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Author(s): N. McDowell, H. Barnard, B. J. Bond, T. Hinckley, R. M. Hubbard, H. Ishii, B. Köstner, F. Magnani, J. D. Marshall, F. C. Meinzer, N. Phillips, M. G. Ryan and D. Whitehead

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N. McDowell · H. Barnard · B.J. Bond · T. Hinckley
R.M. Hubbard · H. Ishii · B. Köstner · F. Magnani
J.D. Marshall · F.C. Meinzer · N. Phillips · M.G. Ryan
D. Whitehead

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Abstract The leaf area to sapwood area ratio ($A_l:A_s$) of trees has been hypothesized to decrease as trees become older and taller. Theory suggests that $A_l:A_s$ must decrease to maintain leaf-specific hydraulic sufficiency as path length, gravity, and tortuosity constrain whole-plant hydraulic conductance. We tested the hypothesis that $A_l:A_s$ declines with tree height. Whole-tree $A_l:A_s$ was measured on 15 individuals of Douglas-fir (*Pseudotsuga menziesii*

var. *menziesii*) ranging in height from 13 to 62 m (aged 20–450 years). $A_l:A_s$ declined substantially as height increased ($P=0.02$). Our test of the hypothesis that $A_l:A_s$ declines with tree height was extended using a combination of original and published data on nine species across a range of maximum heights and climates. Meta-analysis of 13 whole-tree studies revealed a consistent and significant reduction in $A_l:A_s$ with increasing height ($P<0.05$). However, two species (*Picea abies* and *Abies balsamea*) exhibited an increase in $A_l:A_s$ with height, although the reason for this is not clear. The slope of the relationship between $A_l:A_s$ and tree height ($\Delta A_l:A_s/\Delta h$) was unrelated to mean annual precipitation. Maximum potential height was positively correlated with $\Delta A_l:A_s/\Delta h$. The decrease in $A_l:A_s$ with increasing tree size that we observed in the majority of species may be a homeostatic mechanism that partially compensates for decreased hydraulic conductance as trees grow in height.

N. McDowell (✉) · B.J. Bond · N. Phillips
Department of Forest Science, Oregon State University,
Corvallis, OR 97331, USA
e-mail: nate.mcdowell@orst.edu
Tel.: +1-541-7378493, Fax: +1-541-7371393

H. Barnard · R.M. Hubbard · M.G. Ryan
Department of Forest Sciences
and Graduate Degree Program in Ecology,
Colorado State University, Fort Collins, CO 80523, USA

T. Hinckley · H. Ishii
College of Forest Resources, University of Washington,
Seattle, WA 98195–2100, USA

H. Barnard · R.M. Hubbard · M.G. Ryan
USDA Forest Service, Rocky Mountain Research,
240 West Prospect Rd., Fort Collins, CO, 80526-2098, USA

B. Köstner
TU Dresden, IHM-Meteorologie,
Pienner Str. 9, D-01737 Tharandt, Germany

F.C. Meinzer
USDA Forest Service, Forestry Sciences Laboratory,
3200 SW Jefferson Way, Corvallis, OR 97331, USA

J.D. Marshall
Department of Forest Resources, University of Idaho,
Moscow, ID 83844, USA

F. Magnani
CNR-IMGPF, via A. Vannucci 13, 50134 Firenze, Italy

D. Whitehead
Landcare Research, PO Box 69, Lincoln 8152, New Zealand

Present addresses:

H. Ishii, Biosphere Dynamics Research Group,
Institute for Low Temperature Science, Hokkaido University,
Sapporo 060–0819, Japan

N. Phillips, Boston University, Geography Department,
675 Commonwealth Avenue, Boston, MA 02215, USA

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Introduction

The allometric relationship between stem basal or sapwood area and whole-tree leaf area has been recognized since the original work by Huber (Huber 1928; Waring et al. 1982). This relationship was conceptualized into the pipe model (Shinozaki et al. 1964a, b), which proposes that a given unit of leaf area is supplied with water from a constant quantity of conducting pipes. Implicit in the model is the assumption that the ratio of leaf area to sapwood area ($A_l:A_s$) is a constant throughout plant development (Shinozaki et al. 1964a). Consistent with the model, it should be possible to estimate the leaf area of trees if the sapwood area and the whole-tree $A_l:A_s$ are known (Waring et al. 1982). The pipe model has been widely employed in studies that require knowledge of tree or stand leaf area (e.g. Gholz et al. 1976, 1979; Waring et al. 1982; Turner et al. 2000).

