Vessel-length distribution in stems of some American woody plants

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Vessel-length distributions in some trees, shrubs, and a vine have been calculated from measurements of particle penetration and of air-volume flow through the xylem. In shrubs and diffuse-porous species, longest vessels were about 1 m long, but most of them were much shorter, the largest percentage in the 0–10 cm length class. In the two ring-porous species investigated (*Quercus rubra* and *Fraxinus americana*), the longest vessels often were as long as the tree's stem, but most of them were much shorter. In the grapevine (*Vitis labrusca*) which has large-diameter vessels (ca. 300 μm) a small percentage of the vessels was 8 m, but most of them were less than 5 m long. In a given species, lengths of the longest vessel were quite variable, but the distribution of the short lengths was more constant. In general, vessel lengths are correlated with vessel diameters: wide vessels are longer. Even in diffuse-porous species, the slightly narrower latewood vessels are somewhat shorter than the wider earlywood vessels. The method is a simplified version of that described by Skene and Balodis, but using a programmable desk calculator. It works best with diffuse-porous species in which vessels are randomly distributed in the stem, and less well in species with wide vessels, because as vessels reach the length of the stem itself, they cannot be randomly distributed.

Introduction

Although the concept of the vessel, a conducting unit of the xylem consisting of a finite number of individual vessel elements arranged end to end, was established a long time ago, vessels have remained rather elusive structures. By looking at longitudinal sections of xylem, one can see parts of vessels perhaps as long as a dozen elements, but this is only a minute portion of their entire length which often consists of hundreds or thousands of elements. Cinematographic analysis has given us, for the first time, precise information on the general layout of the vessel network in wood and the nature of the vessel ends (Zimmermann 1971, 1978). For example, we know now that vessels generally end in pairs or groups where they gradually taper out over a length of many (often 50 or more) elements. Endings on rays have also been reported for oak (Bosshard et al. 1978), but these ends are of small diameter and therefore quantitatively unimportant for long-distance transport of water.

Some measure of vessel length has been reported by many authors using different methods. Air, mercury, India ink, etc., can be forced through a segment of stem if it contains vessels that are cut open at both ends (see the citations in Greenidge 1952). Maximum vessel lengths are thus obtained. Lengths labeled "maximum" and "minimum" in Greenidge's (1952) Table 1, for example, are in reality "longest measured maximum length" and "shortest measured maximum length" because his method gives no information about the frequency distribution of shorter vessels. This is rather important to note, because we know now that in most species only a very small percentage of the vessels are of maximum length.

Scholander (1958) reported a method of estimating "average vessel length" by measuring water volumes released by a vertically held piece of freshly cut vine when trimmed at the top. This was conceptually a step forward, but it neither takes the longest vessels into account nor does it differentiate length distribution in the shorter ones. It also ignores the fact that drainage is incomplete because of capillarity.

It was not until Skene and Balodis (1968) published their paper on vessel-length distribution in *Eucalyptus obliqua* L'Hérit, that we acquired the concept of the multitude of vessel lengths in wood, although we had ourselves, during the process of studying the vascular system of palms, seen and measured individual vessels (Zimmermann 1973 and earlier papers).

Vessel-length distribution is a fundamental parameter in the hydraulic construction of long-distance transport channels of plants, with relevant implications for physiology, pathology, and other disciplines.

Materials and methods

Application of paint

The principle of Skene and Balodis' (1968) method is to determine the number of vessels that are cut open at both ends in successively shorter pieces of wood. The length of the longest vessel is first determined by injecting air into a piece of stem and cutting it shorter until the first bubbles appear at the far end which is dipped into water. The remaining piece is then

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divided (i.e., marked) into 10–20 segments of equal length. Paint is injected into the stem by air pressure and section after section is cut off the far end. It is important to apply paint from the morphologically upper end of the stem to confine measurements to an axial direction, for the present, and avoid complications of vessels leading from the main stem into branches. Air, paint (oil-based or latex particles in suspensions), or hot wax, would not penetrate vessel ends under the pressures applied in the experiments. We had a paint applicator constructed which is driven horizontally into the wood surface and is fed paint vertically via a transparent plastic tubing which permits observation of the paint level and allows settling of large particles and agglomerates away from the wood surface (Fig. 1). Air bubbles must be avoided as entrapped air blocks resist further paint movement within vessels.

We spent an enormous and frustrating amount of time trying to improve upon the method. Oil-base paint is not only messy, but it creates a very serious problem in that paint-containing vessels are hard to recognize. At the far end where there are only a few, they are easy to recognize and count. At short distances where they are crowded, there may be some obviously paint-filled ones and some obviously empty ones, but many that cannot be counted with certainty because of smudging, insufficient paint content because of contraction during drying, etc. We tried many types of paint and methods of application. We also tried "chemical" methods such as perfusing the stem with lead acetate followed by hydrogen sulfide gas.

A piece of stem, longer than the longest vessel, was collected from the forest, preferably during rain, because the test piece must be completely water saturated. During periods of stress (e.g., an ordinary summer day), the stem may be cut successively shorter from both ends to relax the water tension. The paint applicator was attached to an area of the distal end which had been shaved smooth with a razor blade or microtome. Transparent plastic tubing was attached to it, reaching a height of about 2 m. This was initially filled with a few centimetres of water, and vacuum was applied to remove any superficial air pockets. A suspension of water-miscible (latex) paint was then filled into the tubing and fed by gravity into the stem until the rate of uptake slowed down (ca. 24 h). Air pressure was then applied at the far (upper) end (0.5–1 atm) (1 atm = 101.3 kPa). The applicator was refilled periodically until uptake of liquid decreased. This usually took several days. It is important that vessels are not air blocked. If uptake is rapid, pressure may have to be removed during periods when the liquid level cannot be watched (e.g. overnight). The paint suspension with minimal particle agglomeration was prepared by diluting commercial latex paint of a suitable color (e.g. green, easily seen against the color of the wood) at least 100 times with water. The suspension was left standing for a day or so while the larger particles settled. The supernatant "green water" contained very small particles (less than 1 μm diameter). The size distribution is such that the particles pass neither through the xylem walls nor through pit membranes. On the other hand, they are easily carried along vessels, and through scalariform perforation plates. Pressure injection takes them to the vessel ends and gradually increases their local concentration by lateral water loss (i.e. filtration) until the vessels are virtually packed with particles. At the end of the infusion time, the paint applicator was removed and the stem cut into segments. These were left to dry overnight, and paint-containing vessels were counted.

