

Hydraulic architecture of some diffuse-porous trees

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The rate of flow of a dilute KCl solution through sections of stem, branches, and twigs was measured and expressed in microlitres per hour, under conditions of gravity flow, per gram fresh weight of leaves supplied by that section of xylem. This is called leaf-specific conductivity (LSC). It is not uniform throughout the tree, LSC of the stem being higher than that of branches. Furthermore, vascular junctions, such as the path from stem to branch, represent hydraulic constrictions. Distribution of LSC in the tree is primarily based on varying vessel diameters. Vessel diameters increase from top to bottom in the tree stem. They are smaller in branches than in the main stem, and there is a distinct constriction of diameters at the base of each branch. Functionally this means that when transpiration begins the pressure has to drop more rapidly in the xylem of lower lateral leaves than in those at the top of the tree. It also means that under conditions of water stress peripheral parts of the tree are more vulnerable than the trunk.

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L'auteur a mesuré le taux d'écoulement d'une solution diluée de KCl à travers des sections de troncs, de branches et de ramilles dans des conditions d'écoulement par gravité; il exprime ces valeurs par rapport au poids frais des feuilles approvisionnées par cette section de xylème. Ce paramètre s'appelle la conductivité foliaire spécifique (LSC). Cette valeur n'est pas uniforme tout le long de l'arbre, la LSC du tronc étant plus élevée que celle des branches. De plus les jonctions vasculaires, telles que le passage entre le tronc et les branches, représentent des constrictions hydrauliques. La distribution de la LSC dans l'arbre est surtout reliée à la variation des diamètres des vaisseaux. Les diamètres des vaisseaux augmentent du sommet vers la base dans le tronc de l'arbre; ils sont plus petits dans les branches que dans le tronc, et il y a une constriction évidente des diamètres à la base de chaque branche. Du point de vue fonctionnel ceci signifie que lorsque la transpiration commence, la pression doit baisser plus rapidement dans le xylème des feuilles latérales basses que dans celles qui sont situées dans la cime de l'arbre. Ceci signifie également que dans des conditions de tension hydriques, les régions périphériques de l'arbre sont plus vulnérables que le tronc.

[Traduit par le journal]

Introduction

The most important leaves of a tree are usually those at the top because it is with these that the tree can best compete with its neighbors for a place in the sun. But the highest leaves are also the most 'expensive' ones. Not only are they farthest from the water supply, the roots, but water has to be brought to them against the force of gravity. How, then, can the top leaves of a tree successfully compete for water with the bottom leaves? This paper offers at least a partial answer to this question.

Leonardo da Vinci wrote several hundred years ago, "All the branches of a tree at every stage of its height when put together are equal in thickness to the trunk (below them). All the branches of a water (course) at every stage of its course, if they are of equal rapidity, are equal to the body of the main stream." (Leonardo's note No. 394, translation by Richter 1970). Botanists are aware of the approximate correctness of this observation and have interpreted this constructional principle of a tree as

serving the demands of equal strength and equal conductivity (see Jaccard 1913, 1919, and the literature cited therein). Japanese workers call this simple situation the "pipe model" whereby a tree is regarded as a bundle of thinner stemmed plants (Shinozaki *et al.* 1964). Of particular interest are investigations by Huber (1928). He measured transverse-sectional xylem areas (in square millimetres) of stems and branches and divided these by the fresh weight of all the leaves that were supplied with xylem sap via that transverse-sectional area. This measurement (in square millimetres per gram) is referred to as the Huber value in this paper. It would have to be the same anywhere in the tree if Leonardo's statement were precisely correct, i.e., the transverse-sectional area of the main stem divided by the total leaf weight supplied by that part of the stem should give the same number as the transverse-sectional area of a small branch divided by the leaf weight borne by that branch. This is generally the case but there are

interesting exceptions. In *Abies concolor*, Huber (1928) found values of the order of $0.5 \text{ mm}^2/\text{g}$ in the lower stem and lateral branches. However, the value increased sharply toward the terminal shoot to a maximum of $4.26 \text{ mm}^2/\text{g}$. An illustration of such a tree is reprinted in Zimmermann and Brown (1971) on p. 182 (note that in the first printing of 1971 the legend should say hundredths of square millimetres per gram). Huber (1928) pointed out that this is an interesting expression of apical dominance: the leader has a better water supply system than the lateral branches.

Huber's (1928) investigations are of considerable interest, but they do not describe the water-conducting capacity of the xylem very well. First of all, Huber's values do not take into account the amount of functional xylem. Heartwood does not conduct water and is not visually recognizable in every species. Furthermore, in ring-porous trees, most conduction is through the large vessels of the outermost growth ring. This means that the Huber value is informative only in young small-porous trees where the entire transverse-sectional area of the xylem is conducting.

An even more serious objection to the usefulness of the Huber value is the fact that vessel diameter is of paramount importance for the efficiency of water conduction. Volume flow through a capillary is proportional to the fourth power of capillary radius according to the Poiseuille equation (see Zimmermann and Brown 1971, p. 190). In order to learn something about the efficiency of the xylem, we need to measure hydraulic conductivity and express it per supplied leaf quantity. It is surprising that this has never been investigated, even though interest in these matters was very great 40–60 years ago (e.g., Farmer 1918; Riedl 1937). Experimental procedures to make such measurements are extremely simple, yet they revealed surprising information about the hydraulic construction of trees.

