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The hydraulic architecture of trees and other woody plants

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CONTENTS

SUMMARY

In this paper, we have reviewed how the hydraulic design of trees influences the movement of water from roots to leaves. The hydraulic architecture of trees can limit their water relations, gas exchange throughout the crown of trees, the distribution of trees over different habitats and, perhaps, even the maximum height that a particular species can achieve. Parameters of particular importance include: (1) the vulnerability of stems to drought-induced cavitation events because cavitation reduces the hydraulic conductance of stems, (2) the leaf specific conductivity of stems because it determines the pressure gradients and most negative water potentials needed to sustain evaporation from leaves, (3) the water storage capacity of tissues because this might determine the ability of trees to survive long drought periods. All of these parameters are determined by the structure and function of anatomical components of trees. Some of the ecological and physiological trade-offs of specific structures are discussed.

Key words: Hydraulic architecture, cavitation, embolism, water relations.

I. INTRODUCTION

1. *Water relations of plants*

Much of the study of water relations in plants has emphasized problems of stomatal control, the effects of water stress on growth, and the process of water and mineral uptake by the roots. By comparison, long-distance transport processes in trees and other large plants have been less frequently studied.

The hydraulic design of trees influences the movement of water from roots to leaves, thus different designs could have different consequences for diverse species of trees. We know very little about the advantages and disadvantages of different designs and their contribution to the overall biological strategy and ecological competition among species. In this paper we will cite evidence and present theoretical arguments on the ways in which the structure of the water transport system (the hydraulic architecture) can limit plant water relations, gas exchange throughout the crown of a tree, and, perhaps, even the maximum height that a particular species can achieve. The complexity of the branching structure of many large woody plants requires special treatment, and only recently have techniques been developed to address some of the problems.

2. *Hydraulic architecture*

Trees with very complicated branching patterns sometimes have been reduced by analogy of Ohm's law to just one or a few conductance elements (see section 1.3 below), which is quite adequate for modelling of stand-level water use over days. At a whole-tree level, however, a more complicated branched catena sometimes is desirable in order to answer questions of relevance regarding individual trees, or for the study of the comparative physiology of different species of trees. To look at trees as whole, functional organisms, we need to study their hydraulic architecture.

Some relevant questions to answer through a study of hydraulic architecture are: Since growth rate often is reduced by water stress and since trees grow tall to compete for light, how are trees designed hydraulically to ensure that dominant apices far removed from the ground get better access to water than subdominant apices near the ground? How do trees without apical control ensure that all branches have more-or-less equal access to water regardless of their distance from ground? At times of drought how do trees programme which branches are sacrificed first? How susceptible are trees to water-stress-induced xylem dysfunctions like cavitation and embolism that decrease stem conductance? Are there trade-offs between stem conductance and vulnerability to cavitation and embolism? What structural features of stems allow lianas (woody vines) to supply water to large leaf areas through relatively narrow stems and why not (or do not) trees use these features? Trees invest much more biomass in stem versus leaves than do small plants, and consequently, have potentially large reserves of stored water. Is stored water ever critical to the survival of trees? Does stem conductance or stem vulnerability to cavitation play a major role in the drought resistance of trees? Can we explain some of the differences in life history or phenology of trees (e.g. drought deciduousness) in terms of difference in hydraulic architecture? Does the hydraulic architecture limit the maximum height (in the case of trees) or length (in the case of lianas) that a particular species can achieve? Answers to these questions may be of more than just academic interest, and may provide better ability in predicting the effect of global climate change in species composition of forests, allow us to breed more productive or more stress-resistant trees, or to develop trees with more useful wood.

3. *Nature of the conducting units*

Long-distance water flow occurs through the lumens of non-living tracheary elements (vessels and tracheids) of the xylem and through the lateral pits that interconnect the tracheary elements (Esau, 1965). Pits are thin, porous depressions in the wall where secondary wall material is lacking. A vessel is composed of a series of vessel elements (vessel members) stacked end-to-end and interconnected by perforations at the end walls. Since vessels, like tracheids, are of finite length, water eventually must move from vessel to vessel or from tracheid to tracheid through lateral pit pairs. Vessels can range from less than 1 mm to many metres in length in different species (Zimmermann & Jeje, 1981; Ewers, Fisher & Chiu, 1990). Coniferous trees lack vessels, so they are entirely dependent upon tracheids for their water transport. Tracheids are individual elongated conducting cells ranging in length from a mean of 2 mm in wood of *Juniperus virginiana* L. to a mean of 6 mm in *Sequoia sempervirens* Endl. (Panshin & de Zeeuw, 1980). In young stems tracheids are often 1 mm or less in length.

