

## The hydraulic architecture of balsam fir (*Abies balsamea*)

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Leaf-specific conductivities (LSCs – hydraulic conductivity per dry weight of supplied leaves), Huber values (transverse sapwood area per dry weight of supplied leaves), specific conductivity (hydraulic conductivity per transverse sapwood area) and tracheid diameters were measured throughout the trunk and crown of 20-year-old trees of *Abies balsamea* (L.) Mill. Measured specific conductivity was proportional to the radius to the fourth power of tracheids. LSCs, which indicate the relative water availability to different plant parts, are much higher in the trunk than in first order branches, and lowest in second order branches. The structural basis for this “hydraulic hierarchy” lies both in Huber values and in tracheid diameters. For similar diameter stem segments, there was no statistically significant difference for trunks versus branches in specific conductivity. However, in old parts of the tree, trunks are wider than supported branches and produce wider tracheids resulting in greater specific conductivities than in branches. In vigorous trees with strong apical control, Huber values were 12.0 times greater in the trunk than in similar diameter branch segments. In slow-growing trees with weak apical control, Huber values were 2.2 times greater in the trunk versus similar branch segments.

*Additional key words* – Apical control, hydraulic conductivity, leaf-specific conductivity, tree architecture, xylem conductivity.

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### Introduction

Recently, Zimmermann (1978) measured leaf-specific conductivities (LSCs – hydraulic conductivity per leaf weight supplied) in isolated stem segments throughout the trunk and crown of many dicotyledonous trees. He found that trunks were hydraulically favored over branches, and that there was a hydraulic constriction or bottleneck at the base of each branch and twig. In the present report we examine the conifer *Abies balsamea* to determine how its hydraulic architecture compares to that of dicotyledonous trees, and more importantly, to determine the structural basis for this architecture.

An elegant mechanical plus hydraulic model of tree growth is offered by the “pipe model”, where the plant is considered as an assemblage of “unit pipe systems” (Shinozaki et al. 1964). Each unit pipe supports a unit of leaves, and as the plant develops, new unit pipes are added to the older pipe systems. This model is based on

the frequent observation for many conifers and dicotyledons that the transverse-sectional area of the stem is proportional to the weight of the supported leaves (Shinozaki et al. 1964, Grier and Waring 1974, Waring et al. 1977, 1982, Kaufmann and Troendle 1981, Long et al. 1981, Santee and Monk 1981).

Huber (1928) devised a ratio (the Huber value) which is the xylem transverse sectional area divided by the weight of the supported leaves. According to the pipe model, these values should be constant throughout the plant. However, in the conifers *Abies concolor* and *Picea* sp., Huber values increased towards the top of the plant, and the trunk had much greater values than the lateral branches (Huber 1928). He concluded that the leader was thus better supplied with water and took this as a reflection of strong apical control. Unfortunately, Huber examined only one tree each of *Abies concolor* and of *Picea* sp.

Huber values are of interest from a mechanical point

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of view (Long et al. 1981), but they do not, by themselves, tell us much about water conduction. Xylem conductivity is related not only to xylem transverse-sectional area, but also to the size of the tracheary elements, and to the number of tracheary elements which retain a transport function (Zimmermann 1983).

Recently, Tyree et al. (1983) measured LSCs in the trunk, twigs, and branches of the conifer *Thuja occidentalis*. Through a variety of water relation measurements they demonstrated that LSC values are inversely proportional to localized pressure potential gradients within the plant. This supported theoretical arguments by Zimmermann (1978). In addition, Tyree and co-workers found that LSCs were strongly correlated with stem diameter. However, they did not examine the structural basis for differences in LSCs. In this report we compare similar diameter trunks versus branches in *Abies balsamea* to determine whether differences in LSC are due to differences in tracheid diameter and/or to differences in Huber value. Unlike most of the available conifers, this species lacks resin canals in its wood, which is an advantage since resin canals make measurements of xylem conductivity difficult.

