani *et al*. 2000). Other ideas that remain to be tested include lower light capture per unit leaf area (Niinemets *et al*. 2005); changes in sinks, perhaps through lower turgor pressure (Woodruff *et al*. 2004); and changes in resource use as trees in stands segregate into a dominant or suppressed condition (Binkley *et al*. 2002).

AGE VERSUS SIZE?

Distinguishing between age and size as a causal factor in changing physiology may help distinguish between changes in meristems or gene expression and extrinsic factors, such as water potential or hydraulic conductance acting on the stomata and *A*, that change with size (Mencuccini *et al*. 2005). Several studies demonstrate differences in gene expression for trees of different ages (reviewed in Day, Greenwood & Diaz-Sala 2002), but the driving mechanism is unclear, as is the effect on physiology. A few studies used scions from donors of different sizes and ages grafted to a common (small) rootstock to eliminate size while keeping age differences. These studies differ dramatically in their results. In four species that differ in wood anatomy, grafts or rooted cuttings from tall, older trees reverted to the physiology of young, short trees, suggesting that size caused physiological changes (Mencuccini *et al*. 2005). Shoots from younger trees grafted onto the tops of larger trees had lower *A* than rooted cuttings, and the same *A* as intact shoots in the same position (Matsuzaki *et al*. 2005). By contrast, other studies showed that the physiology (Day *et al*. 2001) or growth (Takemoto & Greenwood 1993) of grafted scions reflected the age of the donor, suggesting that genetic changes in meristems caused the physiological changes. Day *et al*. (2002) also suggested a third possibility – that size might trigger changes in gene expression, perhaps through changes in plant water relations.

TURGOR – A NEW MECHANISM?

Gravitational potential adds 0.01 MPa m^{-1} to the xylem water potential gradient in trees. Unlike the low Ψ_{LEAF} generated by *E* that dissipates at night, the lower water potential from gravity is a chronic part of the environment of leaves on tall trees. In addition to the effects on hydraulic limitation described previously, this potential gradient can alter turgor pressure, affecting cell expansion and division unless plant cells adjust the osmotic pressure to compensate. Woodruff *et al*. (2004) recently showed that foliage on

tall Douglas fir trees had lower turgor pressure than for shorter trees at the time of bud break, because the gravitational gradient in water potential was not offset by osmotic adjustment. They also found slower branch elongation, and thicker leaves on the taller trees, consistent with the lower turgor pressure. Other studies have found that specific leaf area increases with tree height, apparently independent of light environment (Grulke & Miller 1994; Wieser 1997; Thomas & Bazzaz 1999; Day *et al*. 2001; Niinemets 2002; Marshall & Monserud 2003; Koch *et al*. 2004; Nabeshima & Hiura 2004). Because thicker leaves may result from less cellular expansion, these results suggest that a lower turgor pressure may be a common condition for tall trees.

Accepting a turgor limitation requires an entirely different paradigm for thinking about limits to growth, because lower turgor slows down growth by limiting cell expansion and division instead of reducing *A*. It is possible that a lower turgor pressure may slow carbon sinks regardless of carbohydrate supply.

CARBON LIMITATION IN OLDER TREES?

The mechanism proposed in HLH for reduced growth fundamentally assumes that reduced *A* reduces growth. In other words, tree growth is generally constrained by carbon limitation, regardless of age or size. Increasing evidence suggests that trees, particularly mature or taller trees, are not limited by carbon supply (Körner 2003). In a mature tropical forest, non-structural carbon reserves (primarily starch) remained high throughout the year and increased during the dry season when water stress may have reduced growth more than *A* (Würth *et al*. 2005). A mixed-species, mature temperate forest failed to increase wood growth under an increased atmospheric CO_2 and leaf-level *A*, and non-structural carbon reserves increased (Körner *et al*. 2005). A survey of forests in different climatic zones found that non-structural carbon reserves increased during periods of reduced growth (Körner 2003). Finally, we note that sink limitations (severe root pruning) produce mature bonsai trees. These studies suggest that *A* was not 'pushing' or limiting growth, rather that controls over sinks limited the use of available carbon. While we might expect such sink limitations to reduce *A* through an end-product inhibition (Wiemken & Ineichen 2000), the extra carbon may simply flow through trees and be released rapidly below-ground, without changing *A* (Körner *et al*. 2005).