In addition to the tracheary elements, wood (secondary xylem) contains other cell types, including fibres and living parenchyma cells. Fibres are thick-walled cells specialized for mechanical support. Xylem parenchyma cells are involved with water and carbohydrate storage, and may be crucial in defence against disease. Non-living cells cannot, themselves, respond to wounding or parasite entry, but living cells can, and do, respond by excreting gums, lignin precursors, and other substances, or by growing into the vessel lumens to form tyloses (Panshin & de Zeeuw, 1980; Zimmermann, 1983; Bonsen & Kucera, 1990). These and other responses by living cells help to limit the spread of pathogens in the xylem. Some of these protective responses also

are a normal part of heartwood formation, the inner, non-conducting portion of the xylem (Ewers & Cruiziat 1990).

4. *Ohm's law analogy*

The fundamentals of water movement in plants have been understood for some time (Dixon & Joly, 1896; Dixon, 1914; Huber, 1928, 1956; Van den Honert, 1948; Scholander, 1972) and has been reviewed by Zimmermann (1983) and Boyer (1985). Huber (1928) and Van den Honert (1948) made important contributions to our understanding of long distance water flow with the application of the Ohm's law analogy, and Richter (1973) provided a valuable discussion of some misunderstanding and misuse of this principle.

Water flux (F, kg s^{-1}) through the various parts of the soil–plant–atmosphere–continuum (SPAC) is treated as a catenary process, analogous to the current in an electric circuit composed of a series of conductances (or resistances = inverse conductance, Fig. 1). In the Ohm's law analogy the flux of water through a discrete region from A to B, F_{AB}, is proportional to the product of the hydraulic conductance (k_{AB}, kg s^{-1} MPa^{-1}) of that region and the

water potential drop across the structure (ψ_A–ψ_B, MPa, to be precise we should include only the pressure potential component for flow through xylem conduits).

$$F_{AB} = k_{AB}(\psi_A - \psi_B). \tag{1}$$

The Ohm's law (or electrical) analogy can be generalized further to allow for hydraulic capacitances. This usually is done by associating each conductance element with a discrete water-storage capacity value, C_{AB} (kg MPa^{-1}). The effect of capacitance is to cause the water flux into a region (F_A) to be unequal to the water flux going out (F_B) whenever ψ is changing in the region. The magnitude of the differences in fluxes in and out depends upon the product of C_{AB} and the rate of change of ψ with time ($d\psi/dt$, MPa s^{-1}). There are two circumstances under which the Ohm's law equation can be applied without accounting for capacitances: (1) when ψ is not changing with time ($d\psi/dt = 0$) regardless of the size of C_{AB}; this situation is sometimes referred to as steady-state flux or conservative flux. (2) when the product $C_{AB}(d\psi/dt)$ is much smaller than $k_{AB}(\psi_A - \psi_B)$, either because C_{AB} is small or $d\psi/dt$ is small, or both.
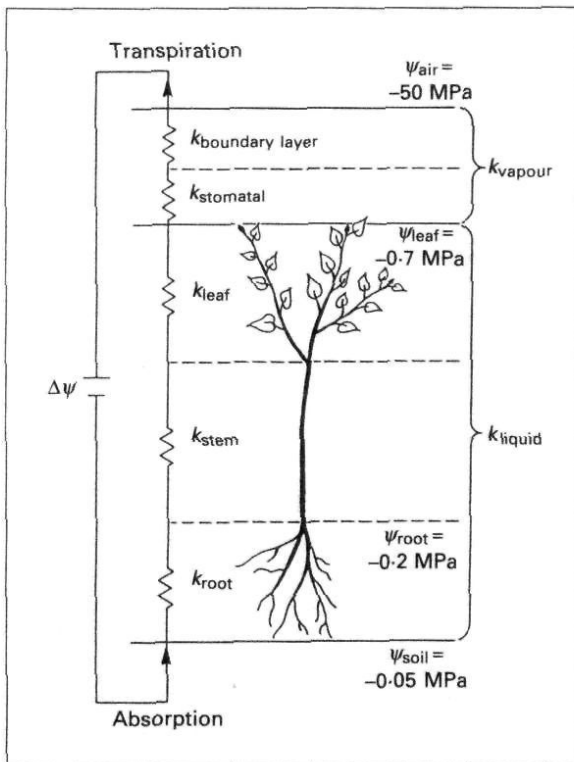
II. WATER FLOW THROUGH PIPES AND THE UNIT PIPE MODEL