Investigation of the pipe model over the last two decades has revealed that $A_1:A_s$ is often dependent on site water balance. Whole-tree $A_1:A_s$ declined with decreasing soil water availability at constant evaporative demand for a study on *Eucalyptus* (White et al. 1998). Furthermore, $A_1:A_s$ declined along gradients of low to high evaporative demand (Waring et al. 1982; Mencuccini and Grace 1995). These observations can be explained using a simple model based on Darcy's Law showing that reductions in $A_1:A_s$ may compensate for increased evaporative demand, thus preventing the development of damaging water potential gradients and minimizing reductions in canopy conductance. This hydraulic model was described by Whitehead and Jarvis (1981) and Whitehead et al. (1984) as:

$$\frac{A_1}{A_s} = \frac{k_s \Delta \psi}{h \eta g_s D} \quad (1)$$

where D is atmospheric vapor pressure deficit (a net radiation term should be added for poorly coupled canopies), g_s is canopy conductance to water vapor, k_s is sapwood permeability of the hydraulic pathway, $\Delta \psi$ is the soil-to-leaf water potential difference including the effect of gravity, η is the viscosity of water at a given temperature and h is tree height. We note that this model is most appropriately applied to cylinders of uniform material, and it is an oversimplification of tree hydraulics in several respects. The path length from bulk soil to leaf, rather than height per se, is the most appropriate term. However, because height is a significant fraction of total path length and is much more commonly measured, we use it here as a surrogate. This model does not include the effects of changing root surface area (Sperry et al. 1998; Magnani et al. 2000) or variation in k_s , due to, for example, partial cavitation or tapering of conducting elements (Niklas 1994; West et al. 1999). $\Delta \psi$ in our application of this model includes the effect of gravity because physiological and architectural behavior responds to the net effect of the soil-to-leaf water potential difference as regulated by leaf and soil water potential and the gravitational constraint on minimum leaf water potential. This model is consistent with both the cohesion-tension theory (Dixon and Joly 1895; Zimmermann 1983) and the concept of the development of a homeostatic mechanism to reduce the occurrence of cavitation and avoid runaway embolism (Tyree and Sperry 1988). Such a homeostatic response may occur via short-term (i.e. minutes to days) adjustment of g_s and leaf water potential, or long-term (i.e. days to generations) adjustment of k_s , h , and $A_1:A_s$. This hydraulic model provides a framework to develop and test hypotheses regarding the interaction between hydraulic architecture, stomatal conductance, and climate.

One hypothesis derived from the hydraulic model is that $A_1:A_s$ will decline with increases in height. This hypothesis assumes that other variables within the hydraulic model are constant with increasing height, or that any changes in these variables with increasing height do not oppose or exceed concurrent changes in $A_1:A_s$. This hy-

pothesis is supported by observations and predictions of a decline in $A_1:A_s$ with increasing tree height or age (Mencuccini and Grace 1996a, b; Grace 1997; Becker et al. 2000; Bond and Ryan 2000; Mencuccini and Magnani 2000; Schäfer et al. 2000). A potential advantage of decreasing $A_1:A_s$ with increasing h is that hydraulic compensation for h may occur, in which g_s is maintained, or reductions in g_s are minimized, as h increases.

An important distinction about compensation of hydraulic constraints must be made to avoid confusion about leaf versus whole-plant physiology. While a decline in $A_1:A_s$ with increasing tree height may mitigate hydraulic constraints to canopy conductance, this does not mean that hydraulic constraints to whole-tree transpiration will also be mitigated. Reduced $A_1:A_s$ may maintain stomatal conductance per unit leaf area while simultaneously reducing the transpiring leaf area per plant relative to whole-plant biomass. Because photosynthesis is closely tied to transpiration, whole-plant carbon assimilation may also decline depending on how light interception is affected. Note that these declines could occur even though leaf-specific stomatal conductance is maintained. The critical distinction is that a change in one parameter *per unit leaf area* does not translate directly into an equal change in another parameter at the *whole-tree scale*. In this paper, we will discuss the role of $A_1:A_s$ versus height only in relation to leaf-specific stomatal conductance.

In light of the recent debate regarding the role of compensatory mechanisms to alleviate hydraulic limitations to water transport (Becker et al. 2000; Bond and Ryan 2000; Mencuccini and Magnani 2000), it is necessary to examine the generality of evidence supporting such mechanisms. The objective of this study was to determine if evidence for the age- or size-related reduction in $A_1:A_s$ is consistent across species and climates. We tested two primary hypotheses: (1) that $A_1:A_s$ declines with increasing height over the lifetime of a species, and (2) that the direction of change or lack of change in $A_1:A_s$ with plant development is consistent across a range of species, maximum heights, and environments. Hypothesis 1 was tested using measurements of *Pseudotsuga menziesii* var. *menziesii*, a long-lived, large-statured conifer native to North America. Hypothesis 2 was tested using data derived from a review of original and published data for a variety of species spanning a broad range of maximum height. To further explore relationships between $A_1:A_s$ versus height and climate or species, we tested relationships between the rate of change of $A_1:A_s$ versus height (the regression slope) and (1) annual precipitation and (2) maximum potential tree height.

Materials and methods

Study site

We tested hypothesis 1 in three even-aged *Pseudotsuga menziesii* var. *menziesii* stands located in the Wind River basin of the Cascade Mountains near Carson, Washington (45°49' N Lat.,

121°57' W. Long.). The climate of this region is maritime, with cool, wet winters and warm, dry summers. Site elevation is approximately 355 m. Annual precipitation is approximately 2,500 mm, with less than 10% of that falling in summer (June through September ~120 mm). The soils are loamy sands and sandy loams developed from two to three meters of volcanic tephra over a basalt flow. Stand ages were determined using increment cores taken at breast height from five or more trees per site. The three sample stands were approximately 20, 40, and 450 years old. Both the 20- and 40-year-old stands originated after clearcuts, whereas the 450-year-old originated after a stand-replacing forest fire (Franklin and DeBell 1988). Average tree heights for the 20-, 40-, and 450-year-old stands were 15 m (14–16), 33 m (29–36), and 57 m (51–62), respectively.