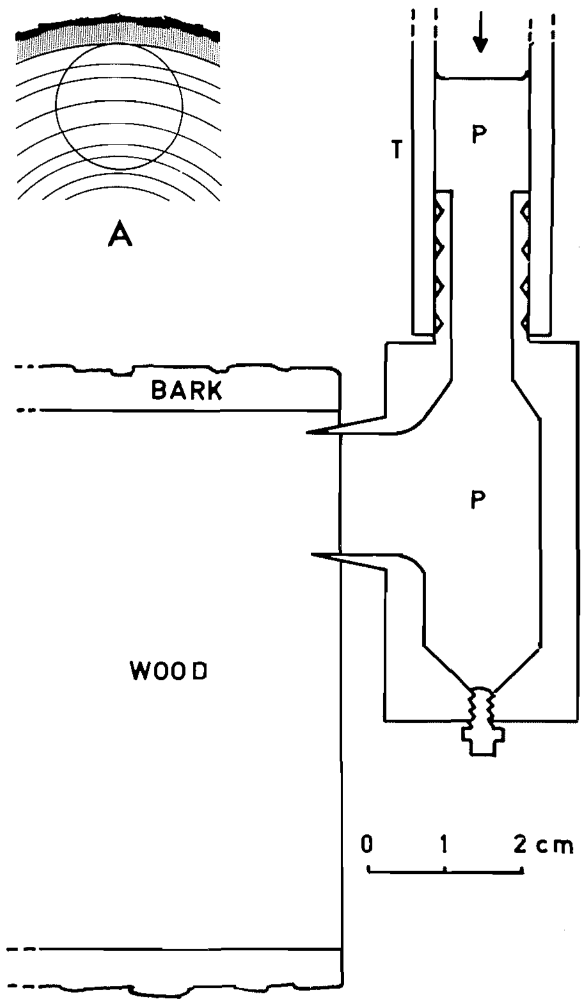

FIG. 1. The paint applicator is tapped into the shaved end surface of a piece of wood near the periphery of the stem to sample the most recent growth rings. The screw at the bottom of the applicator is for easier cleaning. The paint suspension (P) is filled into the applicator via a transparent plastic tubing (T) which permits observation of the paint level. The tubing is about 2 m long; it is refilled when the paint level is low. Pressure is applied at the upper end (arrow). The diagram at A shows how the paint applicator intersects the growth rings. The hatched area marks the bark. The configuration explains why vessel counts are low in the most recent and the oldest growth rings. In ring-porous trees where the earlywood vessels of only the most recent growth rings are conducting, the applicator may have to be moved out into the bark to increase the number of vessels.

Another method used hot wax. The piece of stem was heated to about 80°C either in a water bath or with heating tapes. Hot wax, darkly stained (for example, with Sudan Corinth) was injected into the vessels. The stem was then cooled, cut into segments, and the wax-filled vessels counted.

Air method

In another method, we quantified air flow through a piece of stem at a given pressure. A ca. 1.5 cm diameter cork borer was hammered into one stem end which had been shaved clean on the microtome or manually with a razor blade. Air was injected into this end at measured pressure (we used a gauge with 0.2 psi (1 psi = 6.9 kPa) scale divisions, or a mercury column). The stem was held at an angle, the far end dipping into water. The escaping air was collected with a funnel attached to a pipet, or, for larger volumes, with a 100-, 500- or 1000-mL cylinder (Fig. 2), and the rate of air flow was measured with a stopwatch. At a fixed pressure gradient, the air volume escaping at the far end within a given time is proportional (to a first approximation) to the number of open vessels. As long as we were dealing with a small stem or a piece split from a larger one that did not exceed the dimensions of our microtome clamp (our largest one accepts sizes up to 5 × 5 cm and ca. 1 m length), we could shave the end in the microtome and the escaping air volume from a particular stem of fixed length was directly proportional to the pressure as shown in Fig. 3.

If the stem end was shaved smooth with a microtome, the line went almost through the origin, indicating a negligible end effect. If the stem was sawn at the far end, but not shaved, the relationship remained linear, but an end effect became significant. Although the end effect was readily obtained in terms of pressure (P_e) by measuring air volumes at two pressure levels, the resulting straight line is not parallel to the line that goes through the origin in the absence of a P_e (ends shaved) (Fig. 3). Hence it was not possible to express P_e in terms of stem length and thus make a correction in those cases where the end grain of the wood is not shaved smooth. That is, the end effect was not linearly correlated to flow rates.

If all vessels are of equal diameter, a method of analysis readily presents itself as described below. However, vessel diameters are not monodisperse in semi-ring-porous species. In this case, very much less air flows through the narrow latewood vessels than through the wider earlywood vessels as would be indicated from the fourth-power relationship of tube radii in fully developed Newtonian capillary flow. Rigorous vessel-length distribution calculations based upon air volume rate measurements alone can therefore not be made. We used the air method with diffuse-porous woods in which vessel diameters are reasonably uniform. Even though diameters of individual vessels varied when observed on a single transverse section, we assumed that over their entire length the average diameters are comparable. Comparison of results from air-flow measurements and paint-perfusion experiments support this (see Fig. 8). We also used the air method with certain ring-porous trees (e.g. ash). Here the vessel diameters decrease very abruptly from early- to late-wood. Latewood vessels were not considered in this case because they carry an insignificant amount of the total air flow. Their lengths were measured separately with the paint method. In ring-porous trees, air flow had to be restricted to the vessels of the most recent growth ring, because earlywood vessels of older rings are not functional and may therefore be partially closed by tyloses. These older vessels were plugged with Plasticine with the aid of a small spatula.

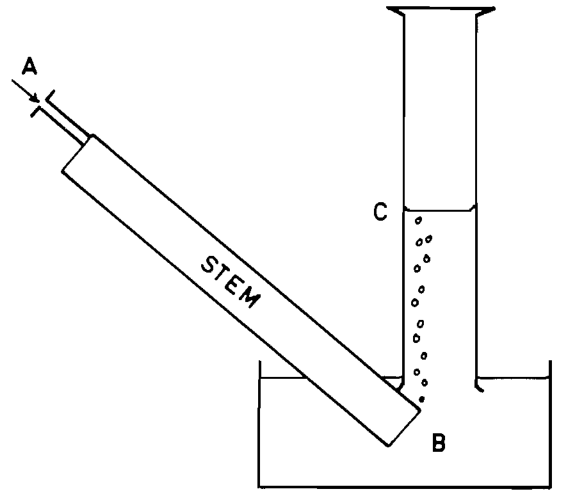

FIG. 2. The air method. Air is applied under measured pressure (arrow) to the shaved surface of a stem via a cork borer at A. The far end of the stem dips into a water-filled container (B). The rate of air flow is measured by collecting air in a pipet via a funnel, or into a graduated cylinder (C).