One could argue about the best measure for leaf quantity. Photosynthesis is often expressed per unit area of leaf surface. This is probably the best measure, but measurement of leaf area becomes totally unpractical when we are dealing with larger trees. For example, in the poplar shown in Fig. 5, left, we are dealing with well over 5000 leaves of a total weight exceeding 2.8 kg. We followed Huber's example and used fresh weight of leaves. This is simple to measure and probably the most reliable measurement of large leaf quantities.

Fresh weight of leaves does vary. For example, detached sugar maple leaves lost ca. 3% of their weight during 3 h until they showed signs of wilting. This is insignificant in respect to our measure-

ments, especially because we always weighed turgescient leaves. Long-term variations of fresh weight are more difficult to assess because absolute weight is a destructive measure. To overcome this and to make our measurements comparable with other physiological parameters such as photosynthesis, we measured fresh weight of leaves per unit leaf surface area. This is discussed in the Materials and Methods section.

Materials and Methods

Measurements were made with three species of maple (*Acer pensylvanicum* L., *A. rubrum* L., and *A. saccharum* Marsh.), with white birch (*Betula papyrifera* Marsh.), with large-toothed poplar (*Populus grandidentata* Michx.), and a few other diffuse-porous trees. Trees were collected in the forest early in the morning to prevent excessive embolism at the cut end. The tree was cut at ground level with a bow saw, its base immediately transferred into a bucket of water, and thus carried to the laboratory. If the tree was too tall to be carried out of the forest in upright position, the cut end was transferred to a water-filled plastic bag which was tied, as air free as possible, around the stem. The tree was then carried horizontally, its cut basal end still in water. On the lawn outside the laboratory, the points at which stems and branches were to be measured were determined and tagged. A sketch of the tree was then made and leaves were collected and put into plastic bags. Leaf weight was recorded in such a way that the total weight of leaves above any checkpoint was known. Stem and branch sections to be measured were sawn from the tree as pieces about 30 cm long, i.e., considerably longer than the needed length, and immediately submerged in water until further use. The section of the stem to be measured was trimmed to length (ca. 7–15 cm, but uniform within one experiment) on a table saw by cutting disks off both ends alternately. This procedure releases any residual tension in the xylem. Both ends were then cut smooth with a razor blade or sliding microtome (for which we have an oversize clamp). A piece of rubber tubing or 'Pluro-Stopper' was then fitted at one end, the wood inserted into a container with water, tubing end up, and briefly vacuum infiltrated to remove air bubbles from the cut surface. Thus prepared, smaller stem pieces were hung from a water-filled pipette and the flow of water through them was measured at intervals of either 30 s or 1 min, depending on the rate of flow. Gravity flow was calculated by dividing measured flow rate by the average height of the water column above the specimen ($(h_1 + h_2)/2$ in Fig. 1, left) and multiplying it by the length of the specimen (l in Fig. 1, left). Pieces too large for a pipette were fitted at their upper end with a Pluro-Stopper ring and supported above a balance (Fig. 1, right). Gravity flow rate was again calculated by dividing the measured flow rate by the intermediate pressure head h_1 and multiplying it by l .

Hydraulic conductivity is normally defined as flow rate per square centimetre per pressure gradient. This concept is not very useful for the purpose of comparing different parts of a tree with each other. We therefore express conductivity not per square centimetre but per fresh weight of leaves supplied. In order to obtain simple numbers, we use the units microlitres per hour per gram (fresh weight of leaves) under conditions of gravity flow and call this 'leaf-specific conductivity' (LSC).

Fresh weight of leaves per unit projected surface area has been measured with several hundred leaves for each species. Results were rather variable and primarily dependent upon leaf size. For example, tiny sugar maple leaves weighed $0.5 \text{ g}/\text{dm}^2$, while very large ones weighed $1.4 \text{ g}/\text{dm}^2$. Average values were

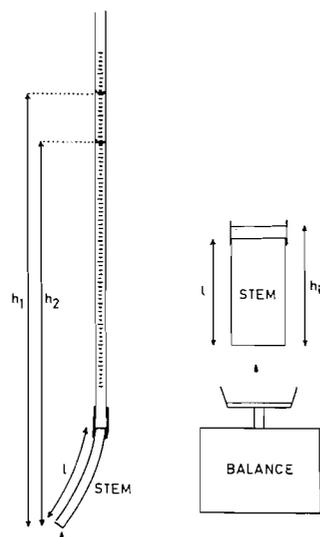


FIG. 1. Left, flow-rate measurements with a small piece of stem. The KCl solution is fed to the stem from a pipette. Gravity flow rate is calculated by dividing flow rate by $(h_1 + h_2)/2$ and multiplying it by the length of the piece, l . Right, flow-rate measurements with larger stem pieces. A Pluro-Stopper ring is fitted to the upper end of the stem. KCl solution flows from this pool through the stem specimen and drips onto the balance. Water-level readings (h_t) and balance readings (amount of water on balance) are taken alternately. Gravity flow rate is therefore measured flow rate divided by the intermediate pressure head h_t times the length of the stem, l .