## Materials and methods

### Plant material

Experiments were run on seven open-grown trees of *Abies balsamea* (L.) Mill. during the period from September through December of 1982. The trees were each 20 years old and growing within 20 m of one another, but they ranged in height from 1.31 to 4.28 m.

### Conductivity measurements

These are made by directly measuring the flow rate of a defined solution (here 5 mM KCl) through stem segments, at a defined pressure gradient (here 10.13 kPa  $m^{-1}$ ). This was done as described by Zimmermann (1978), except that prior to the final trimming of a stem segment, a 1 cm collar of bark was girdled from each end to insure that resin in the bark did not interfere with the conductivity measurements. After the final trimming the stem segments were from 3 to 10 cm long, but all segments from a particular tree were the same length.

### Transverse xylem areas and tracheid diameters

Immediately after making the conductivity measurements the stem segments were immersed in water and the next day 0.5% (w/v) safranin or 0.5% (w/v) crystal violet was perfused through each segment to demarcate the area of the conducting xylem or "sapwood". Median transverse sections of each segment were later prepared on a sliding microtome. Large stems were sectioned as longitudinally split pieces. Measurements of the trans-

verse sectional areas of the sapwood (indicated by the perfused dye), current year's xylem (outer growth ring), and the entire xylem area were made by weighing paper cut-outs from camera-lucida drawings of the sections. For each section ten of the largest tracheids of the outer growth ring were measured with an ocular micrometer. As an approximation of hydraulic diameter the radial and tangential inside diameters of each tracheid were averaged.

### Leaf weights

For water transport, leaf surface area may be more directly relevant than leaf weight, but for practical reasons we measured leaf dry weights and provide conversions to surface area and fresh weight below. Branches and leaves distal to stem segments of interest were put in paper bags in a 50°C oven for 2 to 3 days. The resulting brittle leaves were removed by hand from the branches and twigs. Subsamples measured before and after the 50°C oven treatment showed no measurable dry weight loss due to respiration during this period. The isolated leaves were oven-dried to constant weight at 70°C.

### Definitions, units, and conversion factors

Strong apical control means the leader has greater elongation growth than the lateral branches. This is not necessarily the same as apical dominance (Brown et al. 1967), which refers to the arrest of lateral buds. Leaf-specific conductivity (LSC) = hydraulic conductivity per g dry weight of leaves supplied, Huber value = xylem transverse area ( $mm^2$ ) per leaf dry weight supplied, and specific conductivity = hydraulic conductivity per xylem

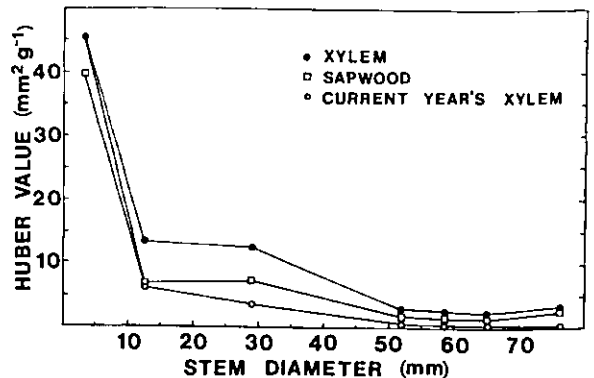


Fig. 1. Huber values versus stem diameter for trunk segments of Tree 3 (compare to Fig. 5). Values were calculated in three ways, i.e., based on the total xylem transverse area (as originally done by Huber 1928), the sapwood area (as done elsewhere in the present study), and the transverse area of the outer growth ring (current year's xylem), each divided by the dry weight of supplied leaves. Total xylem area is the most important mechanically, sapwood area is most relevant hydraulically, and current year's xylem is morphogenetically informative. All three values increase towards top of the tree (to left on graph).

