

The hydraulic architecture of eastern hemlock (*Tsuga canadensis*)

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Received August 22, 1983

EWERS, F. W., and M. H. ZIMMERMANN. 1984. The hydraulic architecture of eastern hemlock (*Tsuga canadensis*). Can. J. Bot. 62: 940–946.

Leaf specific conductivities (LSCs, hydraulic conductivity per gram dry weight of supplied leaves), Huber values (transverse xylem area per gram dry weight of supplied leaves), specific conductivities (hydraulic conductivity per unit transverse xylem area), and tracheid diameters were measured throughout the trunk and crown of 9- to 96-year-old trees of *Tsuga canadensis* (L.) Carr. By definition, LSC = Huber value \times specific conductivity. Specific conductivity is controlled by wood anatomical features, especially tracheid diameter. LSCs, which indicate the relative water supply to different plant parts, decrease acropetally but are higher in the trunk than in branches and are particularly low in second-order branches and at branch insertions. The differential water supply is due to larger Huber values in the leader and to particularly narrow tracheids at branch junctions. In addition, as trunks enlarge they produce wider tracheids, resulting in greater specific conductivity than in supported branches. Based on comparison with results for *Abies balsamea*, the degree of "hydraulic dominance" in the younger parts of conifers is controlled by the Huber value and may be related to the degree of apical control.

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La conductivité spécifique des feuilles (LSC, conductivité hydraulique par gramme de poids sec de feuilles alimentées), la valeur de Huber (surface transversale du xylème par gramme de poids sec de feuilles alimentées), la conductivité spécifique (conductivité hydraulique par unité de surface transversale du xylème) et le diamètre des trachéides ont été mesurés dans tout le tronc et la cime d'arbres âgés de 9 à 96 ans appartenant au *Tsuga canadensis* (L.) Carr. Par définition, LSC = valeur de Huber \times conductivité spécifique. La conductivité spécifique est régie par les caractéristiques anatomiques du bois, surtout le diamètre des trachéides. La LSC, qui est une mesure de l'approvisionnement relatif en eau des différentes parties de la plante, diminue en direction acropète, mais elle est plus élevée dans le tronc que dans les branches et elle est particulièrement faible dans les branches de deuxième ordre et dans la zone d'insertion des branches. Ces différences d'apport d'eau sont dues aux plus grandes valeurs de Huber dans les rameaux terminaux et au fait que les trachéides sont particulièrement étroites à la jonction des branches. De plus, à mesure que le tronc s'agrandit, il forme des trachéides de plus en plus larges, ce qui provoque une plus grande conductivité spécifique dans le tronc que dans les branches. D'après des comparaisons avec l'*Abies balsamea*, le degré de "dominance hydraulique" des parties les plus jeunes des conifères est régi par la valeur de Huber et est peut être relié au degré de dominance apicale.

[Traduit par le journal]

Introduction

As trees increase in size, water and minerals must be transported a greater distance to get to the upper leaves. There have been recent studies on the overall functional xylem anatomy of dicotyledonous trees (Zimmermann 1978, 1983), palms (Zimmermann and Sperry 1983), and conifers (Tyree et al. 1975; Tyree et al. 1983; Ewers and Zimmermann 1984). However, this is the first such study to examine trees of various sizes and ages to understand the xylem architecture from both an ontogenetic and functional point of view.

In the "pipe model theory of plant form" (Shinozaki et al. 1964a, 1964b) the tree is considered as an assemblage of "unit pipes," each of which supports a unit of leaves. This simple and popular model is based on the common observation for many species that there is a fairly constant "Huber value" (xylem transverse sectional area in square millimetres per gram dry weight of supported leaves) throughout the plant and between plants of the same species (Grier and Waring 1974; Waring et al. 1977; Rogers and Hinckley 1979; Kaufmann and Troendle 1981; Santee and Monk 1981).

In conflict with the pipe model, Huber (1928) found that the relative *Leitfläche* (relative conducting area or what we call the Huber value) was not constant throughout individual trees of *Abies concolor* and *Picea* sp. Instead, Huber values increased with height in the tree and were greater in the trunk than in

branches. We have found similar results for *Abies balsamea* (Ewers and Zimmermann 1984).

Huber values are interesting from a mechanical point of view (see Long et al. 1981), but they are not, by themselves, informative about water transport. First of all, we can not assume that all tracheary elements will retain a conductive function. Secondly, the size of individual tracheary elements greatly influences the transport properties of wood (e.g., Siau and Petty 1979; Zimmermann 1983; Ewers and Zimmermann 1984). According to Poiseuille's equation for ideal capillaries, volume flow is proportional to the radius to the fourth power of tracheary elements (Reiner 1960).