as follows: *Acer saccharum* Marsh., $1.01 \pm 0.107 \text{ g/dm}^2$; *A. pensylvanicum* L., $0.971 \pm 0.114 \text{ g/dm}^2$; *Populus grandidentata* Michx., $1.74 \pm 0.166 \text{ g/dm}^2$; *Betula papyrifera* Marsh., $1.79 \pm 0.146 \text{ g/dm}^2$. These values permit the reader to convert our LSC to microlitres per hour per square decimetre leaf area. Although standard deviations are large, conversion is permissible in most cases because we never dealt with a statistical leaf sample in our experiments, but always weighed *all* leaves above a certain point (big and small ones). Conversion requires caution where we deal with petioles or small shoots where only a few leaves are supplied. For example, conductivity of an axis supplying small leaves, based upon fresh weight, comes out too high when converted to leaf area. However, this paper deals primarily with stems and branches. The reader should also realize that our conductivity measurements range over almost three orders of magnitude, from about 1 in petioles to about 1000 in the main stem of birch. In other words, we are dealing with such large variations that errors of 5 or 10% are at the moment not very important, although refinements of techniques are desirable for future work.

Reproducibility of Results

In spite of their simplicity, the experiments were initially confounded by embarrassingly erratic results. Some of the problems have been resolved as follows.

One of the initial problems was that a piece of stem often gives a steadily decreasing flow rate with distilled water. This problem seems to have been first encountered by Huber and Merz (1958) who worked with coniferous wood. They ascribed this decrease to gradual closure of bordered pits. This explanation was quite plausible because (1) the decrease was greater at greater pressure gradients and (2) reversal of flow restored the original flow

rate briefly. However, the explanation became somewhat questionable when similar flow patterns were found in dicotyledonous wood whose bordered pits do not act as valves because of the lack of tori. Kelso *et al.* (1963) ascribed the flow decrease to a plugging of pit pores with tiny gas bubbles. This explanation is consistent with the restoration of flow rate upon reversal of flow direction. Any particles in the water, such as bubbles, even submicroscopically small ones, should decrease flow by lodging against pit pores but would be flushed away when flow is reversed (Fig. 2, left).

The difficulty of flow-rate decrease was eliminated quite by accident. In order to obtain a more distinct decrease of conductivity, distilled water was replaced by tap water in the middle of a flow-rate measurement. It was thought that tap water surely must contain more bubbles and suspended particles to plug the pit pores. The result was surprising: flow rate instantaneously increased to above the initial rate with distilled water and remained constant (Fig. 2, right). We first thought that we were dealing with an electrical phenomenon, that distilled water perhaps flushes cations to the lower stem end, thus building up a streaming potential that was acting against the flow. Further experimentation made this explanation unlikely, and we now think that the phenomenon might be based upon swelling or shrinking of the vessel-to-vessel pit membranes. It is not the purpose of the present paper to discuss this problem further; suffice it to say that all subsequent flow-rate measurements were made with a dilute solution of KCl which gave not only constant flow rates but also generally higher rates than distilled water. Most measurements were made with 5 or 10 mM KCl; in rare cases, with certain larger stems, when a flow decrease could still be detected, the concentration was arbitrarily increased to 100 mM, a concentration which proved to be sufficient in every case.

Another problem is that a piece of wood, no matter how neatly its ends are trimmed, shows an end effect, apparently due to resistance to flow into and out of vessels at the cut ends. Resistance to flow is not proportional to the length of the piece but proportional to the length plus ca. 2.5 cm. When pieces are very short, on the other hand, resistance per length may decrease again by elimination of much of the vessel-to-vessel flow because many vessels are cut open at both ends. These two length-dependent variables were held constant by using pieces of uniform length within any one experiment. In some experiments, we used 15-cm-long sections; in later experiments, we shortened the length to 7 cm for reasons explained later.

Taking all these precautionary measures, the scatter of results is still larger than that of many other biological measurements, and the reported results should be thought of as not more accurate than ± 10 –20%. Although it is hoped that accuracy can be improved in the future, the present results are nevertheless interesting because the difference between stem, branches, junctions, etc., are very large.

In some trees, the magnitude of transpiration was measured on a cut branch before defoliation. The cut end of the branch was supplied with water from a graduated pipette and the transpiration rate was measured in full sunlight and in open shade. As the xylem pressure in this situation is near +1 atm (1 atm = 101.325 kPa), figures obtained in such a way must be regarded as maximum rates. Transpiration rates were expressed per gram fresh weight of leaves so that LSC values in trees could be converted directly to xylem pressure gradients (assuming equal maximum transpiration rate of all leaves).

When all flow-rate measurements of a tree had been concluded at the end of the day, a dye solution was perfused through the stem piece. In the case of branched pieces, two different dyes were used so that the branching of the vascular tissue could be studied in more detail. In other words, on a stem section below a branch insertion, the xylem portion leading into the