Leaf area and sapwood area measurements

Whole-tree leaf area of *Pseudotsuga menziesii* var. *menziesii* was estimated by scaling branch estimates of leaf area to the canopy (Maguire and Batista 1996; Monserud and Marshall 1999). Branch-scale allometric equations were developed through branch harvest and analysis at each of the three stands. For the 20- and 40-year old stands, scaffolding towers were erected to allow access to harvest branches. Six branches were harvested from each of five trees for a total of 30 branches per stand in July 1998. For each tree, branches were harvested from the lower, middle and upper crown on either northeast or southwest facing aspects. Leaves from each branch were immediately sub-sampled and used to determine specific leaf area (S , $\text{cm}^2 \text{g}^{-1}$). Four twigs for measuring S were collected systematically from along the axis of each branch, located at the second twig from each end of the foliated length, and from two twigs in the middle of the foliated length. Leaf area was determined using a video image recorder and AgVision software (Decagon, Pullman, Wash.). The remaining leaves were collected in paper bags, dried at 65°C and weighed. In late August 1998, another 30 branches were harvested from the 20- and 40-year-old stands using a sampling scheme identical to the July sample. These branches were measured for whole-branch leaf weight only. Branches were harvested from six 450-year-old trees. A total of 17 branches from the old trees were analyzed to develop branch-level allometric relationships. Branches were accessed by climbing the trees using fixed ropes. Branches were harvested from throughout the height profile of the crowns. After cutting, branches were lowered to the ground using a second rope. We randomly collected 10% of the foliated shoots from each branch as measured by visual cluster measurements (Ishii and Ford 2001). Leaf samples were collected from each of these shoots and analyzed for S . Both S and total branch leaf weight were measured using identical methods to those used for the younger stands. Independent variables measured at all three stands included branch diameter (20 mm distal from the swollen branch-stem juncture), branch length, foliated length, height above ground, distance from top of tree, and aspect at the position of branch origin. Suitability of these variables was tested using both stepwise and independent regression analysis (Systat 9.0). Only branch diameter (d) was a significant factor for branches from the 20- and 40-year-old stands, and branch length (L) was the only important factor for branches from the 450-year-old stand. For the 450-year-old trees, L was a better predictor of branch leaf area than d because diameter continues to increase even after breakage (e.g. during wind and ice storms); however, the length of a branch is sensitive to such stochastic events (Ishii and McDowell 2002). Scatterplots of branch leaf area versus d or L revealed that variance in leaf area increased with larger values of the predictive variable; a violation of an assumption of linear regression. We therefore developed predictive equations using weighted regression (Monserud and Marshall 1999), a technique that homogenizes variances. The equations for estimating *Pseudotsuga menziesii* branch leaf area (A_1 , projected, cm^2) from branch d (cm) and L (m) are:

$$20\text{-year-old trees } A_1 = 2,958(d)^{1.67} \quad (2)$$

(44% variation explained)

$$40\text{-year-old trees } A_1 = 4,221(d)^{1.60} \quad (3)$$

(70% variation explained)

$$450\text{-year-old trees } A_1 = 1.032(L)^{1.66} \quad (4)$$

(55% variation explained)

Whole-tree estimates of leaf area were obtained via application of the stand-specific branch models (Eqs. 2–4) to measurements of branch d (20- and 40-year-old trees) or branch L (450-year-old trees). Five 20-year-old and six 40-year-old trees were climbed. For the 20- and 40-year-old trees, trees were climbed using the towers for rope anchors and each branch's diameter was measured in two perpendicular directions. The average diameter for each branch was recorded and used to estimate branch leaf area. Leaf areas for each branch were then summed to give total leaf area for the tree. For the 450-year old trees, five trees were climbed using the trees as rope anchors and L was measured for every branch using an extendable measuring tape. Branch leaf area was estimated for each branch using the stand-specific Eqs. 2–4, and then branch leaf area was summed for each tree. Sapwood area was estimated from four increment cores per tree taken at a height of 1.4 m. The sapwood-heartwood boundary was discerned by holding the core up to the sunlight and marking the position of the inner boundary of the translucent section, indicating a decrease in water content. This boundary was verified on a subset of cores (>30 cores) using multiple stains known to be absorbed by living cells. In all cores the boundary indicated by staining matched that from the method using visual examination.