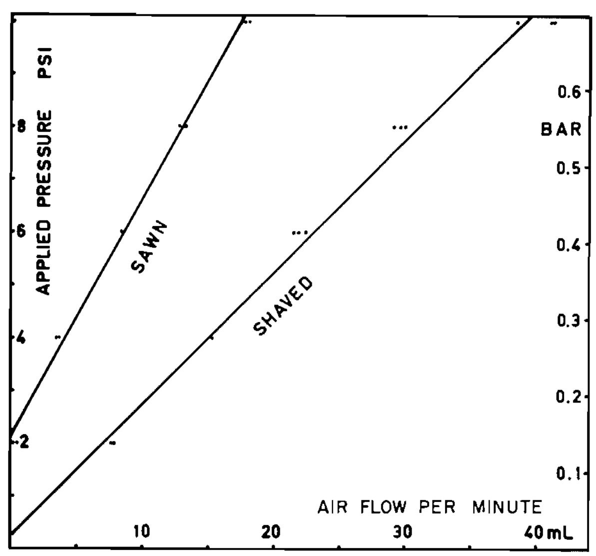

FIG. 3. The rate of air flow through a piece of wood of a given length shown here when the far end of the piece is roughly sawn and when it is shaved. The respective flow rates are approximately linear, but the two lines are not parallel (see text).

The air-flow method was handled as follows. Longest vessel length was first measured as described before. Another piece, slightly longer than the longest vessel was then marked in 10–20 equal segments. Segments were cut off the far end until the first air bubbles appeared. The end was shaved smooth in the microtome and the air volumetric rates measured three times each at two pressure levels. This was repeated with the successively shorter stem piece. Toward the end of an experiment, when the stem piece was short and air-flow rates large, lower pressures were often used. The pressure-rate data were fitted with linear regression curves to obtain the slopes and intercepts (a and b). The latter is equivalent to P_e. We can interpolate or extrapolate to obtain any volumetric rate at an arbitrarily chosen pressure level, P. Volume flow rates multiplied by the stem length and divided by $P - P_e$ yield a value proportional to the number of open vessels of uniform diameter. At the end of this experiment, we still needed the number proportional to the total number of vessels through which air was applied at the entrance (vessel count at zero distance). This was obtained by injecting latex paint, diluted ca. 1:1 with water, or hot wax through the last (shortest) piece of wood after flow rate measurements. The population and percentage of paint- or wax-containing vessels at the far end of this segment within a unit area permitted us to estimate the vessel count at distance zero, and the number of vessel endings within this last piece of stem.

Interpretation of data

Skene and Balodis (1968) plotted their results to show the number of vessels cut open at both ends as a function of stem length. They fitted a regression curve through these points. This curve was then converted to a bar diagram showing the percentage of vessels in each length group. Because the vessel-length distribution was recovered from a smooth cumulative curve, their distribution of vessel percentages in the different length classes decreased smoothly and monotonically. This interpretation was criticized by Milburn and Covey-Crump (1971) who argued that the data could be interpreted as consisting of three straight lines, indicating three distinct length populations. These two interpretations are opposite extremes. In both, individual counts of open vessels at each cut segment were not used, only interpolated numbers. We converted counts directly to percentages by geometrical analysis.

Figure 4 illustrates how the calculations were carried out, using a hypothetical stem with 30% of its vessels (as counted on a transverse section) 18–20 cm long, and 70% 4–6 cm long. If randomly arranged, the vessels produce the counts indicated by the line A–B–C, which is the sum of the counts A–D for the longer vessels, and the counts E–F for the shorter ones (see Appendix A). The total number of infused vessels at distance zero was used to normalize all subsequent counts at sections "downstream." These cumulative ratios will be called "counts" so that they are not confused with the final results, the percentages of vessels in specific length classes. Each count (number of paint-containing vessels) was given the designation, m, with the length of the stem at which they were counted as a subscript (see Fig. 4). Thus m_{22} and m_{20} (counts at 22 and 20 cm) are zero; the first positive count is m_{18}. Beginning at the far end,

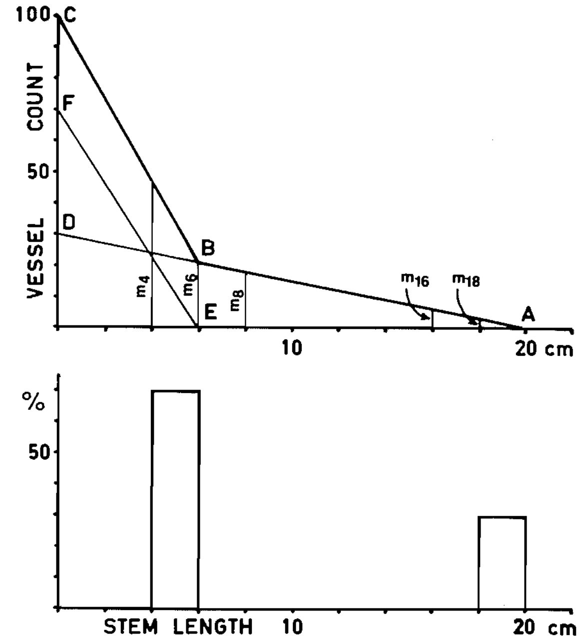

FIG. 4. A hypothetical wood whose vessels are randomly arranged; 30% of the vessels (seen on a transverse section) are 18–20 cm long, 70% are 4–6 cm long. A count of vessels, cut open at both ends, follows the line A–B–C, which is the sum of the counts A–D for the longer vessels and the count E–F for the shorter ones. (Note that the lines E–F and B–C are not parallel.) The resulting bar diagram of vessel-length distribution is shown below.

we calculated the increase of the vessel counts for each point. There are no vessels in the 20- to 22-cm length class. The contribution of vessels in the 18- to 20-cm length class to the cumulative count is, by central difference (see Appendix A), $[(m_{18} - m_{20}) - (m_{20} - m_{22})]$ times the number of steps to go to zero. As m_{20} and m_{22} are zero, this is equal to m_{18} times 10, i.e. 30%. The next calculation, $(m_{16} - m_{18}) - (m_{18} - m_{20})$, for the 16- to 18-cm length class, gives zero, because the number of vessels increases linearly. The calculation continues step by step, yielding zero until the 6-cm length is reached. At this point we calculate $[(m_4 - m_6) - (m_6 - m_8)]$ 3 = 70%. From here to zero, results are again zero. The resulting bar diagram is shown in Fig. 4. It can easily be seen that the curve, obtained from the vessel counts must always be either straight or turn up as we proceed with the calculation. If the count increment toward shorter stem pieces diminishes, the calculator prints a negative percentage. This is not necessarily a counting error, but may merely indicate that the vessels were not randomly arranged. This can be illustrated with a hypothetical oak tree with a stem length of a little over 10 m whereby 40% of all vessels are 10 m long, all with their ends uniformly distributed between 9 and 10 m, and the remaining 60% are 4 m long, randomly arranged