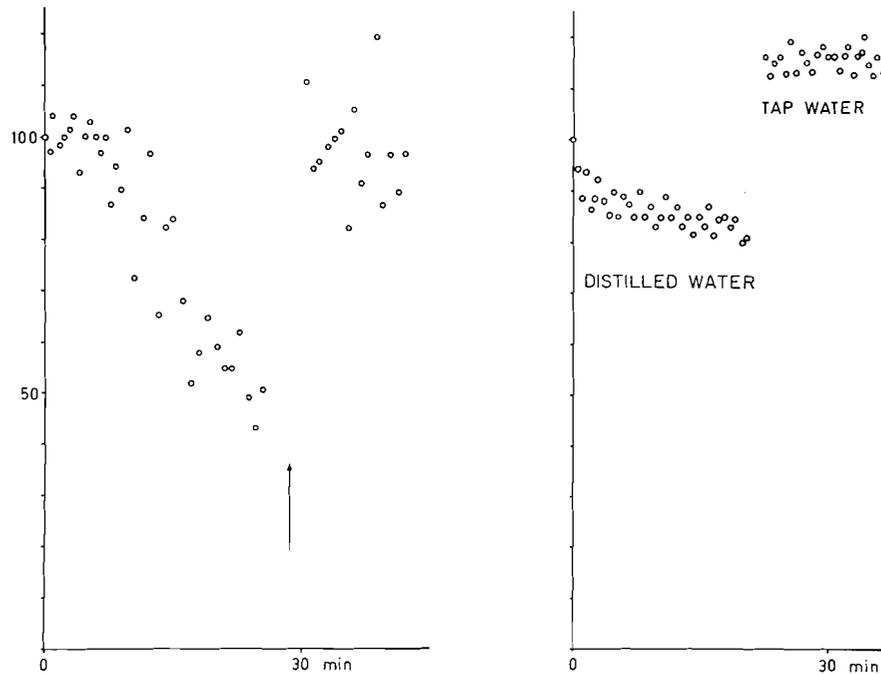


FIG. 2. Left, relative flow rates of distilled water through a piece of sugar maple. The initial rate of 0.0069 ml/min (calculated for gravity flow) is taken as 100%. Within 25 min, the flow rate had diminished to less than half the initial value. The piece was then turned around to reverse the flow direction (arrow); the initial flow rate was thus restored. Right, relative flow rate of distilled water through a piece of sugar maple. The initial rate of 0.0207 ml/min (calculated as gravity flow) is taken as 100%. After the flow rate had decreased to about 80% of the initial value, distilled water was replaced by tap water. This raised the rate to ca. 115% and it remained more or less constant.

branch farther up can thus be recognized by its color. Its area was then determined and the Huber value calculated. Transverse microtome sections were made during the course of the following winter, and vessel diameters were measured.

Results and Discussion

LSC in Stem and Branches

Representative results are shown in Figs. 3–5. LSC's ranged over two orders of magnitude from about 10 to almost 1000 $\mu\text{l} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$ fresh weight of supplied leaves under conditions of gravity feed. In poplar, the stem conductivity remained approximately constant with height (Fig. 3). In birch, there was usually a slight decrease from the bottom to the top of the stem (Fig. 4), and in young maples, there was occasionally a rather distinct increase in conductivity toward the top of the stem (Fig. 5, center and right).

LSC's were consistently lower in branches than in the main stem. This is not surprising because vessel diameters are narrower in branches than in the stem; at the same time, Huber values are similar. If we assume similar vessel densities, conductivity in the stem would have to be greater.

Comparative measurements of hydraulic conductivities in stem and branch wood have been

reported for *Tsuga canadensis* by Tyree *et al.* (1975). Although these were not based upon the quantity of supplied leaves, their conductivity values were considerably lower in branches than in the stem.

The most surprising and perhaps most significant finding of our study was that the xylem path in nodal areas, particularly the junction from stem to branch, represents a distinct hydraulic constriction. The conductivity through junctions is often half, or less than half, that of the branch itself. If we assume equal transpiration rates for all leaves, this would mean that flow velocities are higher in branches than in the stem, are highest in the junctions, and that pressures drop accordingly along the xylem path from stem to branch.

LSC's in Twigs and Petioles

Measurements of LSC were also taken in 1-year-old and current-year twigs and in petioles. We did not make as many measurements as we did on stems and branches because it became clear that the method of measuring conductivity of such small-diameter axes would really require different methods from the ones we used for stems and branches. Only petioles of striped maples and

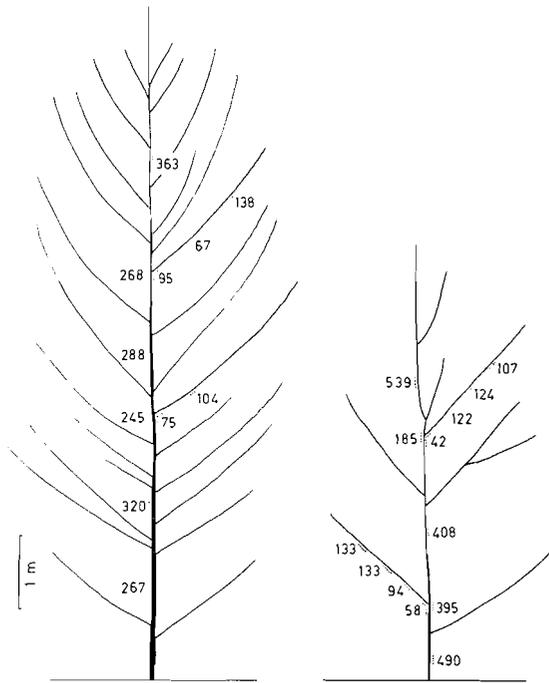


FIG. 3. LSC's along the axes of two open-grown large-toothed poplar trees (*Populus grandidentata* Michx.) in microlitres per hour, under conditions of gravity flow, per gram fresh weight of leaves supplied. Conductivities are much higher in stem than in branches. Branch insertions are characterized by hydraulic constrictions.