Leaf specific conductivity (LSC, hydraulic conductivity² per gram dry weight of supplied leaves) is the best measure we now have of the relative efficiency of the xylem in providing water and minerals to different parts of the tree (Zimmermann 1978). During periods of rapid transpiration, localized pressure potential gradients are inversely proportional to LSCs (Zimmermann 1978; Tyree et al. 1983). In the species so far examined, LSCs are always higher in the trunk than in branches, and there is a hydraulic constriction at the base of each branch (Zimmermann 1978; Tyree et al. 1983; Ewers and Zimmermann 1984). LSCs can be divided into two components since, by definition, LSC = Huber value \times specific conductivity. Specific conductivity

¹Deceased 7 March 1984.

²Hydraulic conductivity is in microlitres per hour under conditions of gravity gradient (10.13 kPa m⁻¹).

TABLE 1. Comparison of trunk versus branch component of a junction. Based on data in Fig. 5. Measurements are described in text

Component	LSC	Mean Huber value	Specific conductivity	Mean radius ⁴ tracheids
Trunk	59	1.9	31.1	12.9 ⁴
Branch	11	1.53	7.2	8.9 ⁴
Trunk/branch	5.36	1.24	4.32	4.41

is defined as hydraulic conductivity per xylem transverse area (millimetres squared).

In our opinion, the pipe model by itself is not useful in predicting water flow in the plant, but it is of some developmental interest. For instance, structural deviations from the pipe model may be related to the degree of apical control (Huber 1928; Ewers and Zimmermann 1984). Apical control means that the leader has greater elongation growth than lateral branches have (Brown et al. 1967). This is not necessarily the same as apical dominance, which refers to the arrest of lateral buds.

In the present study we examine *Tsuga canadensis*, which is unusual among conifers in having very weak apical control. In this species the more or less plagiotropic leader is frequently replaced by a lateral branch (Hibbs 1981). Interestingly, Tyree et al. (1975) found the specific conductivity in large trunks of this species was up to 335 times greater than in small twigs. However, they did not measure LSCs or Huber values. In the present study our objectives were to measure LSCs, Huber values, specific conductivity, and tracheid diameters throughout the trunk and crown of trees to determine the structural basis for differences in LSCs and to determine if there is a relationship between apical control and hydraulic dominance. "Hydraulic dominance" simply means that the leader has greater LSCs than the branches.

Materials and methods

Plant material

Experiments were run on seven forest-grown trees of *Tsuga canadensis* (L.) Carr during the period from August through December of 1982. The trees ranged in age from 9 to 96 years and in height from 0.43 to 15.97 m. After the experiments were completed, the former leaders that remained alive on trees were detected based on pith continuity (see Hibbs 1981).

Conductivity measurements

Unlike most conifers, *Tsuga canadensis* lacks resin canals in its wood. This is an advantage since resin canals make conductivity measurements difficult. Hydraulic conductivity is measured as the flow rate of a defined solution (here 5 mM KCl) through isolated 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 removed from each end. This was done to prevent resin in the bark from interfering with the conductivity measurements. Further details of our procedure are in Ewers and Zimmermann (1984).

Xylem areas and tracheid diameters

After the conductivity measurements were completed, stem segments were perfused with dye to demarcate the sapwood transverse area (i.e., area of conducting xylem). To distinguish between the trunk and branch components of a junction, different color dyes (0.5% safranin and 0.5% crystal violet) were perfused down each. Transverse sections from the middle of each stem piece were later prepared with a sliding microtome. The larger stems were sectioned as longitudinally split pieces. Calculations of the transverse area of the current

year's xylem (outer growth ring), the sapwood, and the entire xylem area (sapwood plus heartwood) were made by weighing paper cutouts from camera-lucida drawings. Except in Figs. 4 and 5 and in Table 1, Huber values and specific conductivities are based on the entire xylem transverse areas, as done by Huber (1928), not sapwood area nor last year's xylem. However, for the trees examined, there was little difference between sapwood area and the entire xylem area.

The transverse sections were also used to measure inside tracheid diameter of 10 of the widest tracheids of the outer growth ring. In transverse section, the tracheid lumens are intermediate in shape between a rectangle and an ellipse. As an approximation of hydraulic diameter, we simply averaged the radial and tangential diameters of each tracheid.

Leaf weights

For water transport, leaf surface area may be more relevant than leaf weight, but for reasons of practicality we measured leaf dry weight and provide the following conversion factors. Based on 18 subsamples of 20 leaves each, the fresh weight to dry weight ratio was 2.33 with a standard error of 0.028. This did not vary significantly during the period of the experiments. The ratio of leaf dry weight to projected surface area (one side only) was 1.39 ± 0.031 g/dm². This conversion factor varied slightly with position in the tree; the ratio was 1.49 ± 0.020 near the top, 1.39 ± 0.042 in the middle, and 1.29 ± 0.057 near the base of the trees.

Leaf dry weights were measured as follows. Branches and leaves distal to the stem segments of interest were put in paper bags in a 40°C oven for 2 days. By this time the leaves had abscised from the stems. The isolated leaves were then thoroughly dried to constant weight at 70°C. Based on subsamples, the 40°C oven treatment resulted in no measurable dry weight loss from respiration.