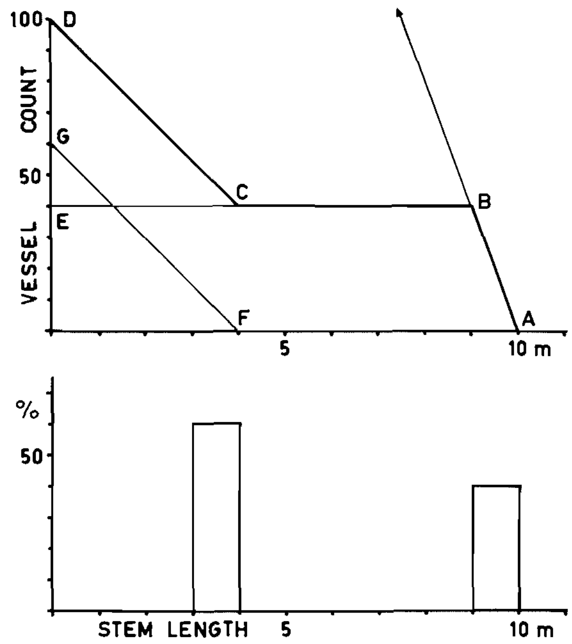

FIG. 5. Vessel count in a hypothetical ring-porous tree with 40% of its vessels 10 m long and not randomly arranged (all ends are at 0 and 10 m, respectively). In addition, 60% of the vessels are 3–4 m long, randomly arranged. The vessel count (vessels open both ends) follows the line A–B–C–D. The first calculation at A gives a vastly exaggerated vessel percentage (400%) which is followed by a negative number (−360%). Addition of the two results in the 40% bar of the figure below.

(Fig. 5). At 9 m we count all long vessels. The count does not change as the stem is cut shorter, until the shorter vessels are reached.

The calculations based on completely random distribution of the ends of 10-m-long vessels throughout the entire stem first gives an exaggerated value of 400% for 10-m vessels. The next class, represented by 9-m vessels, however, yields a virtual count at −360%. The net for the two classes is 40%.

Similar considerations apply if the vessel count begins with a piece of stem that is shorter than the longest vessels. Assume that we begin to count vessels of the stem shown in Fig. 4 with a 10-cm-long piece. The first printout is then an exaggerated percentage (90%), but it is followed immediately by a negative number (−60%). This means that 30% of all vessels are in a length class 9 cm or longer. We often repeated air-flow measurements with short stem pieces to measure more accurately the vessel distribution in shorter length classes. The vertical line indicating maximum vessel length then bears an arrow pointing to the right (e.g. Fig. 6).

A continuing summation of all percentages was built into the program. It permitted us to check at the end if our total was 100%, i.e. if no entry error was made. Another short program eliminated negative numbers, starting at distance zero and ending with the longest vessels.

Results

In paint experiments, we had separate counts for each growth ring. In wood with small vessels, paint was usually applied to a total of 10 000 – 30 000 vessels. Depending on the growth rate of the tree, up to 20 rings were included in a single application (Fig. 1, at A). Vessel-length distribution in individual growth rings was similar; only the results of total counts are presented here.

The length distribution histograms are presented in Figs. 6–8, 11 and 12. There are usually so few vessels in the longer length classes that the bars are not higher than the thickness of the baseline of the graph. We therefore show the end of the longest length class as a small vertical line. In those cases where the longest vessels exceeded the length of the stem at the beginning of the experiment, the vertical line bears an arrow pointing to the right. This means that the longest length class includes vessels that are longer. The discussion concerning Fig. 5 should make this clear. It should be noted that while length distribution in a given species appears similar when measured in different specimens, maximum lengths often vary considerably.

Shrubs

In *Ilex verticillata* (L.) Gray a few vessels are almost as long as the shrub is tall, but most are very short (Fig. 6). The first air appeared at a stem length of 130 cm, but the air-flow rates through the successively shortened stem were such that the length of more than 99.5% of the vessels fell into the 0- to 10-cm class. We repeated the experiment with a 26-cm-long segment and 2-cm subdivisions. (The narrower bars in Fig. 6.)

In *Vaccinium corymbosum* L. 85% of the vessels were in the 0- to 10-cm length class, about 6.5% in the 10- to 20-cm class (Fig. 6, center). The rest were longer, the longest in the 1.3- to 1.4-m class. We repeated these measurements beginning with a 40-cm-long piece and 5-cm segments; results were similar.

In *Viburnum cassinoides* L. a 140-cm-long stem was collected in the forest and vessel length was measured with the air method. The piece already contained a few vessels cut open at both ends. Vessel-length distribution in 10-cm classes is shown in Fig. 6. We repeated the measurements with a 55-cm-long piece at 5-cm intervals with very similar results.

Viburnum dentatum L. was also tested in an air experiment. Longest vessels were 150 cm, and the distribution of the shorter ones was similar to that in *V. cassinoides*.

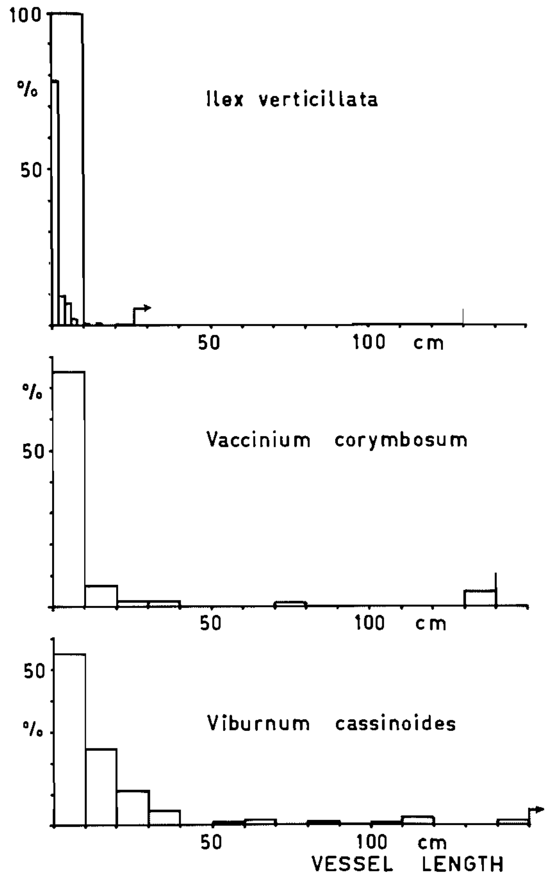

FIG. 6. Vessel-length distribution in three shrub species, measured by the air method.