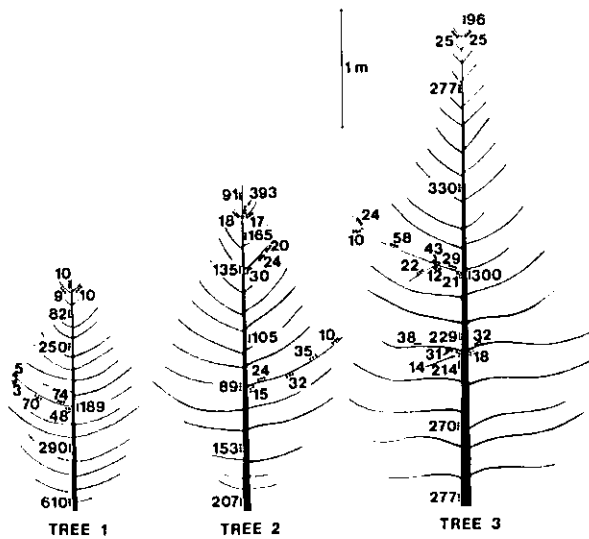


Fig. 2. Leaf-specific conductivities (LSCs) along the axes of three open-grown 20-year-old trees that varied in vigor and in apical control. LSCs are in  $\mu\text{l h}^{-1}$  at  $10.13 \text{ kPa m}^{-1}$  per g dry weight of leaves supplied. Conductivities are higher in the trunk than in branches, and higher in first order than in second order branches. Branch insertions have hydraulic constrictions.

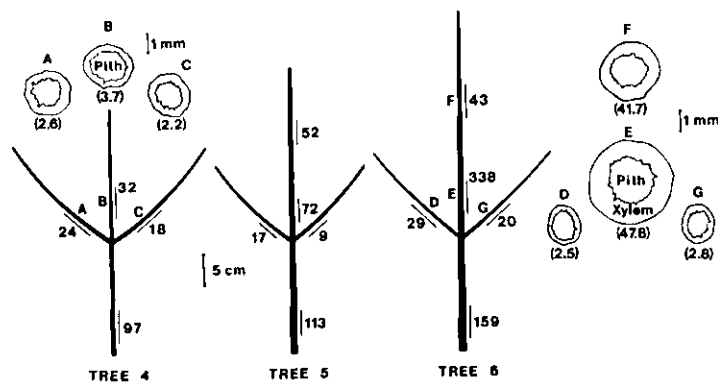
transverse area. It is important to note that these measurements are not totally independent. By definition,

$$\frac{\text{conductivity}}{\text{leaf dry wt}} = \frac{\text{xylem area}}{\text{leaf dry wt}} \times \frac{\text{conductivity}}{\text{xylem area}} \quad (1)$$

or,

$$\text{LSC} = \text{Huber value} \times \text{specific conductivity} \quad (2)$$

Hydraulic conductivity is in  $\mu\text{l h}^{-1}$  under conditions of gravity gradient ( $10.3 \text{ kPa m}^{-1}$ ). Huber (1928) calculated Huber values from the entire xylem transverse area. Except in Fig. 1, our Huber values and specific conductivities were all based on transverse sapwood area, since the heartwood tissue is not involved in conduction.



Based on 18 subsamples of 20 leaves each, the leaf fresh weight to dry weight ratio was  $2.08 \pm 0.022$  (mean  $\pm$  SE). The ratio of leaf dry weight to projected surface area (one side only) was  $2.34 \pm 0.048 \text{ g dm}^{-2}$ . This value varied slightly with position in the tree; the ratio was  $2.39 \pm 0.030$  at the top,  $2.34 \pm 0.028$  in the middle, and  $2.30 \pm 0.078$  near the base of the trees.

## Results

Vigorous trees had strong apical control. That is, the leaders had much greater elongation growth than the adjacent laterals. In contrast, in stunted individuals the annual elongation growth for the leader was about the same as for the uppermost laterals, that is, there was poor apical control (Figs 2 and 3).