Results

LSCs are given in microlitres per hour per gram at 10.13 kPa m⁻¹. These values can be converted to the SI units used by Tyree et al. (1983), that is, kilograms per second per metre per megapascal, merely by multiplying our numbers by 3.8 × 10⁻⁶. It should be noted that with this conversion factor, LSCs will be expressed in terms of leaf surface area in square metres rather than leaf dry weight in grams.

Within individual trees, LSCs were higher in the trunk than in first-order branches and were particularly low in second-order branches and at branch insertions (Figs. 1, 2, 5, 7, Table 2). Near the base of the tree, LSCs were greater by severalfold in the trunk than in branches. However, LSCs steadily decreased in going up the trunk, such that LSCs near the tip of the leader were only slightly greater than those of adjacent laterals (Figs. 1, 2).

In terms of LSC values, small trees were similar to the tops of large trees (Figs. 1, 2). With increasing tree size, LSCs increased dramatically at the base but only slightly at the top (Figs. 1, 2, 6).

As with LSCs, Huber values were higher in the trunk than in first-order branches and were lowest in second-order branches (Figs. 3, 5, 7, Table 2). However, unlike LSCs, Huber values increased in going up the trunk and out along the branches (Figs. 3, 4, 7). Vigorous trees had a sharper acropetal increase in Huber values than did the slow-growing trees (Fig. 7). With increasing tree size, Huber values tended to increase both at the base and the top of the tree (Fig. 6).

Like LSCs, tracheid diameters decreased acropetally (Figs. 3, 8). Measured specific conductivity (x) was correlated to the mean inside diameter of the largest tracheids ($y = 0.0004x + 10.6$, $r = 0.69$, $df = 37$, $p < 0.001$). With increasing tree size, tracheid diameters and measured specific conductivity increased near the base of the tree (Fig. 6).

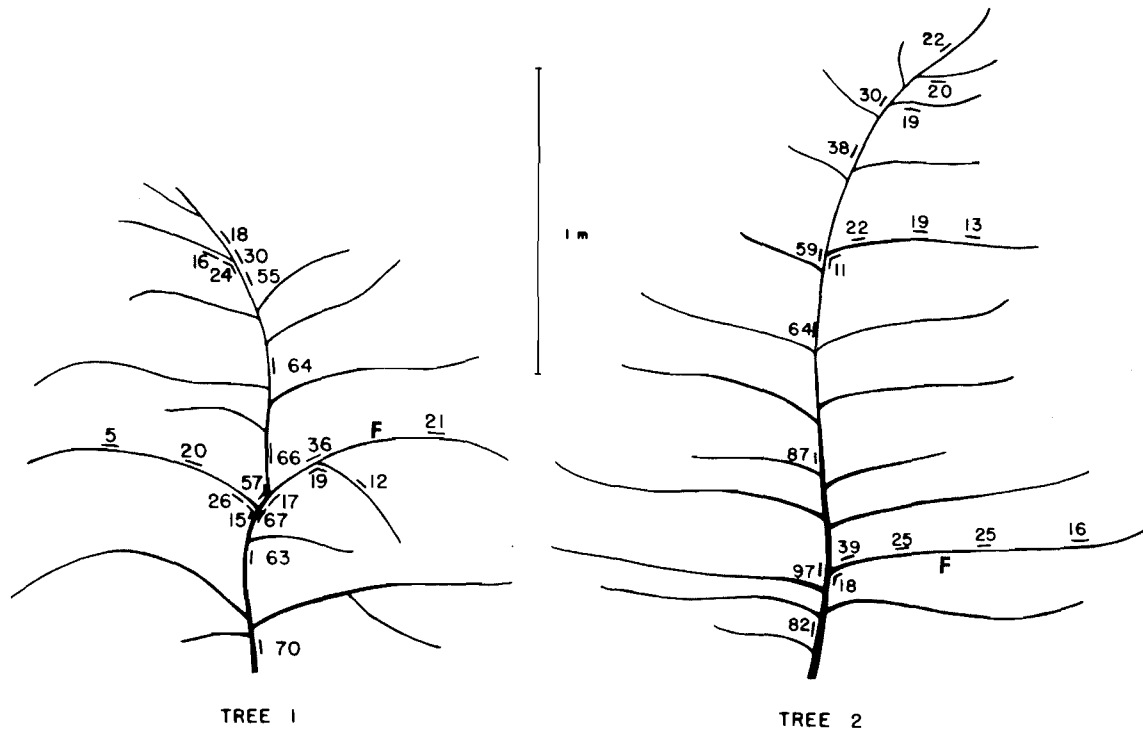


FIG. 1. LSCs along the axes of a 19-year-old (tree 1) and a 12-year-old plant (tree 2). LSCs are in microlitres per hour at 10.13 kPa m^{-1} per gram dry weight of leaves supplied. F, former leader. Conductivities are higher in the trunk than in branches and tend to decrease acropetally. Branch insertions have hydraulic constrictions. For LSCs, tree size is more relevant than tree age (compare with Fig. 6).