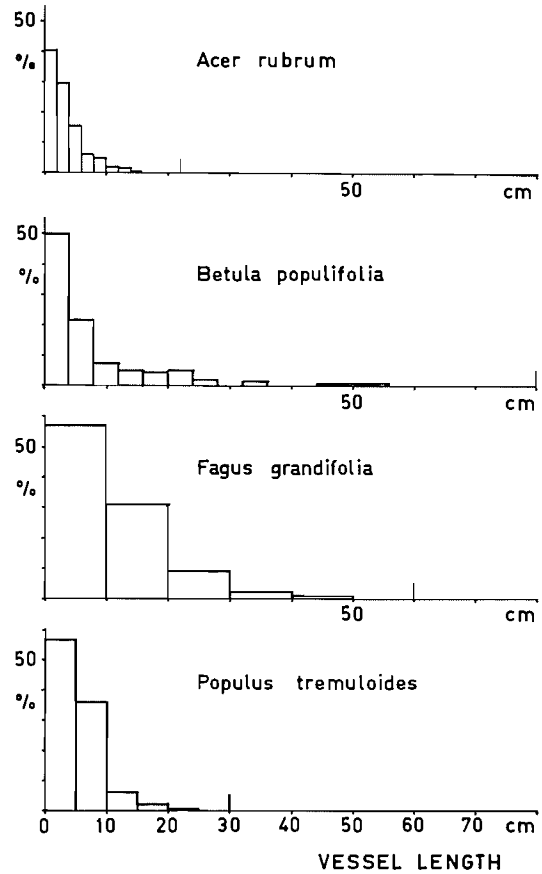

FIG. 7. Vessel-length distribution of four diffuse-porous tree species.

Tree species with small-diameter vessels

Acer rubrum *L.*

More than a dozen vessel-length distribution measurements were made using various methods. The longest vessel length was 42 cm, but it was more often of the order of 25–35 cm. Figure 7 shows a good representative graph, obtained with the paint-infusion method. This tree had been growing as a codominant in a young forest stand. The stem was sampled at a height of ca. 2 m at a diameter of 13 cm. The stem was split and similar sections were measured with the air and the paint methods separately. The results were similar.

Acer pensylvanicum *L.*

This species had a vessel-length distribution similar to that of red maple, although the longest length in this case was 45 cm. Measurements were made with the air method on a stem piece 14 cm in diameter. This was a fully mature tree; the species rarely gets larger than that in our area.

Acer saccharum *Marsh.*

Figure 8 shows the results of an air-flow experiment (top) and a paint-infusion experiment (bottom), both made with pieces of the same stem, ca. 13 cm in diameter. The longest vessels found with air flow were in the 36- to 40-cm length class. It is possible that this difference in the two pieces is real, but possibly the paint did not fully penetrate the longest vessels (but note that in the case of *Betula populifolia*, the longest vessels were found with the paint method!). The paint infusion involved a total of 10 786 vessels in growth rings 1975–1980. We consider the two results similar, because longest vessel length is variable.

Betula populifolia *Marsh.*

Longest vessel lengths were between 30 and 40 cm. The length distribution shown in Fig. 7, obtained from a stem of ca. 7 cm diameter, is representative, although the longest vessels were unusually long in this particular case (80 cm). This shows that the small latex paint particles could move easily across scalariform perforation plates.

Fagus grandifolia *Ehrh.*

The stem samples were from rather small trees (ca.

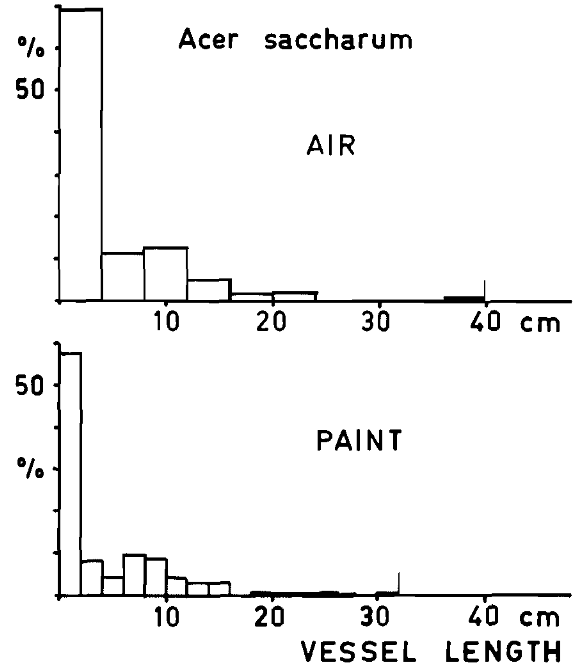

FIG. 8. Vessel-length distribution in *Acer saccharum*, measured by the air and paint method.

10 cm diameter). Figure 7 shows measurements taken with paint counted in growth rings 1961–1979. Maximum vessel lengths varied from 60 cm (the tree shown in Fig. 7) to 120 cm.

Populus tremuloides *Michx.*

Figure 7 indicates the results of a paint-injection experiment. Vessels of six growth rings were counted (Table 1). The longest vessels fell into the 25- to 30-cm length class. In other experiments maximum length ranged up to 65 cm, but the distribution of shorter vessels was similar.