In all trees LSC values were higher in the trunk than in lateral branches and were particularly low in second order branches (Figs 2–4, Tab. 1). Likewise, there were very low LSCs at junctions between the trunk and branches and between first and second order branches (Fig. 2). In stunted individuals (e.g., Trees 1 and 4 in Figs 2 and 3) the LSCs tapered off near the top of the tree. In contrast, in vigorous trees (e.g., Trees 3 and 6 in Figs 2 and 3) the LSCs were high throughout the trunk such that even near the tip of the leader the trunk LSCs were much higher than those of lateral branches.

Like LSC values, Huber values were higher in the trunk than in branches (Figs 3–5, Tab. 1). Unlike LSCs, Huber values increased sharply in going up the trunk of vigorous trees (e.g., for Tree 3 from  $2.6 \text{ mm}^2 \text{ g}^{-1}$  at the base to  $39.8$  near the top, Fig. 5), but slightly decreased in going up the trunk of stunted individuals with weak apical control (e.g., for Tree 1 from  $8.0 \text{ mm}^2 \text{ g}^{-1}$  at the base to  $4.7$  near the top, Fig. 4).

Inside tracheid diameters and specific conductivity consistently decreased in going up the tree and out along the branches (Figs 4–6). Specific conductivity was strongly correlated with tracheid diameter ( $y = 2.66x - 37.7$ ,  $r = 0.72$ ,  $df = 31$ ,  $P < 0.001$ ) and even more strongly correlated with the radius to the fourth power of the tracheids (Fig. 7).

If we compare similar diameter stem segments of

Fig. 3. Huber values (in parentheses) and leaf-specific conductivities (LSCs) along the upper axes of three open-grown 20-year-old trees that varied in vigor. Tree 4 was 1.31 m tall, Tree 5 was 2.3 m, and Tree 6 was 3.12 m. For Trees 4 and 6 transverse xylem areas of 1-year-old stem segments are diagrammed (A–C, D–G, respectively). In Tree 6, which was the most vigorous and which had the greatest apical control, the leader had particularly large LSC and Huber values, as well as a wide pith.

Tab. 1. Comparison of means for similar diameter trunk versus branch segments. Statistical significance was determined via Student's *t*-test. NS indicates means not significantly different at 0.05 level of probability. Measurements described in text.

Parameter	Trunk	Branches	<i>P</i>	Trunk/ Branches
<b>Vigorous trees</b>				
LSC	186	26	<0.001	7.2
Huber value (mm <sup>2</sup> g <sup>-1</sup> )	36	3	<0.002	12.0
Specific conductivity	10	17	NS	0.6
Tracheid diameter (μm)	20	19	NS	1.1
<b>Slow-growing trees</b>				
LSC	41	27	NS	1.5
Huber value (mm <sup>2</sup> g <sup>-1</sup> )	4.5	2	<0.001	2.2
Specific conductivity	9	13	NS	0.7
Tracheid diameter (μm)	23	20	NS	1.1