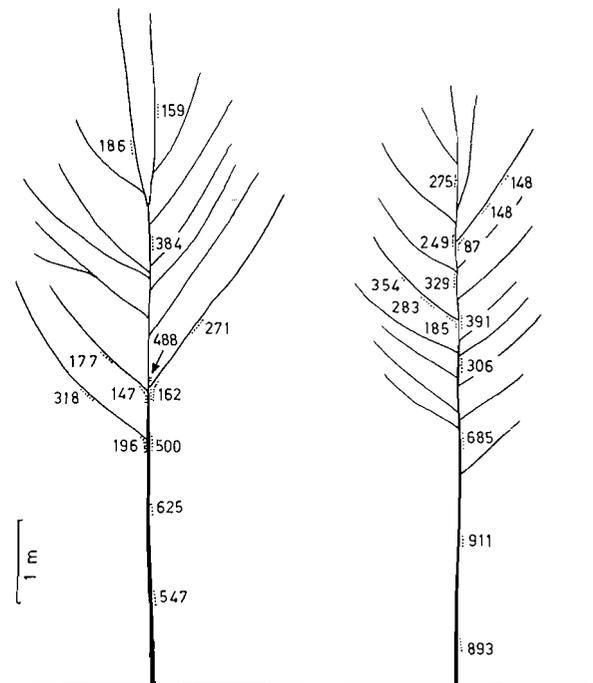


FIG. 4. LSC's of two codominant birch trees (*Betula papyrifera* Marsh.) in microlitres per hour, under conditions of gravity flow, per gram fresh weight of leaves supplied. Conductivities are highest in the stem, particularly the basal part. Branches have lower conductivities, and branch insertions are hydraulic 'bottlenecks.'

large-toothed poplar were used because they are relatively large. Petioles were fitted to small-diameter plastic tubing with Duco cement.

LSC's of last year's twigs (i.e., those with two xylem growth rings) were between 10 and 30, those of leaf-bearing shoots and of petioles were between 5 and 10, and those of the petiolar junction were between 1 and 3. These results must be regarded as tentative. It would be desirable to investigate petiolar conductivities more thoroughly with a more suitable method. Nevertheless, they seem to be based upon anatomical features. Isebrands and Larson (1977) have shown, in their painstaking work with *Populus deltoides*, that there is a constricted zone in the xylem path as it enters the petiole from the shoot. In a later paper in which they specifically address the hydraulic implications of their anatomical findings, they report sums of the fourth powers of the inside vessel radii. Their results show clearly a hydraulic constriction near the base of the petiole (Larson and Isebrands 1978).

Relation of LSC to Flow Velocity

It is obvious that a given volume of xylem sap, on its way from roots to leaves via a given path, must

flow faster along those portions of the path that have a lower conductivity. If the number of vessels along the path is the only variable and the diameters remain the same, the velocity would be inversely proportional to conductivity. As will be shown in the anatomical part of this paper, it is primarily the vessel diameters that vary and the number of vessels remains, at least roughly, constant. In this case, conductivity is inversely proportional to the square of velocity because flow rate is proportional to the fourth power of the vessel radius and velocity to the square (see Zimmermann and Brown 1971, p. 191). If we assume that all leaves transpire equally, we can translate LSC values into a velocity-proportional figure by taking the reciprocal value of the square root of LSC. This has been done in Table 1 for the tree shown in Fig. 5, right. A factor of 20 has been chosen arbitrarily to obtain a figure that could reasonably represent flow velocity in metres per hour (cf. the measurements of Huber and Schmidt (1936), listed also in Zimmermann and Brown (1971), p. 195).

In the diffuse-porous trees, shown in Figs. 3–5, LSC values are generally lower in the branches than in the stem. This means that flow velocities

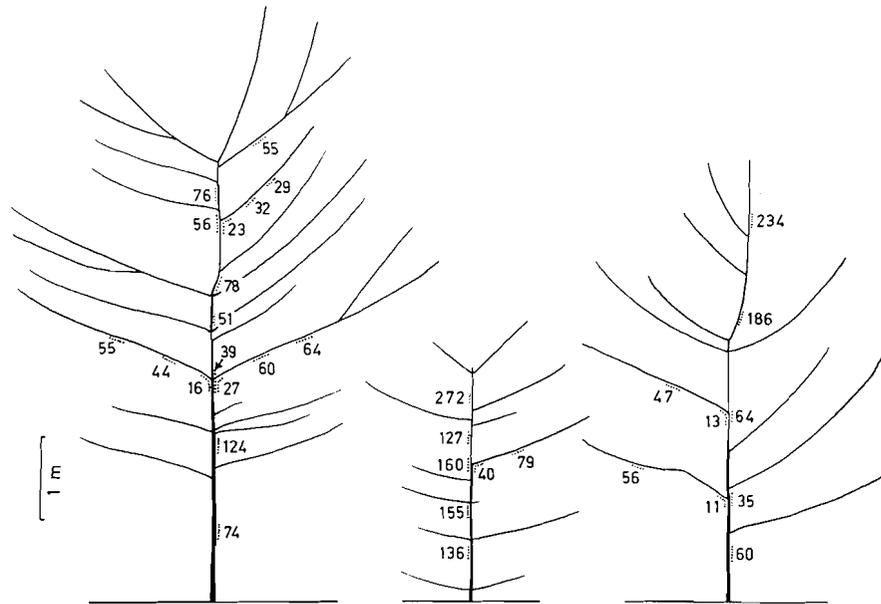


FIG. 5. LSC's of three sugar maples (*Acer saccharum* Marsh.), grown in open shade, in microlitres per hour, under conditions of gravity flow, per gram fresh weight of leaves supplied. Conductivities are usually higher in stem than in branches and often increase towards the top. Hydraulic constrictions characterize the xylem pathway in its transition from stem to branch.