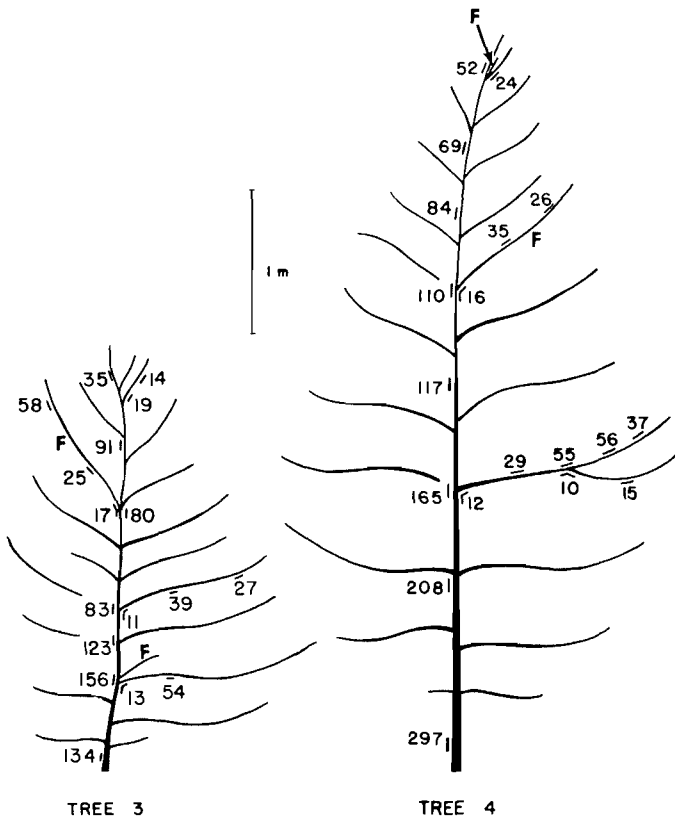


FIG. 2. LSCs (microlitres per hour per gram at 10.13 kPa m^{-1}) along the axes of two 19-year-old trees. F, former leader. Arrow indicates former leader with aborted apex. Conductivities are higher in the trunk than in branches and are particularly low in second-order branches and at branch insertions.

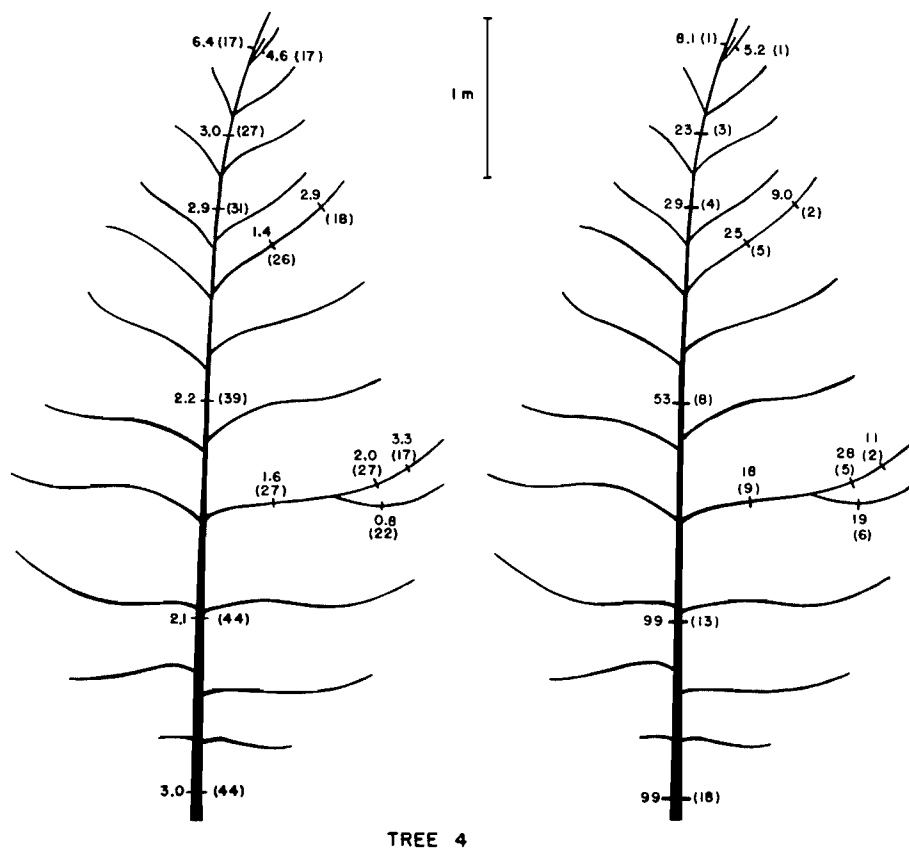
TABLE 2. Comparison of means for trunk and branch segments of similar diameter. Statistical significance determined by Student's *t*-test. NS, not significantly different at 0.05 level of probability