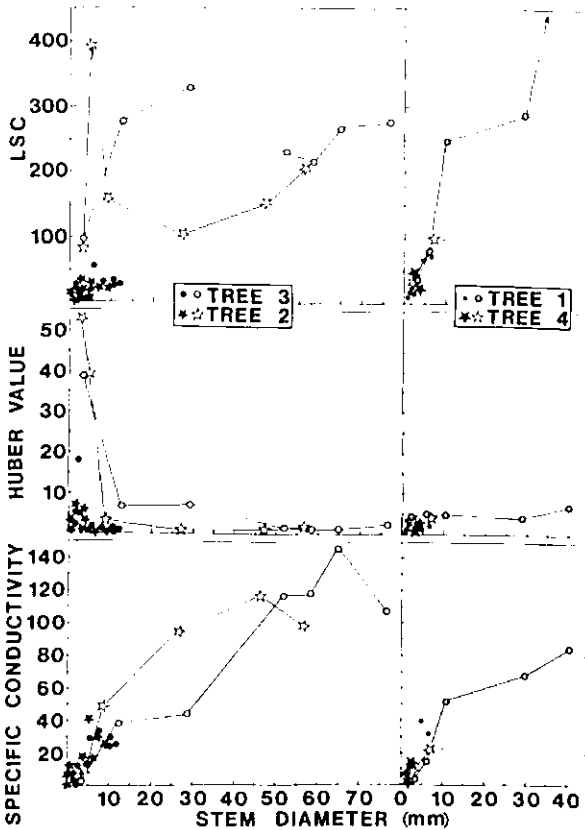


Fig. 4. Leaf-specific conductivity (LSC), Huber value (mm<sup>2</sup> g<sup>-1</sup>), and specific conductivity as functions of stem diameter. Results shown for two fast growing trees (3 graphs on left) and two stunted individuals (3 graphs on right). The connected (open) symbols represent 1- to 20-year-old trunk segments and the solid symbols 1- to 10-year-old branch segments. Differences between similar diameter trunks and branches in LSC were due to differences in Huber values. In vigorous trees LSCs and Huber values were much greater in trunk than in stem segments, but for stunted individuals these distinctions were less pronounced. See statistical summary in Table 1.

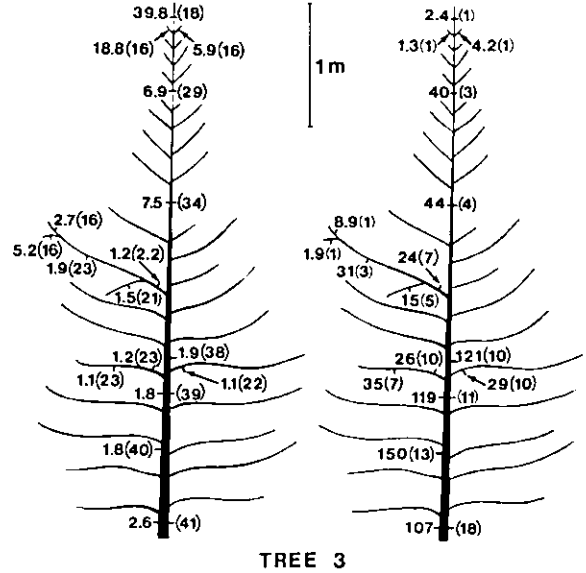


Fig. 5. Left diagram shows Huber values (mm<sup>2</sup> g<sup>-1</sup>) and mean inside tracheid diameters (μm - in parentheses); right diagram shows specific conductivities and stem ages (years - in parentheses) along the axes of a fir tree. Compare to LSCs in Fig. 2. Mean tracheid diameters are for ten of the widest tracheids in the outer growth ring. In going up the tree and distally along branches tracheid diameter and specific conductivity decrease but Huber value increases.

trunks versus lateral branches, the LSC and Huber values were much higher in the trunk. These differences were much greater in vigorous than in slow-growing trees (Fig. 4, Tab. 1). For instance, for vigorous trees, on the average LSCs were 7.2 times greater in the trunk than in comparable diameter branch segments, versus 1.5 times greater in the trunks versus branches of stunted individuals (Tab. 1).

There was no statistically significant difference between similar diameter trunk versus branch segments in specific conductivity or in tracheid diameter (Tab. 1). However, with increasing stem diameter there were steady increases in both of these parameters. This was true both for fast- and slow-growing trees and for branches as well as trunks (Figs 4 and 6). In the older plant parts, where the trunk was of much greater circumference than the supported branches, the trunks had much greater specific conductivity and greater mean tracheid diameter. However, near the top of the tree, where trunk segments were not much wider than adjacent laterals, there was little difference between stem types in these parameters (Figs 4-6).

In cases where the leader had been damaged or destroyed, a new leader was formed from a lateral branch. Like the original leader, the new leader had greater LSC and Huber values than the adjacent laterals (Fig. 8).