Prunus serotina *Ehrh.*

This species is considered a semi-ring-porous species because its earlywood vessels are somewhat wider than the latewood vessels. To illustrate the semi-ring-porous characters we measured the hydraulic diameters (assuming vessels to be elliptical in transverse section) in seven successive growth rings (1974–1980) on a stem transverse section in the microscope. Each growth ring was divided into five tangential bands, and maximum and minimum diameters of 20 vessels were measured in each band. The overall hydraulic diameter was then calculated for each band (Fig. 9) (Appendix B). The 1980 growth ring was incomplete at the time of sampling. We do not know why the vessel diameters were so much larger in this new ring. The results were pooled and the overall population frequency of the hydraulic diameters was calculated for diameter classes at 5-μm intervals (Fig. 10). Vessel-length distribution was measured with

TABLE 1. Numbers of vessels, cut open at both ends, in stem pieces of *Populus tremuloides* Michx. The numbers were obtained by counting paint-containing vessels on cut stem surfaces with a stereomicroscope

	Distance from application (cm)					
Growth ring	0	5	10	15	20	25
1980	470	110	14	3	1	0
1979	1 222	198	30	7	1	0
1978	5 292	1516	307	71	8	1
1977	5 233	1098	125	22	5	2
1976	5 202	1460	170	39	7	1
1975	5 288	1048	123	26	4	2
Total	22 707	5430	769	168	26	6

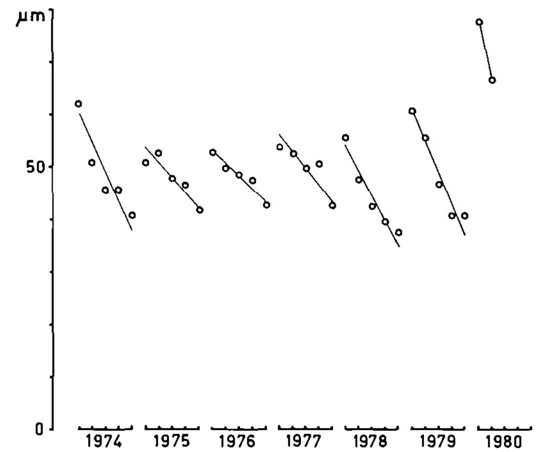

FIG. 9. Hydraulic vessel diameters in five successive tangential bands within the growth rings of 1974 to 1980 in *Prunus serotina*. For the sake of clarity, linear regression lines have been added within each growth ring, showing the gradual diameter decrease from early- to late-wood.

paint, applied to a total of 29 307 vessels. The longest vessels were in the 40- to 50-cm length class, but over 85% of the total number fell into the 0- to 10-cm class (Fig. 11, left). As length appears to be correlated with diameter, we made separate counts for early- and late-wood. This was done in tangential zones of 0.6 mm width at the beginning and end of the 2.5 mm wide 1977 growth ring (Fig. 11, right). The solid bars indicate earlywood vessels. The longest ones (0.8%) are in the 40- to 50-cm length class. The dashed lines indicate the distinctly shorter latewood vessels, the longest ones of these (0.9%) are in the 20- to 30-cm length class. This was a stem piece of ca. 15 cm diameter, taken from a codominant tree of a young hardwood stand.

Species with large diameter vessels

It has been known for many years that wide vessels

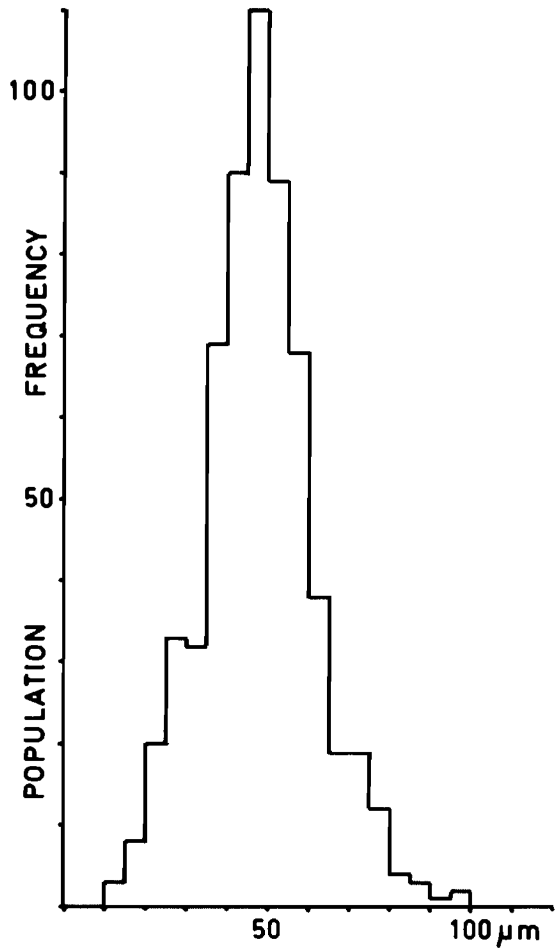

FIG. 10. Overall population frequency of hydraulic vessel diameters of the wood of *Prunus serotina*.

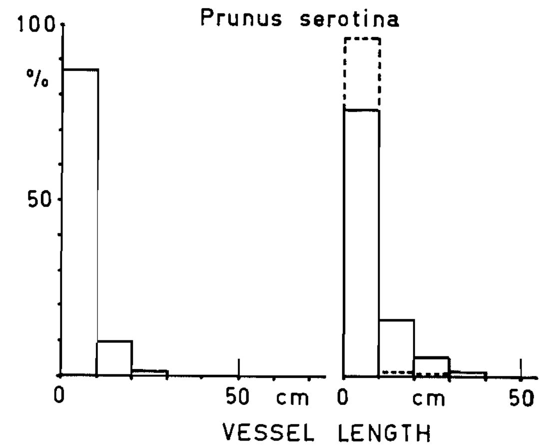

FIG. 11. Vessel-length distribution in *Prunus serotina*, a semi-ring-porous tree in which earlywood vessels are distinctly wider than latewood vessels. Overall vessel-length measurements of growth rings 1974–1980 are shown on left, longest vessels were 50 cm. Separate counts for early wood (solid lines) and late wood (dashed lines) are shown on the right.

are longer than narrow vessels (Greenidge 1952). It will be noted that the vessel-length scale in Fig. 12 differs considerably from those of Figs. 6–8, and 11.

Fraxinus americana *L.*

We conducted seven experiments; the results were variable, but show generally that there are some very long vessels of the order of 10 m, and some shorter ones of one to several metres in length (Fig. 12). Ring-porous trees, which require considerable stem lengths for experimentation, were initially cut in the forest and hand-carried to the lawn area outside the laboratory. This limited the size of the trees. The air experiments were done with trees of ca. 10 cm diameter at breast height (dbh) (Fig. 12, top). Later, we felled larger trees in the forest and carried out the paint infusion on the tree where it fell. The paint experiment shown in Fig. 12 (center) was done in this way (dbh 19 cm).

Quercus rubra *L.*

An example of *Quercus rubra* is shown in Fig. 12.