How might a sink limitation apply to the problem of tree and forest growth changes with height and age? Retaining the dominant paradigm for forest growth of a carbon limitation, and focusing on mechanisms that reduce *A* will overlook factors controlling sinks. This seems clear, but virtually all studies focusing on growth reductions with tree height have assumed a carbon supply limitation and looked for a reduction in *A*. But if excess carbohydrates do not reduce *A* in mature trees, a sink limitation may not produce an *A* signal.

If a sink limitation does regulate growth rate with tree size or age, how would the sink limitation change with tree

size or age to produce the observed patterns in tree growth and height? For slowing growth on an individual site, a declining turgor pressure with tree height (Woodruff *et al.* 2004) offers a potential sink-limiting mechanism, because slower or less complete cell expansion may limit the use of available carbohydrates (Alves & Setter 2004). In addition, cell division may be more sensitive to turgor pressure than cell expansion (Kirkham, Gerloff & Gardner 1972), enhancing a sink limitation. How this process might act throughout the tree (on foliage and wood lower in the tree where turgor would be higher) remains unclear. If water availability were the only difference amongst sites, a turgor-caused sink limitation might explain the different rates of tree height and biomass growth, and different maximum heights reached for the same species growing on different sites. Sites with lower water availability would operate under lower Ψ_{LEAF}, have lower turgor pressure and reach a sink limitation at a lower height. However, nutrition and climate also play a role in site differences. Temperature does have a stronger effect on the rate of cell division than on *A* (Körner 2003), which suggests that a cold environment will produce shorter trees with slower growth – a prediction supported by an observation (Körner 1998). Poor nutrition does appear to restrict growth more than *A* (Schulze 1982), perhaps because plants in nutrient-poor conditions use more annual *A* below the ground (Giardina *et al.* 2003). We also cannot rule out some genetic causes to a sink limitation, because many trees and other woody plants seem to have a constrained size far below theoretical limits.

A PATH TO DEFINITIVE TESTS

Most of the studies in Table 1 (including our own) examined HLH or other ideas about the causes of growth differences with tree size using leaf-level measurements (e.g. g_s, *A*, leaf-specific conductance, Ψ_{LEAF}), key indicators [e.g. response of g_s to vapour pressure deficit, leaf or wood ^{13}C:^{12}C isotopic ratio, relative to standard ($\delta 13C$)] or indices (growth per unit leaf area, relative growth rate, G_s estimated from sap flow). These techniques were appropriate for identifying if a hydraulic limitation differs between tall and short trees, and a reasonable strategy for exploratory work. However, they failed to link (or incompletely linked) physiological behaviour with the patterns that we are attempting to explain (tree and stand growth, tree height and height growth).

Growth efficiency (wood growth per unit leaf area) can be used to compare the carbon balance for trees of different sizes, generally integrated over a year or years (Waring 1983). However, processes other than *A* or wood growth can affect this ratio, making it difficult to map differences in growth efficiency back to physiological differences. Wood growth receives only 20–30% of the annual carbon fixed in *A* (Ryan, Lavigne & Gower 1997b), and appears to be the most malleable component amongst sinks (Waring & Pitman 1985; Ryan *et al.* 2004). In addition, not all leaf area receives the same light or has the same photosynthetic capacity. Therefore, shifts in annual partitioning of *A* or

differences in light or photosynthetic capacity could cause differences in growth efficiency, independent of differences in *A*, whether caused by hydraulic limitation or not.

Leaf-level measurements of g_s and *A* survey only a small portion of the foliage, generally for a limited time. Differences in leaf physiology are difficult to relate to G_s and canopy *A*, because the distribution of leaf area, photosynthetic capacity and light also strongly controls canopy behaviour. Furthermore, differences in photosynthetic capacity can cause differences in *A* and g_s unrelated to hydraulic limitation.