Tree numbers	Trunk	Branch	<i>p</i>	Trunk/branch
2 and 4				
LSC	49.2	26.3	<0.05	1.9
Huber value	3.5	2.0	<0.05	1.75
Specific conductivity	15.8	14.9	NS	1.1
Tracheid diameter (μm)	21.5	19.3	NS	1.1
1 and 3				
LSC	49.8	25.8	NS*	1.9
Huber value	2.5	1.8	<0.001	1.4
Specific conductivity	20.25	15.0	NS	1.35
Tracheid diameter (μm)	20.0	19.2	NS	1.0

*NS owing to much variation in LSCs.

At the junctions between a trunk and branch, LSCs, Huber values, tracheid diameters, and specific conductivities were all greater for the trunk than for the branch component. In the example shown (Fig. 5, Table 1), a 5.36 times greater LSC was attributed to a 1.24 times greater mean Huber value and a 4.32 times greater measured specific conductivity. The mean radius to the fourth power of tracheids was a good predictor (ca. 2% error) of the measured difference in specific conductivity (Table 1).

With increasing stem diameter there were increases in LSC, tracheid diameter, and specific conductivity but decreases in Huber value (Figs. 7, 8). If we compare similar diameter stem segments of trunks versus lateral branches, the LSC and Huber values were higher in the trunk. The more vigorous trees had a greater difference between trunks and branches in Huber values than did the slow-growing trees (Fig. 7, Table 2). How-



TREE 4

FIG. 3. Left diagram shows Huber values (square millimetres per gram) and, in parentheses, mean inside tracheid diameters (micrometres). Right diagram shows specific conductivities (microlitres per hour per square millimetre at 10.13 kPa m^{-1}) and, in parentheses, age of stem segments (years). In going up the tree and out along branches tracheid diameters and specific conductivity decrease. Hydraulically, this is partially compensated by the acropetal increase in Huber values.

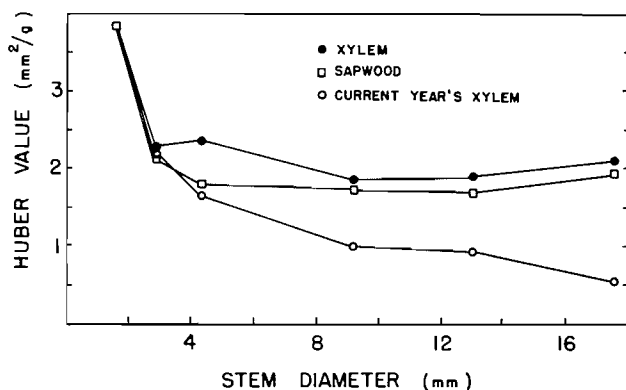


FIG. 4. Huber value versus stem diameter for trunk segments of tree 2. Values were calculated in three ways, i.e., based on the total xylem transverse area (as originally done by Huber 1928), the sapwood area (as in Fig. 5 and Table 1), and the transverse area of the outer growth ring (current year's xylem) each divided by the dry weight of supplied leaves. Total xylem area is mechanically relevant, sapwood area is the most hydraulically important, and current year's xylem is informative from a morphogenetic viewpoint. All three values increase acropetally (to left on graph).

ever, for all trees there was no statistically significant difference between comparable diameter trunk and branch segments in specific conductivity or in mean tracheid diameter (Figs. 7, 8, Table 2). Near the top of the tree, the leader was similar to adjacent lateral branches in mean inside tracheid diameter and

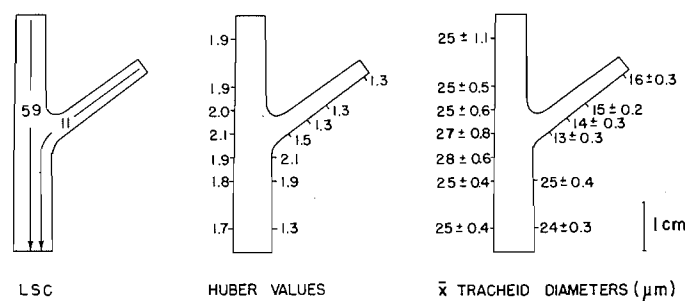


FIG. 5. LSCs, Huber values, and mean tracheid diameters (\pm standard error) for a junction. After the conductivity measurements, different color dyes were perfused to distinguish the trunk and branch components. The trunk has a greater LSC as a result of greater Huber values and wider tracheids. As we approach the junction, branch Huber values slightly increase, while tracheid diameters decrease. See summary in Table 1.

in measured specific conductivity (Fig. 3). However, in the older plant parts the trunk segments had much greater girth, LSCs, tracheid diameters, and specific conductivities than in supported branches (Figs. 1, 2, 3, 5, 7, 8).