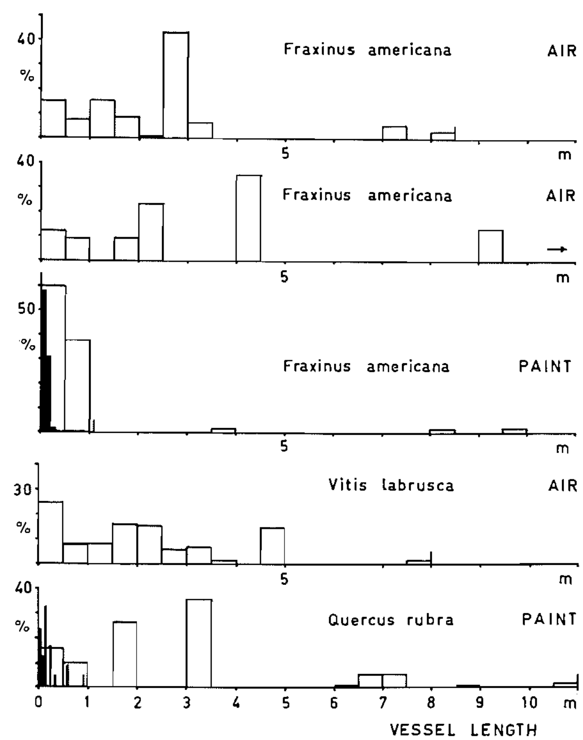

FIG. 12. Vessel length of two ring-porous tree species and a vine. Narrow (black) bars give lengths of latewood vessels. Note that the scale is different from those of Figs. 6–8 and 11. Vessel lengths of diffuse-porous trees and shrubs are comparable to lengths of late-wood vessels of ring-porous trees.

Longest vessels were in the 10.5- to 11-m class; shorter ones were one to several metres long.

Vitis labrusca *L.*

One specimen was measured with the air method; its top diameter was 1.8 cm, the bottom 2.7 cm. The experiment, carried out in the laboratory with air, was somewhat of an adventure as the vine was initially 14 m long. This was cut shorter until bubbles appeared from a first vessel at a length of 7.5 m. Air-flow rate measurements were made at 0.5-m intervals; the end of the vine was always shaved in the microtome. This may sound unbelievable, but we had the microtome at the edge of a bench. The vine was flexible enough that one end could be fitted into the microtome clamp while the remainder of the vine seemed to occupy the rest of the laboratory. The results are given in Fig. 12. We made two further measurements, beginning with 1-m-long pieces. The results matched the original one, 68 and 70% of the vessels were longer than 1 m. Two further air experiments were later done with 1-m pieces from other grapevines. In these cases 51 and 88% of the vessels were longer than 1 m.

Discussion

Greenidge's (1952) maximum lengths are greater than ours, often by a factor of two. We do not know why this is the case. Greenidge does not give measurements of tree sizes, except heights of some ring-porous species, but his Methods section implies that he generally used larger trees than we did.

The most important single finding is perhaps the fact that in all species so far investigated, only few vessels belong to the longest length class. In diffuse-porous tree species and shrubs short vessels are far more numerous than long vessels. An extreme case is *Ilex verticillata*, a shrub with some vessels 130 cm long (ca. 0.01%), but most of them (99.5%) shorter than 5 cm. In most species, however, the percentages of the individual length classes increase as length decreases in a way comparable to *Eucalyptus obliqua* investigated by Skene and Balodis (1968).

While, after considerable early difficulties, we finally obtained reliable results with small-porous species, the results with large-porous species (ash, oak, and grapevine) were far less consistent. There are a number of reasons for this. One reason is that vessel numbers are necessarily small (see Fig. 1, at A). Another reason is the fact that the length of the longest vessels is comparable to tree height. This does not permit true random distribution.

It has been known for years that the wide vessels of ring-porous trees are long and the narrow vessels of diffuse-porous trees are relatively short (e.g. Greenidge 1952). This implies a correlation between vessel diameter and length. The present study confirms this trend. We not only know now that the narrow latewood vessels of ring-porous trees are short (Fig. 12); we have also found that the slightly narrower vessels of the latewood of small-porous species are shorter than the wider earlywood vessels (e.g. Fig. 11). However, while diameter distribution describes a symmetrical bell-shaped curve in many cases (e.g. Fig. 10), the distribution of length is asymmetric. We are therefore refraining, for the present, from trying to establish a mathematical correlation.

Although the cohesion theory of sap ascent is generally accepted today, two questions remained: how can tensile water remain stable over several years and how can water get around injuries such as double sawcuts? We believe that these questions are answered by the structural nature of the xylem. Safety and stability reside in compartmentalization. Long and wide vessels serve efficiency, narrow and short ones provide safety. Even ring-porous trees which depend on their wide and long vessels for efficient conduction, and whose functional longevity is restricted to one growing season, have narrow and short latewood vessels that remain functional for many years. Although these are not sufficient to supply water to a fully developed crown, they can carry water to the top in early spring during early cambial activity which produces earlywood vessels before the leaves unfold.

Water movement around injuries such as sawcuts is easily explained by the presence of many short vessels and the nature of their network. Vessels run at different angles in successive layers of a growth ring, the axial path of water conduction thus fans out tangentially from any given point (Zimmermann 1971; Zimmermann and Brown 1971).

Vessel length is also a factor in tree pathology, particularly wilt diseases (e.g. Ayres 1978). Microorganisms introduced by insects into new xylem injuries can initially be swept up and down to the ends of the injured vessel by the retreating water. The longer the vessels, the further an infection can be carried during the initial injury.

Three-dimensional wood anatomy has been a badly neglected field of research. Cinematographic analysis is a tool with which we have been able to follow individual vessels, look at their ends and reconstruct their three-dimensional network. Measurements of vessel-length distribution has shown that wood contains many more short than long vessels. This is a feature of considerable importance for the safety of water conduction.

Acknowledgments

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Appendix A
Vessel length distribution analysis

The recovery of vessel length distribution from experimental data reproduced in Fig. 13 by Skene and Balodis (1968) involved the implicit assumption of a general shape for the distribution profile which was then quantified. The slope of cumulative count-distance data was required to increase smoothly and monotonically with distance. Multi-modal vessel length classes were not admissible. Milburn and Covey-Crump (1971) simply imposed another distribution form (three straight lines) to represent discrete length groups without much improvement in rendering the actual distribution. Both techniques involved the most important assumption of a completely random distribution of vessel ends, and slopes of the cumulative counts-distance plot were averaged over considerable lengths of the stem.