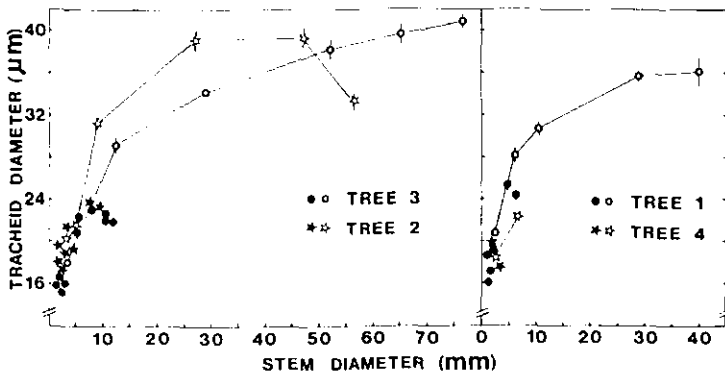


Fig. 6. Stem diameter versus mean tracheid diameter ( $\pm$  SE) for ten of the widest tracheids of outer growth ring. The connected (open) symbols represent 1- to 20-year-old trunk segments and the solid symbols 1- to 10-year-old branch segments. With increasing stem diameter, trunks and branches have similar increases in tracheid diameter. However, trunks increase in girth faster than do branches.

## Discussion

The hydraulic architecture of *Abies balsamea* is remarkably similar to that reported by Zimmermann (1978) for dicotyledonous trees. For all the taxa in which LSCs have been measured, there is a hydraulic hierarchy, with the trunk favored over first order branches, which in turn are favored over second order branches (Figs 2 and 3; Zimmermann 1978, Tyree et al. 1983). The greater LSCs in the trunk allow the upper leaves on the tree to compete with the lower leaves for water and minerals (Zimmermann 1978, Tyree et al. 1983).

In the present study we make use of the fact that LSC is

the product of the Huber value and the specific conductivity (Eqs 1 and 2). As a result of this mathematical relationship we can determine to what extent differences between stem types in LSC are due to differences in Huber value and/or differences in specific conductivity. In *Abies balsamea*, both of these factors contribute to the hydraulic hierarchy.

Ontogenetically, the initial basis for the hierarchy lies in the Huber value. In 1-year-old stem segments the Huber values are much greater in the leader than in

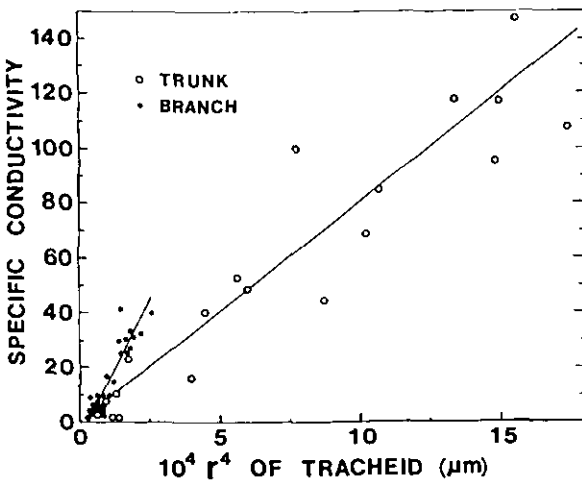


Fig. 7. Specific conductivity versus mean radius to the fourth power of tracheids. Results combined from Trees 1-4 (Figs 2, 3 and 5). Each point represents a single stem segment. Trunk segments ranged from 1 to 20 years old, branch segments from 1 to 10 years. The  $r^4$  relationship is consistent with Poiseuille's equation for flow through ideal capillary tubes. The reason for differences in regression lines for trunks vs. branches (Trunks:  $y = 0.0008x + 1.12$ ,  $r = 0.94$ ,  $P < 0.001$ . Branches:  $y = 0.0020x - 5.57$ ,  $r = 0.92$ ,  $P < 0.001$ ) is not clear, but may be due to the fact that only the larger tracheids in the outer growth ring were measured, not the sum of the radii to the fourth power of all transporting tracheids.