Discussion

The large LSCs in the trunk of trees help allow the upper leaves to compete with lower leaves for water and minerals (Zimmermann 1978; Tyree et al. 1983). Differences between stem segment in LSCs can be mathematically assigned to dif-

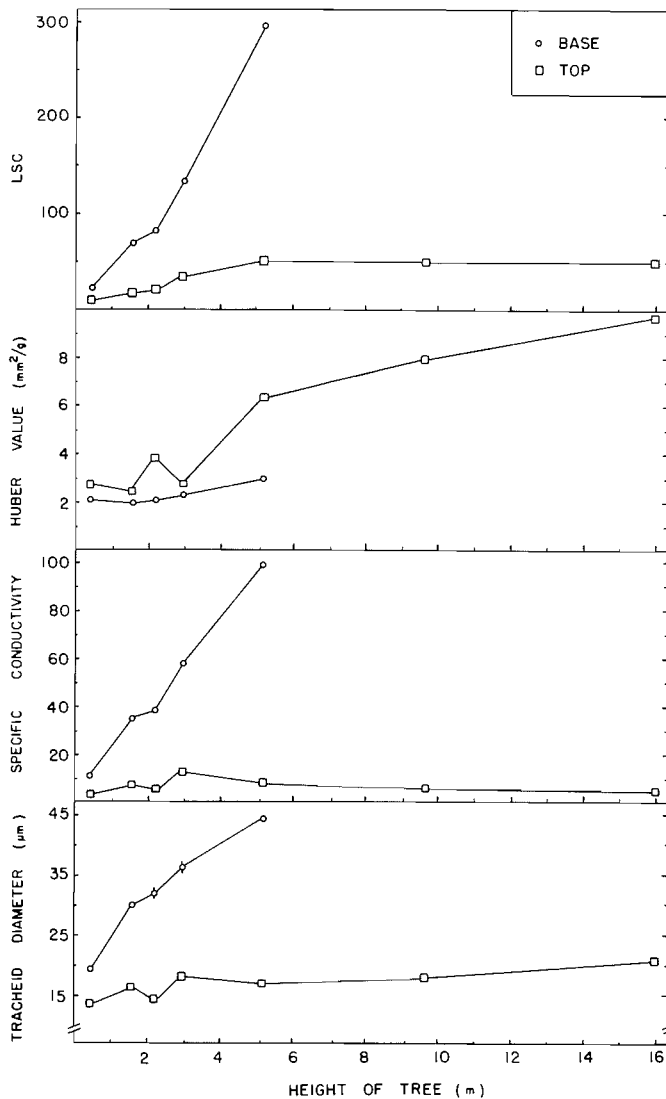


FIG. 6. Tree height versus LSC, Huber value, specific conductivity, and mean tracheid diameter (\pm standard error). Measurements were made on trunks at 15 cm from ground (base) and 20 cm from tip of leader (top). Trees were from 9 to 96 years old. For the two tallest trees, measurements were made only at the top.

ferences in Huber value and (or) to differences in measured specific conductivity (Ewers and Zimmermann 1984). Specific conductivity is a function of wood anatomical features including especially the diameter of tracheary elements (Farmer 1918; Huber 1956; Tyree et al. 1975; Ewers and Zimmermann 1984). Thus, we now have the necessary tools and information to analyze the structural bases for the unequal water supply to different plant parts.

As young trees of *Tsuga canadensis* enlarge, they develop greater LSCs all along the leader but especially near the base of the trunk. This is due mostly to greater specific conductivities, which apparently result from wider tracheids in large trees (Fig. 6). However, the increase in specific conductivity as trunks enlarged was not as great as would be predicted by Poiseuille's law for ideal capillary tubes (Reiner 1960). This is probably because large trunks have many small as well as large tracheids; for practical purposes, in this study we measured only the wider tracheids, not the sum of the radii to the fourth power of all tracheids. In addition, other factors, such as tra-