A close examination of data in Fig. 13, however, reveals that the assumption of complete randomness of vessel ends for all vessels within the stem may not be sustained for long vessels within a stem segment which itself constitutes a major proportion of the tree trunk or branch. The absolute number of open vessels between points *W* and *X*, a distance greater than 0.45 m for example, did not increase. This would suggest that no vessel ends of long vessels ($\gtrsim$2.8 m) existed in this zone. (The slightly higher count at *W* may be experimental error.) Vessels between 2.8 and 3.2 m long may, however, be within the stem, only displaced. Again between points *Y* and *Z*, about a 50% increase in number of open vessels was recorded, a trend which was not maintained in the shorter sections. Within this zone, a large number of vessel endings may reside. This

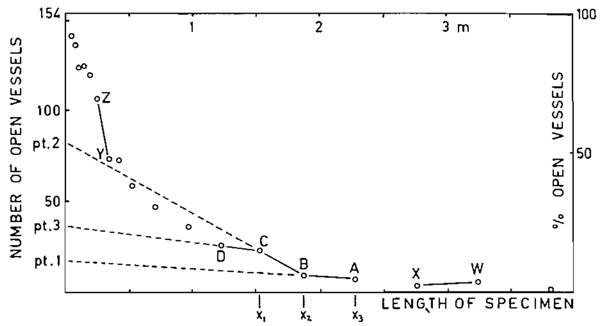

FIG. 13. Reproduced data of Skene and Balodis (1968).

feature might not have been apparent had counts at points *Y* and *Z* not been recorded; i.e. if measurements had been made at insufficiently close intervals.

The method of analysis in both papers above was essentially of the same type for which the assumption of completely random vessel ends is necessary. Starting with Milburn and Covey-Crump's method, we observe that the vessels' lengths were divided into discrete classes, each class represented by the longest vessel in the group. That is, only this length represents the group. Analysis of the situation whereby all actual vessel lengths (the analog condition) are admissible is considerably more complicated. Let us illustrate their technique with points *C*, *B*, and *A* in Fig. 13 with counts m_1, m_2, and m_3 at planes x_1, x_2, and x_3, respectively. For complete randomly dispersed vessel ends belonging to all length groups, the total number of vessels in the length class x_1 to x_2 is given by:

$$\text{[A-1]} \quad n_{12} = -\left[\left.\frac{dm}{dx}\right|_{12} - \left.\frac{dm}{dx}\right|_{23}\right] x_2$$

where dm/dx is the slope of line between adjacent points *B*–*C* or *A*–*B*. The number n_{12} corresponds to the count between points 1 and 2 on the ordinate axis. On substitution for the slopes, it is readily seen that:

$$\text{[A-2]} \quad n_{12} = \left[\frac{m_1 - m_2}{x_2 - x_1} - \frac{m_2 - m_3}{x_3 - x_2}\right] x_2$$

which for equal intervals $x_2 - x_1$, $x_3 - x_2$ yields the central difference form which we also employed in the main text.

As the spacing between counts, h, shrinks (or $x_2 - x_1$ and $x_3 - x_2$ approach zero) the count versus distance curve becomes smooth, and the limit of number of cells in any length class (which is now very narrow) becomes:

$$\text{[A-3]} \quad \lim_{h \to 0} n_{12} = x \frac{d^2 m}{dx^2} h$$

This second differential in finite difference form yields [A-2] above, and it is the form used by Skene and Balodis.

The critical assumption in the analysis of Skene and Balodis, and Milburn and Covey-Crump is that of complete randomly dispersed vessel ends. This may not be so as mentioned earlier. In a stem segment recovered from a tree trunk or branch of length L, the population of vessel ends belonging to a particular length class x_i (assumed straight in the stem), may depend upon the distance from the plane of the origin. This is particularly important for long vessels that may have no endings in the middle of the stem. Thus the local population density of a length class, n_{x_i} should be defined in terms of a probability function, f, i.e.

[A-4] $n_{x_i} = n_0 \cdot f(x, L, x_i)$ at variable distance x from chosen origin

The function may have the property that the higher the L/x_i ratio, the more random the vessel ends for the length class. For complete randomness,

[A-5] $f(x, L, x_i) = 1$

and n_0 is a uniform population density for each length class as determined by techniques shown above.

The adoption of different forms for the function such as

[A-6] $f(x, L, x_i) = \exp - \left(\frac{x_i - x}{L}\right)\beta$; for $x < x_i$

may be useful except that it involves an arbitrary constant β. However, the function approaches unity as x_i approaches zero. That is, complete randomness is almost achieved for short vessels.

As is apparent in Fig. 13 and in the data of this study, the connection of adjacent points with straight lines yields a cumulative curve whose slopes vary widely from one length class to another. Moreover the absolute magnitude of the slopes does not always increase as the stem is cut shorter. This feature is utilized to adjust locally for a nonrandom distribution of a class group as an improvement over previous methods. Real and virtual counts are admitted for any length class. In Fig. 13 the length class BC has a projected population of n_{12} if randomly distributed. For class CD, however, the population is a negative value, n_{23}. The implication is that n_{12} includes an overprediction. All vessels longer than x_1 are now assumed to have an upper bound total count equal to n_{03} with the virtual count n_{23} used to adjust n_{12} directly for the preceding length class. This is strictly an intuitive approach. It should yield a good approximation of the actual vessel length distribution when the origin (or plane at which paint or air is injected) is near one extreme end of the tree trunk, and intervals between vessels length classes are short.

The difference between results of this approach and lower bound populations for long vessels obtained by direct subtraction of consecutive counts will not be significant. Yet for shorter vessels, the complete randomness condition will most often be satisfied. The technique admits multi-modal length distributions.

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Appendix B
Concept of hydraulic diameters

The choice of a length scale to describe an equivalent diameter for a combined system of tubes of varying flow areas and cross-sectional shapes, and transporting a fluid all in one direction, is arbitrary. While the resistance to flow due to friction at the wall is proportional to the total wetted perimeter, the volumetric rate of flow is related simply to the sum of the cross-sectional areas if a uniform average flow velocity may be assumed for all tubes. Under steady-state flow conditions, the wetted perimeter times a length scale would allow the same through-put as the sum of the cross-sectional areas, as long as form drag is negligible. (In xylem vessels, form drag is produced by perforation plates and vessel ends.)

That is

$$\gamma_H \times \text{wetted perimeter} = \text{sum of cross-sectional areas of tubes}$$

where γ_H is a "hydraulic" radius. By comparison with flow in a single circular tube, it can be shown that

$$4\,\gamma_H = \text{diameter}$$

which in the present situation will also be defined as the "hydraulic" diameter.