We suggest that providing a direct link between physiology and tree response will clarify the causes of patterns of tree growth. The best test would measure the annual carbon balance of the tree: total *A*, wood growth, height growth and wood growth/*A*. This is very difficult for an individual tree of any size, because trees are difficult to enclose or measure frequently. Paradoxically, estimating carbon balance is somewhat easier for a stand of similar trees, and two methods are available. Firstly, carbon sinks can be measured and summed to estimate *A* (Möller, Müller & Nielsen 1954; Ryan *et al.* 2004). This method is likely simpler and more accurate than estimating *A* from leaf-level measurements and a model, but it requires many measurements of soil and above-ground respiration, and has its own uncertainties (Ryan *et al.* 2004). Secondly, the net ecosystem exchange of carbon can be measured with eddy covariance (Baldocchi, Hicks & Meyers 1988), and *A* estimated by adding an estimate of ecosystem respiration, either from night eddy covariance measurements corrected for temperature or by concurrent measurements of soil and above-ground plant respiration. Neither method would apply to individual trees because below-ground sinks cannot be assigned easily to an individual. For individual trees, canopy *A* can also be derived from G_s (estimated from sap flow and corrected for aerodynamic coupling), and measurements of photosynthetic capacity, leaf area and canopy light absorption. Finally, canopy *A* models might be used to help integrate leaf-level measurements and provide a partial link to tree or stand carbon balance.

CONCLUSION

The patterns for tree and stand growth with increasing tree height – slowing height growth, decline in tree and stand wood growth and slower growth where trees of the same species reach lower heights – are so regular, that it is difficult to discard a simple, universal explanation. However, we do not yet have one. Our review shows that hydraulic limitation appears to operate in many trees (but not all), and lowers *A*, g_s and tree water use in older, taller trees where it occurs. However, HLH failed to account for the reduction in *A* in *Eucalyptus* (Barnard & Ryan 2003; Ryan *et al.* 2004), the only study that explicitly linked measurements of whole-forest carbon budgets with a test of HLH. In addition, the reductions in *A* seen at the leaf level for studies in Table 1 are unlikely to account for reductions in wood production measured in many studies (30–90%)

(Ryan *et al.* 1997a), unless other sinks also decline with tree height growth, and reduced *A* only reduced wood production. That strategy for carbon allocation seems unlikely, because fluxes to respiration, below-ground foliage and wood production appear to change in concert with changes in canopy *A* (Giardina *et al.* 2003; Ryan *et al.* 2004; Litton, Ryan & Raich unpublished results). If larger trees are not carbon limited, and growth is limited by sinks through lower turgor pressure, genetic change or some other unknown mechanism, any reduction in *A* may not be important for growth or carbon balance.

One benefit from testing HLH is the increasing knowledge that old, tall trees are physiologically and morphologically different in many ways from the young, short trees commonly measured. Many of the studies in Table 1 show that older, taller trees have lower g_s, *A*, Ψ_{LEAF}, turgor pressure, ^{13}C discrimination and branch expansion, but higher specific leaf area. Some studies also show that short and tall trees operate in a different micro-environment, with different access to resources. The distribution of leaf area within stands also changes from a thin, shallow layer at canopy closure to a much deeper, more complicated arrangement in older stands (Brown & Parker 1994; Parker, Davis & Chapotin 2002). These physiological and structural differences likely alter ecosystem fluxes of carbon (Pregitzer & Euskirchen 2004) and water (Roberts *et al.* 2001; Moore *et al.* 2004), and should be considered in physiologically based modelling of forest growth or ecosystem fluxes. These changes should also be considered when extrapolating any measurements of tree physiology.

In the original description of HLH, Ryan & Yoder (1997) did not consider compensation, or adjustments made by the tree to mitigate the effects of increased path length and hydraulic resistance. These include increases in the diameter of conducting elements and the sapwood to leaf area ratio, and decreases in minimum Ψ_{LEAF}. These compensating factors do appear to at least partially mitigate a hydraulic limitation to leaf gas exchange, and also contribute to the increasing list of height-related physiological changes in trees. The costs of these compensating factors on the carbon balance of the tree, and their effect on drought tolerance may be important but have yet to be considered.

Many of the studies of physiological changes with height and age suggest that the critical signal seems to be height and its effects on xylem water potential. Perhaps this is why the response appears similar for all trees, although the signal might act through different response pathways. The effects of height-induced changes in Ψ_{LEAF} have yet to be examined for triose phosphate uptake limitation, phloem transport or the activation of genetic expression. Woody plants are complex organisms, and we believe that further progress in understanding age- or height-related physiological changes will best come from considering the whole organism.

Future studies on the causes of height and growth decline in trees should consider whether trees are carbon limited, and if not, whether such limitation changes with tree growth. A growing carbon surplus as trees grow taller might explain some of the disparate results seen when comparing the physiology of trees of different sizes. If *A* is not forcing growth, but rather growth slows down in response to some 'sink limitation', trees may have many pathways to shunt excess carbon.

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