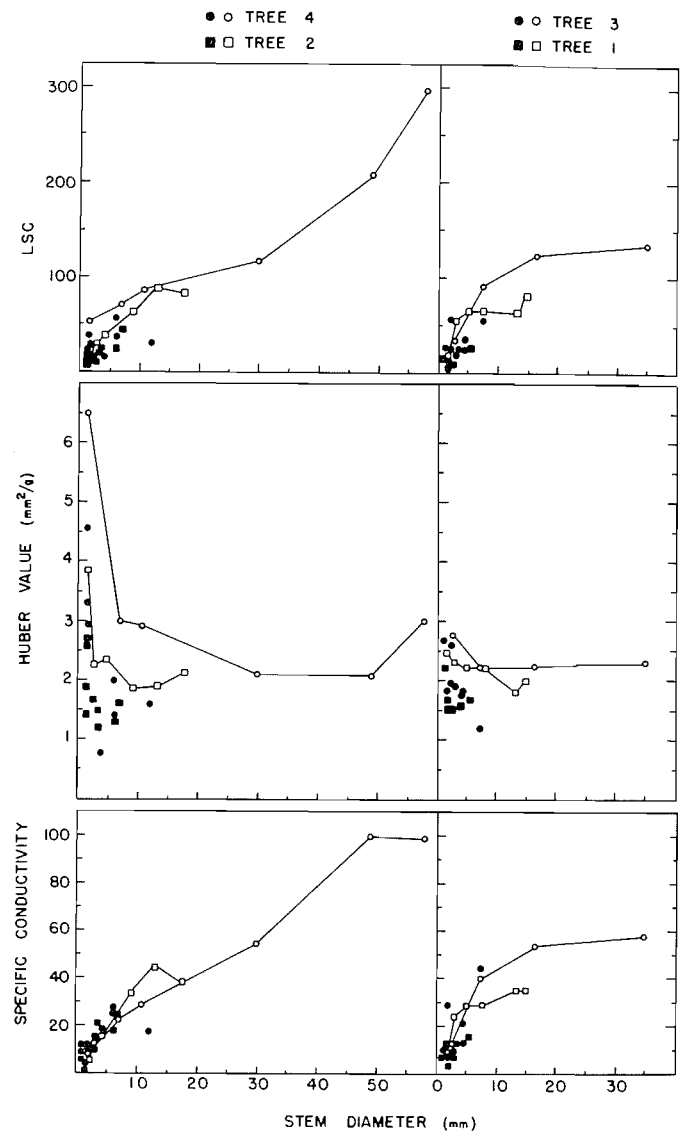


FIG. 7. LSC, Huber value, and specific conductivity as functions of stem diameter. Results shown for two vigorous trees (three graphs on left) and two slow-growing trees (three graphs on right). The connected (open) symbols represent trunk segments and the solid symbols branch segments. Junctions between trunks and branches are not included. Note that $LSC = \text{Huber value} \times \text{specific conductivity}$. See statistical summary in Table 2.

cheid length, number of pits, and size of pit pores, might also influence the measured specific conductivity (Tyree et al. 1975; Siau and Petty 1979; Zimmermann 1983).

Since LSCs are inversely proportional to resistance to water flow, greater LSCs in larger plants must at least partially compensate for the greater distance water must move to get to the upper leaves. For instance, when LSCs are twice as great, the pressure potential gradient required to move water at a given rate will be one-half as steep (Zimmermann 1978, 1983).

At junctions between the trunk and branches, the greater LSCs in the trunk component are due both to greater Huber values and to greater specific conductivity (Fig. 5 and Table 1). The older the junction, the greater the hydraulic disparity between the trunk and branch component (Figs. 1 and 2). Throughout the plant, Huber values are greater in the trunk than in branches (Figs. 3 and 7). In addition, there is a fairly consis-

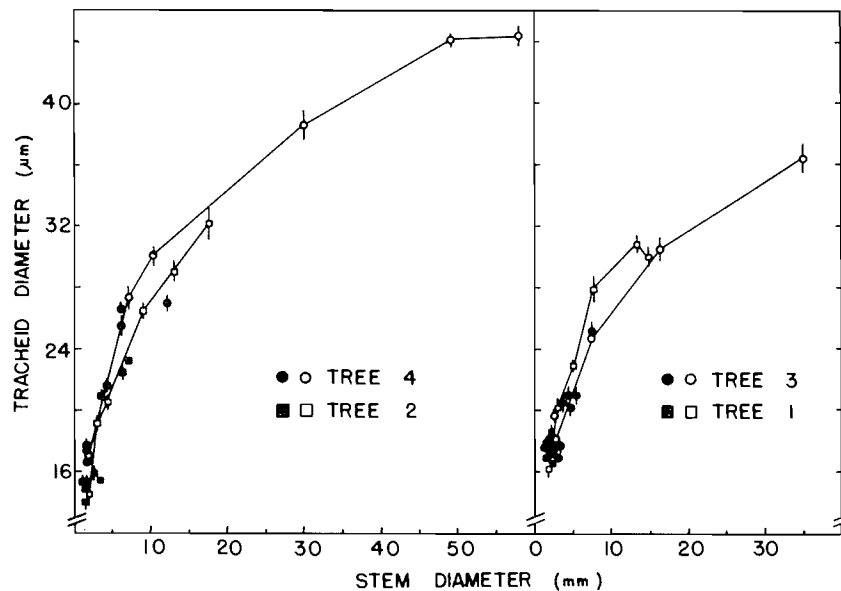


FIG. 8. Stem diameter versus mean tracheid diameter (\pm standard error) for 10 of the widest tracheids of the outer growth ring. Results shown for two vigorous trees (left) and two slow-growing trees (right). The connected (open) symbols represent trunk segments and the solid symbols branch segments, with junctions excluded. With increasing stem diameter trunks and branches have similar increases in mean tracheid diameter. However, trunks enlarge faster than branches.

tent correlation between stem diameter and specific conductivity (Fig. 7). The trunk increases in girth faster than branches; in the older plant parts the trunk has much greater specific conductivity than in branches, which results in very high LSCs in the trunk component. As we approach the branch junction, there are slight increases in Huber values but decreases in tracheid diameter. As a result, the branch component of the junction has particularly low LSCs (Fig. 5 and Table 1).