Meta-analysis

Published and original data sets that included whole-tree $A_1:A_s$ and tree height were used in a meta-analysis test of hypothesis 2 using the study-specific regression slopes and associated variances from linear regression of $A_1:A_s$ versus tree height (MetaWin 2.0, Rosenberg et al. 2000; also see Hedges et al. 1999). Slopes of linear regression ($\Delta A_1:A_s/\Delta h$) were selected as the effect metric because most data sets with samples distributed throughout the height continuum showed that $A_1:A_s$ changed linearly with height, and the majority of data sets included measurements throughout the height continuum rather than clusters of measurements for short and tall trees. On a theoretical note, however, $A_1:A_s$ should decline non-linearly with height, as predicted from Eq. 1. Citations for this review are provided in Table 1. Data sets were excluded from the analysis if they confounded tree height with other variables known to affect $A_1:A_s$, such as light environment (Kaufmann and Troendle 1981; O'Hara and Valappil 1995), nutrient availability or silvicultural manipulation (Brix and Mitchell 1983), site quality (Dean and Long 1986), vapor pressure deficit (Mencuccini and Grace 1995), groundwater access (Zimmermann et al. 2000), soil waterlogging (Santiago et al. 2000) or stand density (Keane and Weetman 1987; Long and Smith 1988). Although this reduced the inference population from which we may draw conclusions, the restricted data set is necessary to test the relationship between tree height and $A_1:A_s$. Variability due to effects of site and species was further reduced by standardizing each data set relative to the largest values of $A_1:A_s$ and height within each respective data set. This should remove differences associated with site and species, while allowing the regression slopes to be used to indicate the effect of height on $A_1:A_s$. The slopes of the regressions both before and after standardization are presented and included in the meta-analysis. Three outliers were excluded from the *Pseudotsuga menziesii* var. *glauca* data set. One of these trees was a suppressed individual and the other two were grown in stands that had wide spacing and larger than average crowns (J.D. Marshall, unpublished data). Stand spacing (or "density") had been shown to dramatically change $A_1:A_s$ in conifers (Oren et al. 1986a; Keane and Weetman 1987; Long and Smith 1988). In a few studies the sample trees did not include trees that had reached maximum potential height for that site. In these cases we calculated maximum potential height based on local site index curves or observa-

Table 1 Summary of studies and results of regression analysis of leaf area:sapwood area ($A_l:A_s$) versus tree height. Values include range of tree heights, diameter at breast height (DBH), and study-level mean $A_l:A_s$. The slopes, P -values and R^2 from regressions of raw data ($A_l:A_s$ in $m^2\text{ cm}^{-2}$, tree height in meters) as well as standardized data are presented. Slope P -values and R^2 are identical for raw and normalized data for all cases. To save space, the variety of *Pseudotsuga menziesii* (var. *menziesii* and var. *glauca*) was abbreviated *v. m* and *v. g*. All studies presented were used in the meta-

analysis except for *Abies balsamea*, which was excluded due to lack of information regarding variance about the regression slope. Citations include studies from which data was obtained or studies that may be used for further reference. (1) this study, (2) Monserud and Marshall (1999), (3) Ryan et al. (2000), (4) Mencuccini and Grace (1996a), (5) Van Hees and Bartelink (1993), (6) Vanninen et al. (1996), (7) Albrektson (1984), (8) Barnard (2000), (9) Bartelink (1997), (10) Ryan and Whitehead, unpublished data, (11) Köstner et al. unpublished data, and (12) Coyea and Margolis (1992)

Species	n	Height(m)	DBH(m)	$A_l:A_s$	Raw slope	Std. slope	R^2	P	Citation
Negative slopes, tracheid bearing species									
<i>Pseudotsuga menziesii v. m</i>	15	13–62	0.15–1.53	0.46	–0.003	–0.24	0.36	0.024	1
<i>Pseudotsuga menziesii v. g</i>	23	5–33	0.05–0.81	0.33	–0.004	–0.22	0.20	0.046	2
<i>Pinus ponderosa</i>	5	9–34	0.19–0.98	0.12	–0.002	–0.05	0.91	0.011	3
<i>Pinus ponderosa</i>	19	4–41	0.05–0.71	0.09	–0.003	–0.62	0.40	0.004	2
<i>Pinus monticola</i>	21	4–44	0.05–0.74	0.22	–0.004	–0.42	0.44	0.001	2
<i>Pinus sylvestris</i>	8	8–24	0.70–0.35	0.09	–0.002	–0.56	0.85	0.001	4
<i>Pinus sylvestris</i>	4	3–22	0.40–0.23	0.13	–0.006	–0.93	0.89	0.057	5
<i>Pinus sylvestris</i>	9	5–33	0.90–0.45	0.20	–0.007	–0.67	0.74	0.003	6
<i>Pinus sylvestris</i>	14	5–25	n/a	0.19	–0.008	–0.55	0.32	0.036	7
Negative slopes, vessel bearing species									
<i>Eucalyptus saligna</i>	37	6–26	0.06–0.30	0.25	–0.044	–0.48	0.34	<0.001	8
<i>Fagus sylvatica</i>	6	3–23	0.31–0.28	0.54	–0.041	–0.83	0.53	0.103	9
<i>Nothofagus solandrii</i>	11	5–14	0.39–0.67	0.13	–0.013	–0.64	0.42	0.033	10
Positive slopes									
<i>Picea abies</i>	28	7–31	0.07–0.45	0.36	+0.017	+0.79	0.46	<0.001	11
<i>Abies balsamea</i>	~50	n/a	0.02–0.21	0.71	+0.031	n/a	n/a	0.001	12

tions. Two data sets for *Pinus sylvestris* included foliar weight rather than area; for these studies we converted weight to area using S measured at nearby sites. Sapwood area measured at breast height (1.4 m) was used for all studies. Verification of accuracy of sapwood estimates was impossible from the published data sets. Although both age and height may interact with $A_l:A_s$, we have used only height as the independent variable in statistical analysis for this study.