must be higher in branches than in the stem. Huber and Schmidt (1936) called this the birch-type velocity distribution. The 'bottle neck' of stem-to-branch junctions requires that velocities are particularly high there. Huber and Schmidt (1936) did record this in one of their figures, without apparently recognizing the significance of this finding. Their Fig. 17 (reprinted as Fig. 11.11 in the textbook on tree physiology by Kramer and Kozlowski (1960)) shows a photograph of an oak with flow velocities drawn in at various points in the tree. The highest velocity is clearly shown at a branch insertion.

Xylem sap velocities in shoot tips and petioles must be considerably higher than those of stem and branches, and the highest velocities in the whole tree must be located at the point where xylem sap enters the petiole. Anatomically, this must be the "constricted zone" of the petiolar node, as it has been described by Isebrands and Larson (1977). In Table 1, representative LSC values for petioles and petiole junctions have been added for comparative purposes. These were obtained with striped maple, a species whose stem and branch LSC values are very similar to those shown for sugar maple in Fig. 5.

Relation of LSC and Transpiration Rate

It is rather interesting to compare LSC values

TABLE 1. Leaf weights, flow rates, LSC's and velocity-proportional figures for the sugar maple shown in Fig. 5, right

Weight of leaves above, g	Flow rate, ml/h, under conditions of gravity flow	LSC	$20/\sqrt{\text{LSC}}$
17.2	4.02	233.7	1.3
204.5	37.98	185.7	1.5
77.3	3.6	46.6	2.9
80.5	1.02	12.7	5.6
467.4	29.8	63.8	2.5
70.0	3.92	56.0	2.7
94.3	1.07	11.3	5.9
884.5	27.5	35.3	3.4
1352.6	81.2	60.0	2.6
Petiole junction		1-3	20-11
Petiole		5-10	9-6

NOTE: Positions on the tree can be identified on Fig. 5, right by LSC numbers. Petiole measurements have been made with striped maple (see text).

with transpiration rates. It is obviously very difficult to make accurate transpiration rate measurements at all points in a standing tree. We simply made occasional transpiration-rate measurements on small detached branches before the leaves of those parts were weighed. In full sunlight, the highest transpiration rates were of the order of $400-600 \mu\text{l} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$ fresh weight of leaves and in open shade were about $100-300 \mu\text{l} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$. These are maximum values because water was supplied under atmospheric pressure to the twig from a pipette,

while in nature, water in the xylem is normally under tension. Information about the order of magnitude of transpiration permits us to estimate pressure gradients as they might occur throughout the tree.

Relation of LSC to Pressure Gradients

The results of our measurements are perhaps most important when the effects of LSC on pressure gradients throughout the trees are considered. Under conditions of no transpiration, e.g., before sunrise or during a rainy day, we assume that pressure gradients are strictly hydrostatic within the tree, i.e., the pressure is 0.1 atm lower for every metre height. As soon as transpiration begins, gradients become steeper, depending on the rate of flow of xylem sap and the conductivity of the xylem. In the trees shown in Figs. 3 and 4, stem LSC values range from about 250–900. Maximum transpiration rate is of the same order of magnitude. This means that in order to move that much water along the xylem (i.e., 250–900 $\mu\text{l}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ leaves) we need a pressure gradient equivalent to the gravity gradient to overcome resistance to flow because our definition of LSC contains the gravity gradient. The total gradient up the stem would therefore be about 0.2 atm/m under conditions of maximum transpiration, namely 0.1 atm/m to overcome gravity and 0.1 atm/m to overcome resistance to flow. This has indeed been anticipated by calculation from vessel diameters and maximum sap velocities (Zimmermann and Brown 1971, p. 191).

Figures 3–5 show that pressure gradients must vary axially under transpirational condition because LSC values are not very uniform along the stem. Nodal areas are occasionally slightly constricted even along the straight path of the stem (both junctions in the Fig. 5, left; the lower junction in Fig. 5, right; etc.). Wherever LSC values are lower, flow velocities must be greater and pressure gradients must be steeper. Where LSC values are very high, as in the basal parts of the birches, pressure gradients must be small. All maple species we tested were shade-grown trees like those shown in Fig. 5. Their LSC numbers were low, but we would expect their transpiration also to be low at their site in the shade. It is interesting to speculate what would happen if such a shade-grown tree were suddenly exposed to full sunlight, if cambial activity would respond to the greater demand for water by producing wood with an increased LSC.

The most important consideration is the pressure gradient from stem into a lateral branch. Velocities in branches must be greater than in the stem and pressure gradients must be steeper. Significantly,

the passage of water from stem to branch must involve a sharp pressure drop because of the nodal constriction.