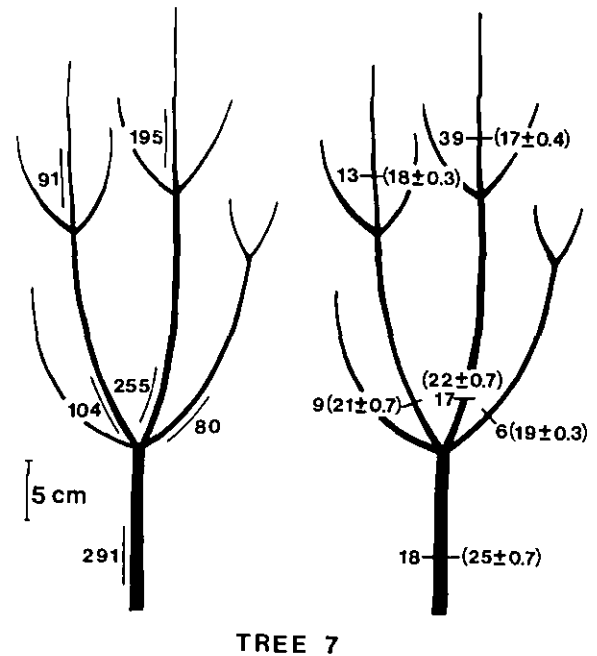


Fig. 8. Leaf-specific conductivities (LSCs - left diagram), Huber values (right), and tracheid diameters ( $\mu\text{m}$  - in parentheses  $\pm$  SE) along the upper axes of a tree in which the original leader was destroyed two years earlier. The largest branch has the greatest LSCs and would probably have become the new leader. The larger LSCs in the future leader are due to greater Huber values; there is little difference between branches in tracheid diameters or in specific conductivity ( $\approx$  LSC/Huber value).

adjacent laterals, while there is little initial difference between stem types in specific conductivity (Figs 3–5, Tab. 1). That is, the initial difference in LSCs is due to greater relative transverse sapwood area in the leader. However, in the older parts of the tree the trunks have much greater specific conductivity than the branches they support, in addition to larger Huber values. The greater specific conductivity is due to wide tracheids in the old trunk (Fig. 5).

When comparisons are made within and between different taxa of plants there is a strong correlation between specific conductivity and the diameter of the tracheary elements (Farmer 1918, Rivett 1920, Huber 1956). Similarly, within trees of *Abies balsamea*, measured specific conductivity was proportional to the mean radius to the fourth power of the largest tracheids (Fig. 7). This relationship is as predicted by Poiseuille's law for volume flow through ideal capillary tubes (Reiner 1960). For most conifers, as stems enlarge they produce wider tracheids (Fig. 6; Sanio 1872, Bannan 1965, Olesen 1982). The trunk of *Abies balsamea* increases in girth faster than do branches; the old trunk has wider tracheids than the supported branches (Figs 5 and 6).

Despite Huber's (1928) evidence to the contrary, there is a persistent belief in the literature that for a given species there is constant relationship between supported leaf weight and xylem transverse area (see Introduction). Perhaps this relationship holds true only for trees with weak apical control. Another consideration is that foresters tend to make these measurements only in the older parts of trees, and that they have usually compared different size trees (e.g., at 1.3 m), rather than different parts of the same plant (e.g., Grier and Waring 1974, Waring et al. 1977, Rogers and Hinckley 1979). In *Abies balsamea*, Huber values often appear to be roughly constant in the older parts of the trunk but usually increase sharply near the top of the tree (Figs 1, 4 and 5).

Results in this report support Huber's (1928) suggestion that apical control and hydraulic dominance are linked. By hydraulic dominance we mean the leader is hydraulically favored over laterals. Vigorous trees with strong apical control have particularly large Huber values near the tip of the leader, which, based on LSCs, results in greater hydraulic dominance compared with stunted individuals (Figs 2–5, Tab. 1). Whether the hydraulic architecture of fir trees influences future growth and developmental patterns, or merely is their result, awaits further experimentation.

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