We used a subset of data from Table 1 to test the null hypotheses that the slope of $A_l:A_s$ versus height and maximum potential height were independent of climate. Mean annual precipitation data was used from each published study to investigate the relationship between $A_l:A_s$ versus height and climate. Precipitation was used in place of other environmental variables such as D or temperature because it was the most widely available and most consistently measured. We used only studies in which the P -value of the slope was <0.10 and in which documented maximum potential height was available. For maximum potential height we used either the height of the tallest individual if sampled trees included the tallest trees in the study area, or estimates of potential height based on local observations if sampled trees did not include the tallest individuals in the study area.

The meta-analysis includes multiple cases from the same species (Table 1); however, meta-analysis techniques are not currently able to evaluate the impact of non independence associated with replication within species (Gurevitch and Hedges 1999). We determined if replication within species affected our overall result in two ways. First, the meta-analysis was repeated 16 times using a unique combination of cases each time and never including more than one case per species. If the results of these 16 analyses were the same as the overall meta-analysis, we concluded that replication within species did not affect the overall result. The second approach was to group the cases by species and repeat the analysis; if species were not significantly different from each other then we concluded that replication within species did not skew the overall result (J. Gurevitch, personal communication).

Results

Whole-tree $A_l:A_s$ varied with total tree height for *Pseudotsuga menziesii* var. *menziesii* (ANOVA, $P=0.03$, $n=14$). Orthogonal polynomial contrasts in the ANOVA showed that $A_l:A_s$ varied linearly with tree height ($P<0.01$). Regression analysis verified that linear regression provided the best fit to the data, with a slope of -0.003 ($R^2=0.36$, $P=0.02$, Fig. 1).

$A_l:A_s$ declined with increasing tree height for nearly all studies in the meta-analysis (Table 1). Meta-analysis of the whole-tree studies revealed a common negative slope of $A_l:A_s$ versus height ($P<0.05$, $n=13$ whole-tree studies, Table 2). The significant decline in $A_l:A_s$ versus height was evident when analyzed using either standardized or absolute values of $A_l:A_s$ and height (Table 2). There was no effect of replication within species on the overall outcome. A negative slope of $\Delta A_l:A_s/\Delta h$ resulted from each of the 16 unique analyses of the meta-data that had no replication of species. In no case did the 95% confidence intervals overlap zero. Likewise, replicated species (species with more than one data set in the meta-analysis, *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Pinus sylvestris*) were not significantly different from each other ($n=3$, $P=0.99$).

Although the meta-analysis revealed a significant and consistent negative relationship between $A_l:A_s$ and h , there were two significant exceptions (Table 1). *Abies balsamea* and *Picea abies* both exhibited positive relationships between $A_l:A_s$ and h . A similar increase in $A_l:A_s$ with height has been previously observed for *Picea abies* (Oren et al. 1986a). We note that the *Abies balsamea* data set could

Table 2 Meta-analysis results of the slope of leaf area:sapwood area ($A_l:A_s$, $m^2\ cm^{-2}$) versus tree height (m). Slopes were used as the effect size and were generated separately for each study via regression of $A_l:A_s$ versus tree height (Table 1). The within-study

	n	Mean slope	$Q(p)$	95% confidence interval
Raw data	13	-0.0027	0.64	-0.0044 to -0.0010
Standardized data	13	-0.3594	0.76	-0.5974 to -0.1215

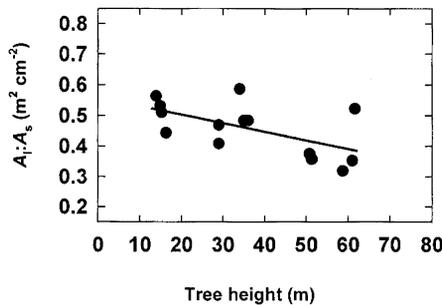


Fig. 1 Leaf area:sapwood area ($A_l:A_s$) versus tree height for *Pseudotsuga menziesii* var. *menziesii* trees in Wind River Experimental Forest, Washington. The regression line is: $A_l:A_s = -0.003 + 0.559(\text{height})$, $R^2 = 0.36$, $P = 0.02$