Vertical gradients of negative xylem pressures have been measured repeatedly on tree stems since Scholander *et al.* (1965) introduced their pressure bomb. In very tall trees, the measured pressure gradients have been conspicuously low. Scholander *et al.* (1965) measured gradients in Douglas fir and redwood over height differences of 50 m and more. Although pressures drifted more deeply into the negative region during midday, gradients did not appear to become steeper under transpirational conditions as they should have. Tobiessen *et al.* (1971) addressed this problem specifically by taking measurements on a 90-m-tall *Sequoiadendron* on which an elevator had been installed. Even though they took pressure measurements under conditions of minimal transpiration, the measured gradient was always less than 0.1 atm/m. The explanation of these phenomena is very simple in view of our LSC measurements, if we assume that the hydraulic construction of very tall trees is comparable with our small trees. Pressure measurements are made on leaves or shoot tips. These are taken from a lateral branch. But our LSC measurements indicate that pressure gradients due to flow resistance are steeper along a branch than along the stem. Pressures in the tip of a lateral branch must therefore be considerably lower than pressures in the main stem at the same height as long as xylem sap is moving. The only way to measure pressure gradients in the stem is to suppress transpiration in the lateral branch on which the measurements are to be taken. Thus one would permit the pressure of the twigs to equilibrate with the pressure of the stem at the same height. One could enclose twigs to be measured in plastic bags the day before measurement and defoliate the rest of the branch. Hellkvist *et al.* (1974) recognized this problem and enclosed lateral branches on which measurements were to be taken in large polyethylene bags. This did not seem to eliminate the problem entirely as their pressure gradients occasionally were even reversed at the very top of the tree (i.e., the xylem pressure at the very top of the tree was higher than 2 or 3 m below). Bagging has the disadvantage that the temperature in the bags can be considerably higher than that of the surrounding air, especially if they are sunlit. This causes condensation on the inner surface of the plastic bag and thus maintains transpiration of the leaves. Double bagging would minimize this problem.

Hellkvist *et al.* (1974) measured pressure gradients not only up the stem but also along lateral

branches. They found distinctly steeper gradients along branches than up the stem. This confirms the presence of lower conductivity in branches than in the stem.

Anatomical Basis of Conductivity Distribution

A logical next step of these investigations was to look for quantitative anatomical differences of the xylem path in the stem, branches, and branch insertions. At the end of some of the experiments, we perfused the stem and branch sections with dye solutions as described in the Materials and Methods section. This enabled us to measure the transverse-sectional area of the conducting xylem and calculate the Huber value (square millimetres of xylem transverse-sectional area per gram of supplied leaf weight; Huber 1928). This was of particular interest at the junction of stem and branch where the xylem path of the branch could be followed into the stem by a different colored dye. We could also measure vessel diameters which are of considerable importance for hydraulic conductivity.

Huber values were generally around 0.7–0.8 mm²/g throughout the tree, but we did occasionally find values as low as 0.5 or as high as 1.7 mm²/g. Branch xylem areas were occasionally somewhat constricted inside the stem proximal to the branch attachment, and there was occasionally a slight bulge in the basal part of the branch just outside the attachment. This may have been due to cambial stimulation at the point of greatest mechanical stress (comparable with the thickening of the stem base). We also found occasionally conspicuous areas of branch xylem at the point of attachment that contained nonconducting vessels. Cine analysis showed occasional gum deposits in these vessels which seems to indicate that they were injured and nonfunctional. Xylem area measurements were in general not very illuminating in explaining the distribution of LSC in the tree. A detailed analysis of vessel diameters, on the other hand, turned out to be very much more interesting.

Both *Populus* and *Betula* have many radial vessel groups (the wood anatomist calls these radial multiples). It is in these groups where vessels end; this can be seen clearly in a 16-mm film, made by photographing successive transverse images of individual sections with a movie camera (see Zimmermann 1971, 1976). The common tangential walls of these vessel multiples are where water passes from one vessel to the next on its way up the stem. These common walls are completely occupied with bordered pits, usually in a honeycomb fashion. This is an extremely efficient way of mak-

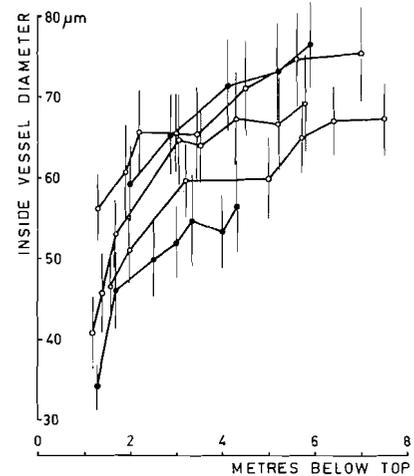


FIG. 6. Inside tangential diameters of the largest vessels in the most recent growth rings of the stems of three birches (O) and two poplars (●). Each point is the average of 30–150 measurements; vertical lines indicate standard deviations.

ing a very large pit membrane area accessible to water passage because the secondary walls (the pit borders) arch over the primary wall (the pit membranes) thus providing mechanical strength without interfering with water movement from vessel to vessel.

When vessels run in radial pairs or groups, their radial diameter is reduced because vessel-to-vessel walls are flat, not curved. Radial diameter measurements are therefore only meaningful if one deals with solitary vessels. As both birch and poplar have large numbers of radial multiples, we decided to use tangential diameters. Microtome sections were made from appropriate samples throughout the tree and tangential vessel diameters were measured in 30–150 of the largest (hydraulically most important) vessels in stained (i.e., previously conducting) areas of the most recent growth ring.