From the literature, it is clear that there is much variation between taxa in the ratio of leaf area to stem sapwood area (e.g., see Waring et al. 1977; Kaufmann and Troendle 1981). This ratio is roughly equivalent to the Huber value. Many workers report constant Huber values within particular species. However, these reports are based mostly on measurements only in the older plant parts, often only at 1.3 m (e.g., see Grier and Waring 1974; Rogers and Hinckley 1979; Santee and Monk 1981). As noted earlier in this report, for *Abies concolor*, *Picea* sp. (Huber 1928), *Abies balsamea* (Ewers and Zimmermann 1984), and *Tsuga canadensis* (Figs. 3–7) the Huber value varies considerably with the precise position in the tree.

For the species in which LSCs have been reported, differences within individual plants are more striking than differences between taxa. For instance, within one tree of *Tsuga canadensis*, LSCs ranged from 10 to 297 $\mu\text{L h}^{-1} \text{g}^{-1}$ at 10.13 kPa m^{-1} (Fig. 2). For *Abies balsamea*, LSCs ranged from 3 to 610 $\mu\text{L h}^{-1} \text{g}^{-1}$ (Ewers and Zimmermann 1984). With the appropriate conversions, for *Thuja occidentalis* LSCs ranged from 4 in 1-mm diameter stem segments up to 124 in trunks 100 mm in diameter (Tyree et al. 1983). Zimmermann (1978) reported LSCs in diffuse-porous dicotyledonous trees to range from 10 in small twigs to 1000 in trunks. Zimmermann's LSCs were based on the fresh weight of leaves; dry weight LSCs would be about 2.5 times as great (F. W. Ewers, unpublished data).

The very large LSC values in the trunks of dicotyledonous trees (up to ca. 2500) are the result of large vessels, which have low resistance to water flow (Zimmermann 1978). We might expect even larger LSCs to occur in ring-porous trees and in

lianas, which have the largest vessels in the plant kingdom. However, this can not be determined without direct measurement since as noted above, LSCs depend not only on the size of the tracheary elements but also on the relative sapwood transverse area.

Based upon the two species that have been examined in detail, there appears to be a relationship between apical control and hydraulic dominance. In *Tsuga canadensis*, which has weak apical control, LSCs are only slightly greater near the tip of the leader than in lateral branches (Figs. 1, 2). In contrast, in trees of *Abies balsamea* with strong apical control, the LSCs of the leader are up to 17 times greater than in branches (Ewers and Zimmermann 1984). Most importantly, slow-growing individuals of this species have poor apical control and are similar to *Tsuga canadensis* in having poor hydraulic dominance near the top of the plant (Ewers and Zimmermann 1984).

Differences between trees of *Tsuga canadensis* and *Abies balsamea* in their degree of hydraulic dominance can be explained exclusively by Huber values. The pattern of measured specific conductivities and tracheid diameters is nearly identical for both species (Figs. 3, 7, and 8) (Ewers and Zimmermann 1984). However, in vigorous trees of *Abies balsamea*, Huber values are on the average 12 times greater in the trunk than in comparable-diameter stem segments (Ewers and Zimmermann 1984). In contrast, in vigorous trees of *Tsuga canadensis*, Huber values were only 1.75 times greater in the trunk than in comparable-diameter branch segments (Table 2).

The hydraulic architecture of a tree might influence its future growth and branching patterns. Branches with greater LSCs can more effectively compete for water and minerals. Therefore their leaves might photosynthesize more efficiently, which could result in more vascular tissue in the subtending stems. In *Tsuga canadensis*, where there is often little hydraulic difference between 1-year-old trunk versus branch segments, it is not surprising that, on the average, the leader is replaced 6.7 times in 10 years. Leader replacement occurs without meristem death 2.4 times in 10 years (Hibbs 1981). In contrast, in *Abies balsamea* the leader has a decided advantage over laterals.

Even the 1-year-old portion of the trunk is hydraulically dominant. Perhaps for this reason in this species the leader is never replaced except when damaged.

To summarize, hydraulic dominance near the top of the leader may be linked to the degree of apical control, but further study is needed to effectively make such a conclusion. The trunk of *Tsuga canadensis* is hydraulically favored over branches partly as a result of greater sapwood transverse area relative to leaves supplied (the Huber value). In addition, the hydraulic dominance of the trunk over branches becomes more pronounced in the older plant parts as a result of large tracheids in the old trunk.

Acknowledgements

We thank Ms. Monica Mattmuller for skilled technical assistance and Dr. P. Barry Tomlinson, Dr. Jörg J. Sauter, Mr. John S. Sperry, and Ms. Ann Lewis for critical review of the manuscript.

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