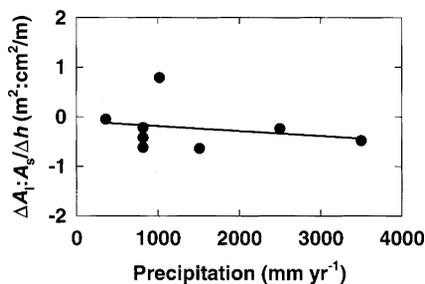


Fig. 2 The slope of $A_l:A_s$ versus tree height ($\Delta A_l:A_s/\Delta h$) as a function of mean annual precipitation (mm year^{-1}). Data sets for which annual precipitation was available included *Nothofagus* in New Zealand, *Pinus ponderosa*, *Pinus monticola*, and *Pseudotsuga menziesii* var. *glauca* sites in Priest River, Idaho, the *Pseudotsuga menziesii* var. *menziesii* site in Wind River Experimental Forest, Wash., the *Pinus ponderosa* site in Oregon, and the *Picea abies* site in Germany. The regression line is: $\Delta A_l:A_s/\Delta h = -0.087 - (0.001 \text{ Precipitation})$, $R^2 = 0.06$, $P = 0.57$

not be included in the meta-analysis due to lack of variance estimates (only the slope was available from Coyea and Margolis, 1992). *Fagus sylvatica* exhibited a negative slope of marginal significance ($P = 0.103$, Table 1). We note that this is not an attribute particular to this species, because Schäfer et al. (2000) observed a large and significant reduction in $A_l:A_s$ with h in *Fagus sylvatica*.

Climate does not appear to regulate the slope of $\Delta A_l:A_s/\Delta h$ for the studies included in this analysis. The lack of significant heterogeneity among all studies (Q in Table 2) is evidence that $\Delta A_l:A_s/\Delta h$ is independent of the large differences in climate across these studies (J. Gurevitch, personal communication). Plotting $\Delta A_l:A_s/\Delta h$ versus mean annual precipitation for the subset of studies

variance estimate was the variance about the slope of each regression. The significance (P -value) of model heterogeneity is $Q(p)$; a non-significant Q indicates homogeneity within the data set

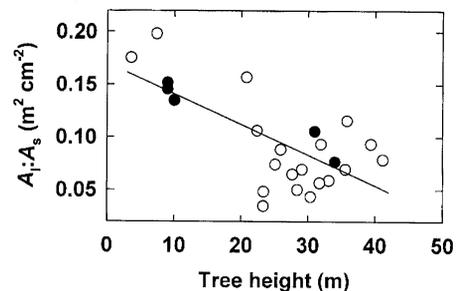


Fig. 3 $A_l:A_s$ versus tree height for two *Pinus ponderosa* stands. The site in Oregon (shaded circles) received 360 mm of precipitation annually, and the Idaho site (open circles) received 817 mm annually. The regression lines for each site were statistically indistinguishable (see text). The pooled regression line for both data sets is: $A_l:A_s = -0.003 + 0.171 \cdot (\text{height})$, $R^2 = 0.47$, $P < 0.001$

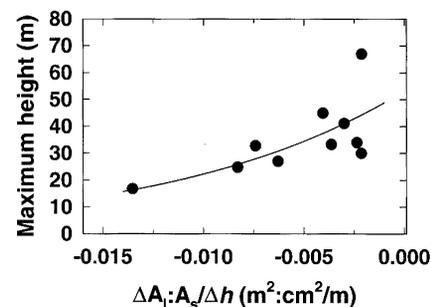


Fig. 4 Whole-tree $\Delta A_l:A_s/\Delta h$ versus maximum tree height. $\Delta A_l:A_s/\Delta h$ is the regression slope from Table 1 for each study. Maximum potential height is either (1) the tallest individual tree height if sampled trees included the tallest trees in the study area, or (2) estimates of potential height based on local observations if sampled trees did not include the tallest individuals in the study area. Studies were included only if the P -value of the slope was < 0.10 and if well-documented maximum tree heights were available. The included studies are: *Pseudotsuga menziesii* var. *menziesii* and *Pseudotsuga menziesii* var. *glauca*, *Pinus ponderosa* (both studies), *Pinus monticola*, *Pinus sylvestris* (all studies listed in Table 1), *Nothofagus solandrii* and *Eucalyptus saligna*. The equation for the best fit line is: $\text{Maximum height} = 53.4 \exp(87.5 \cdot \Delta A_l:A_s/\Delta h)$, $n = 10$, $R^2 = 0.45$

that had precipitation data supports the conclusion that climate (as indexed by precipitation) does not regulate $\Delta A_l:A_s/\Delta h$ (Fig. 2). The independence of $\Delta A_l:A_s/\Delta h$ from site water availability can also be seen by comparing $\Delta A_l:A_s/\Delta h$ for *Pinus ponderosa* trees growing on a site of relatively high precipitation (817 mm year^{-1} , Priest River, Idaho) and low precipitation (360 mm year^{-1} , Metolius, Oregon, Fig. 3). Neither the slope nor the intercept was

significantly different between these two locations ($P > 0.54$) despite the two-fold difference in precipitation.