Inside tangential vessel diameters of the most recent growth ring of the stem are plotted against the distance from the top (the terminal shoot) of the stem in Fig. 6. It can be seen that vessel diameters increase as one moves down along the stem. This has been known to plant anatomists for many years. Largest diameters are normally found in the roots, but we have not investigated roots. This vessel distribution makes sense from a functional point of view. Evolution tends to favor larger, and therefore more efficient, vessels. However, larger vessels involve greater risk. Smaller vessels are safer water conductors. Pressures are always more negative in the top of the tree, smaller, i.e., safer, vessels are always found there (Zimmermann 1978).

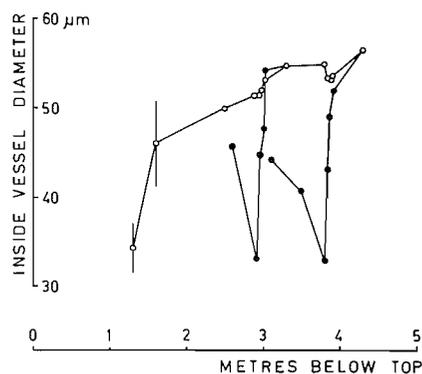


FIG. 7. Inside diameters of the largest vessels in the most recent growth rings of a poplar stem (O) (same tree as the bottom curve in Fig. 6). In addition, two branches are shown (●), attached to the tree 3 and 4 m below the top. Vessels of branches are very narrow just a few centimetres above their attachment. Branch vessels inside the stem (identified by dye perfusions) very quickly reach the diameter of the stem's own xylem. Standard deviations are comparable at all points. They are drawn in only at two points for the sake of clarity.

Figure 7 shows a single poplar tree, the same as the bottom curve in Fig. 6. In addition to stem vessel diameters (open circles), vessel diameters are shown for two branches (closed circles), attached 3 and 4 m below the top, respectively. In Fig. 7, points distal to the branch insertion are plotted from the junction upwards (i.e., to the left in the graph). Furthermore, we measured only five points of the branch, namely three points at the junction itself (ca. 3 cm below the insertion in the stem, at the insertion, and ca. 3 cm above the point of attachment of the branch) and two points 30 and 60 cm (or 40 and 80 cm) distal to the attachment. The interesting feature of branch insertions is the fact that vessel diameters are very constricted about 3 cm distal to the attachment of the branch. Vessel diameters increase drastically as one follows the xylem proximally into the stem. Inside the stem, below the branch attachment, vessel diameters, as recognized by the color of the dye that had been perfused from the branch into the stem, very quickly increase to the same values as those of the stem proper. This means that although cambial activity of the stem immediately below the branch is still under the control of the branch, diameters are somehow influenced by the stem itself.

From this finding, we concluded that the hydraulic constriction of the branch insertion is primarily due to the constriction of vessels although other factors like number of functional vessels may be involved to a lesser degree. It also showed that the three-dimensional xylem anatomy

of branch insertion is a very much neglected field worthy of further anatomical investigation.

Physiological Significance of LSC Distribution in the Tree

In the absence of transpiration, before sunrise or during a rainy day, pressures throughout the tree are relatively high and presumably equal at equal heights. As soon as transpiration begins in the morning, resistance to flow drops the pressures in all parts of the tree. The slope of the pressure gradient along the xylem path must be inversely proportional to conductivity. The smaller the LSC, the steeper the required pressure gradient to move water past that point. As we follow a given quantity of water mentally from roots to leaves, we can visualize that the pressure of this water drops slowly as we move up the stem, it drops sharply as it enters a branch. The pressure drops more along the branch than along the stem (although if the branch is horizontal, the drop is not due to gravity); it drops again very sharply as it enters the petiole from the twig. Lowest pressures are thus always found in the leaves. Resistances are higher along the path of water from roots to lower lateral leaves than along the path to the leaves at the top of the stem. This should at least partly compensate for the disadvantage of height to which water has to be brought to the top leaves. It is possible that critically low pressures which cause stomatal closure are reached earlier, or as early as, in the exposed leaves of lower lateral branches than in the top of the tree. This might be at least partly the mechanism by which lower lateral leaves are prevented from taking all xylem water during times of shortage and thus drying out the leaves at the top of the tree. Another mechanism is of course the lesser illumination of the bottom leaves.

During periods of severe drought, pressures will always be lowest in the most peripheral parts of the tree, and this is where embolism will occur in the xylem when water loss by transpiration exceeds water supply to a lethal degree. Leaves will embolize first, next probably the twigs. The hydraulic architecture delays damage by embolism in the stem xylem. It is important for the survival of a tree that peripheral parts are sacrificed first and that the safety of the main stem is maintained. This is particularly crucial for palms, because palms do not have a vascular cambium and must maintain their primary stem xylem functional throughout their entire life-span. Indeed, we have found earlier that the leaf attachment in palms represents a considerable hydraulic constriction. Xylem pressures in the

leaves must therefore always be considerably lower than those of the stem, whenever transpiration goes on and water moves (Zimmermann 1978).

Acknowledgments

These experiments were started in spring 1976 and were the subject of Patricia Caffrey's student research project during the summer of 1976. However, none of these early results are reported because it was not until late August 1976 that the ion effect was discovered. Miss Monica Mattmüller assisted in every phase of this work. Her untiring help is greatly appreciated.

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