To investigate the potential relationship between tree size and the sensitivity of $A_1:A_s$ to height, we plotted $\Delta A_1:A_s/\Delta h$ versus maximum potential tree height (Fig. 4). A positive relationship was found (Fig. 4). For this analysis we used data sets from the meta-analysis with significant ($P < 0.1$), negative slopes and that had accurate documentation of maximum potential height. The equation for the best fit line is:

$$\text{Maximum height} = 53.4 \exp(87.5 \cdot \Delta A_1 : A_s / \Delta h), \quad (5)$$

$$n = 10, R^2 = 0.45$$

Discussion

The meta-analysis revealed similar responses of $A_1:A_s$ to increasing tree height across a broad range of species (Table 1, Table 2). The common decrease in $A_1:A_s$ with increasing height supports the hypothesis that trees may respond to increasing hydraulic constrictions by maintaining a lower ratio of $A_1:A_s$ (Meinzer et al. 1997; Becker et al. 2000; Schäfer et al. 2000). However, a number of unanswered questions arise from the meta-analysis. These include: 1. Why was $\Delta A_1:A_s/\Delta h$ positive for *Abies balsamea* and *Picea abies*? and 2. What mechanism(s) may regulate the species specific differences $\Delta A_1:A_s/\Delta h$? We will focus the remainder of the discussion on these questions.

The positive relationship between $A_1:A_s$ and tree height for *Abies balsamea* and *Picea abies* must be rationalized in light of Eq. 1. If Eq. 1 is applicable to describe the hydraulic system of woody plants, then, to maintain homeostasis with no increase in the water potential gradient, an increase in $A_1:A_s$ with tree height will require a decrease in canopy conductance or an increase in k_s in conditions where D and h remain constant. Indeed, in *Abies balsamea*, Coyea and Margolis (1992) found that k_s of stemwood increased more rapidly than tree height such that $A_1:(A_s \cdot k_s)$ declined with tree height. They concluded that the *Abies balsamea* data conformed to the hydraulic model (Eq. 1) because the increased k_s more than offset the increase in $A_1:A_s$ with height. Although increasing k_s with tree height has been documented for many species, it is typically insufficient to prevent height-related reductions in hydraulic conductance (Mencuccini and Magnani 2000). An alternative hypothesis is that the fraction of leaf area that is actively transpiring is reduced with height, or the hydro-active sapwood area increases, such that the functional $A_1:A_s$ decreases with height. Köstner et al. (unpublished data) found that standardizing the leaf area by light interception resulted in constant $A_1:A_s$ values across a range of heights. However, Oren et al. (1986b) observed that 92% of the leaf area actively transpired for *Picea abies* and concluded that the functional $A_1:A_s$ increased with height. It is possible that another variable in Eq. 1 such as $\Delta\psi$ changed with tree size for *Picea abies* and *Abies balsamea* and we were unaware of it. Barnard (2000) and McDowell et al. (2002) both found increases in $\Delta\psi$ via

declines in mid-day leaf water potential with increasing tree size. Likewise, a parameter not even included in Eq. 1 may have changed for *Picea abies* and *Abies balsamea*. For example, increasing root surface area may act to increase the capacity of trees to supply foliage with water (Sperry et al. 1998; Magnani et al. 2000). Further work on these species with positive $\Delta A_1:A_s/\Delta h$ values is needed, with an emphasis on understanding the trade-offs between $A_1:A_s$, height, and other important characteristics of the hydraulic system.

The advantage of an increase in $A_1:A_s$ with height for *Picea abies* and *Abies balsamea* is unknown. Increasing $A_1:A_s$ does increase the photosynthetic area relative to respiring sapwood biomass, which could act to increase net carbon uptake if canopy conductance remains constant. However, if canopy conductance declines in an equal and opposite fashion to the increased leaf area, then whole-tree carbon gain will remain unchanged or will even decrease due to higher respiration costs associated with the high leaf area. Alternatively, retaining leaves may provide a mechanism to recycle nutrients more efficiently. Both *Picea abies* and *Abies balsamea* grow in cold, nutrient poor ecosystems where nutrients may be more limiting than water. Retention of nutrients within leaves can allow greater retranslocation of nutrients to growing canopy (Waring and Ludlow 1998; Waring and Running 1998). However, Oren and Schulze (1989) found that retranslocation of nutrients to new leaves in *Picea abies* came from leaves on the same upper-canopy branches rather than from lower canopy leaves. Therefore, holding lower canopy branches is unlikely to provide an advantage for nutrient retention. Retaining lower canopy branches may act to shade out competing vegetation, making soil resources more available (Waring and Major 1964). We conclude that the mechanisms and advantages of increasing $A_1:A_s$ with tree height for *Picea abies* and *Abies balsamea* remain unknown.

Providing a mechanistic explanation for differences in species-specific $\Delta A_1:A_s/\Delta h$ is impossible given the lack of controlled investigations where $\Delta A_1:A_s/\Delta h$ is measured within a given species growing in different climatic and edaphic conditions. Furthermore, the lack of studies that matched our criteria for inclusion in the meta-analysis hampers our ability to interpret patterns. For example, among the studies with negative $\Delta A_1:A_s/\Delta h$, the vessel-bearing species had an average $\Delta A_1:A_s/\Delta h$ of -0.0326 , nearly one order of magnitude greater than the average slope of tracheid bearing species (-0.0042). However, the limited sample size of vessel bearing species makes statistical comparisons impossible. Despite the limited sample size, we can examine patterns from the meta-analysis data set that allow us to generate testable hypotheses as to the controls over $\Delta A_1:A_s/\Delta h$.

We expected that site water availability would be negatively related to $\Delta A_1:A_s/\Delta h$ because forests with greater precipitation or greater soil moisture availability tend to hold more leaf area per unit sapwood area (Waring et al. 1982; White et al. 1998). If this hypothesis were true it would indicate that the driving force for a decline in

$A_1:A_s$ with increasing height was sensitive to water availability. However, the decline in $A_1:A_s$ with increasing height occurred independently of precipitation. This lack of change in $\Delta A_1:A_s/\Delta h$ with precipitation was true when compared across species (Fig. 2) and within species (*Pinus ponderosa*, Fig. 3). It is possible that another, more physiologically meaningful parameter such as soil water potential or atmospheric vapor pressure deficit during the growing season is a better predictive parameter than mean annual precipitation. However, it seems likely that mean annual precipitation was strongly correlated with these more direct measures of water availability. Therefore, it appears that water availability has no effect on the decline in $A_1:A_s$ as height increases among the sites investigated in this study.

The independence of $\Delta A_1:A_s/\Delta h$ from precipitation indicates homeostasis between water availability, hydraulic path length and $A_1:A_s$. This is because mean annual precipitation is positively correlated with both $A_1:A_s$ and maximum tree height. Small trees in wet environments have greater $A_1:A_s$ values than trees of similar size in drier environments (Waring et al. 1982). Likewise, trees in wetter environments tend to grow to greater maximum heights. So although trees in wet environments have greater $A_1:A_s$ at small heights and greater maximum heights than dry site trees, the change in $A_1:A_s$ with a unit increase in height is invariant with water availability. This suggests that another variable, such as hydraulic path length, exerts stronger regulation over $\Delta A_1:A_s/\Delta h$ than site water availability.

There is a trend for trees with greater maximum potential heights to have less negative values of $\Delta A_1:A_s/\Delta h$ (Fig. 4). The relationship shown in Fig. 4 is derived from the significant, negative slopes from studies used in the meta-analysis where accurate measurements of maximum potential height were available. This positive relationship suggests trees able to maintain high $A_1:A_s$ as they grow taller are able to grow to greater final heights. However, the regression equation is of little predictive value for trees with small $\Delta A_1:A_s/\Delta h$ values due to increased scatter in this range. Nonetheless, the positive relationship between maximum potential height and $\Delta A_1:A_s/\Delta h$ may account for some of the variation observed in $\Delta A_1:A_s/\Delta h$ among species and sites.

A decline in $A_1:A_s$ with increasing tree height has been hypothesized to prevent reductions in stomatal conductance associated with hydraulic constraints (Becker et al. 2000). McDowell et al. (2002) investigated this hypothesis by comparing measured values of leaf-specific g_s for *Pseudotsuga menziesii* var. *menziesii* trees in this study to values modelled with Eq. 1 using either (1) measured values of $A_1:A_s$ for each tree height, or (2) $A_1:A_s$ set at the value for 15 m trees ($0.51 \text{ m}^2 \text{ cm}^{-2}$) for all tree heights. $\Delta\psi$ (including the effect of gravity) and g_s values are from McDowell et al. (2002). This analysis is nearly identical to that performed by Schäfer et al. (2000) on individual *Fagus sylvatica* trees within one stand except that in this case trees from different aged stands were compared. Modelled and measured g_s were within 10%

of each other when $A_1:A_s$ was allowed to vary. However, when $A_1:A_s$ was held constant, modelled and measured g_s deviated from each other. Measured g_s for the 32-m-trees was only 5% lower than modelled g_s , but for the 60-m trees the modelled g_s was 45% lower than the measured g_s . This large difference between measured and modelled g_s for the 60 m trees suggests that adjusting $A_1:A_s$ becomes more critical in regulating g_s as trees become taller. This result for trees from different aged stands is similar to that found for individual *Fagus sylvatica* trees within one stand (Schäfer et al. 2000). However, in both the analysis by McDowell et al. (2002) and the one by Schäfer et al. (2000), the decline in $A_1:A_s$ with increasing tree height did not prevent a reduction in g_s , it only minimized the reduction. Other studies of whole-tree $A_1:A_s$ and stomatal conductance also show evidence that conductance declines despite declining $A_1:A_s$ with increasing tree height (Mencuccini and Grace 1996a; Mencuccini and Magnani 2000, Ryan et al. 2000; Ryan and Whitehead unpublished data). It is important to point out that Barnard (2000) found that $A_1:A_s$ reduction with tree height fully mitigated hydraulic limitations to stomatal conductance in *Eucalyptus saligna*; however, these trees were only at half of their maximum height. It remains to be seen if these *Eucalyptus* trees can maintain complete compensation through the rest of their height development. Therefore, the overwhelming majority of studies suggest that the decline in $A_1:A_s$ with increasing tree height acts to minimize, but not eliminate, size related reductions in canopy conductance.

A reduction of the leaf area: sapwood area ratio of trees with increasing height has been proposed as a homeostatic mechanism that may alleviate decreasing hydraulic conductance, thereby allowing canopy conductance to be maintained throughout height development (Becker et al. 2000). Nearly all of the cases included in this study support the idea that $A_1:A_s$ decreases in response to increasing tree height. However, these compensatory shifts in $A_1:A_s$ do not appear to fully mitigate the observed decline in stomatal conductance with tree height.

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