1. *Poiseuille's law*

Many studies have applied Poiseuille's law to model xylem transport. In the nineteenth century Hagen and Poiseuille independently arrived at an equation (modified here for our purposes) for fluid flow through a bundle of perfectly cylindrical pipes:

$$k_h = (\pi\rho/128\eta) \sum_{i=1}^{n} (d_i^4), \tag{2}$$

where k_h is the hydraulic conductivity (= conductance per unit pressure gradient of a bundle of pipes of different diameters) and is the proportionality constant between flux (F, kg s^{-1}) and pressure gradient (dP/dx, MPa m^{-1}) causing the flux; ρ is the density of the fluid in kg m^{-3}, η is the dynamic viscosity of the fluid in MPa s^{-1}; d is the diameter (m) of the ith pipe; and n is the number of pipes in the bundle. For xylem tissue, the conduit diameters can be measured and the sum of their diameters to the fourth power calculated to determine the theoretical hydraulic conductance [eqn (2)]. The value of eqn (2) is that it demonstrates the marked effect of a few large vessels on the hydraulic conductivity of stems. It is not unusual for the median vessel diameter to be $\frac{1}{2}$ to $\frac{1}{4}$ the diameter of the largest vessels, but eqn (2) tells us that the hydraulic contribution of one large vessel four times the median size will contribute the same to conductivity as $4^4 = 256$ median diameter vessels!

Since xylem conduits (tracheids or vessel ele-

Figure 1. The simplest Ohm's law analogy. The total conductance is seen as resultant conductance (k) of the root, stem, leaf, stomates and boundary layer in series. The conductances in the vapour phase are much less than in the liquid phase. Water flow is driven by the differences in water potential between the soil (ψ_{soil}) and the atmosphere (ψ_{air}) (from Ewers & Cruiziat, 1990)

ments) are rarely circular in cross-section and since only a small error in measuring diameter is magnified to the fourth power in eqn (2), it is not surprising that measured conductivity often is less than the theoretical conductivity predicted by Poiseuille's law. The agreement is improved somewhat by using versions of the law for pipes that are elliptical or rectangular in cross-section as seems appropriate for a stem.

For most woods, the actual conductivity is from 20 to 100 % of the theoretical conductivity (Tyree & Zimmermann, 1971; Zimmermann & Brown, 1971; Gibson, Calkin & Nobel, 1985; Calkin, Gibson & Nobel, 1986; Ewers et al., 1990). Since the tracheids of conifers tend to be rather short (e.g. about 1–3 mm in stems less than 10 yr old (Panshin & De Zeeuw 1980), and water must pass through bordered pits to advance to the next tracheid, it seems plausible that when the measured values disagree with eqn (2) in conifers it is because of the low conductance of the bordered pits.

When disagreement is found in stems having vessels many centimetres to metres in length, it is difficult to know if the disagreement is caused by one or more of the following problems: (1) low conductance of pit membranes at vessel ends, (2) non-ideal geometry of the cross-section, (3) the spiral, curved, or otherwise nonlinear shape of vessels in the stem, making the actual length of the transport pathway greater than the measured stem length (4) an unrepresentative number of vessels measured. Omitting one vessel three times the median diameter will have the hydraulic effect of omitting $3^4 = 81$ vessels of median diameter. This problem can be acute when one is not confident that a particular vessel is actually conductive. Some have ascribed the non-agreement to turbulent (non-laminar) flow in vessels caused by ridges in walls, but this seems unlikely. Although turbulent flow will cause a nonlinear relationship between flow and pressure gradient in individual conduits and also in the whole stem, nonlinearity is rarely found in vessel-bearing stems (Sperry & Tyree, 1988, 1990; Sperry, Tyree & Donnelly, 1988).

2. The unit pipe model

In the 'pipe model theory of plant form' (Shinozaki et al., 1964a, b), the plant is viewed as an assemblage of 'unit pipes', each of which supports a unit of leaves (Fig. 2). This model is supported by the observation that the xylem cross-section of a tree is generally proportional to the mass of leaves supported by that stem segment (see for example, Long, Smith & Scott, 1981; Rogers & Hinckley, 1979). The pipe model has been useful in predicting canopy leaf mass or leaf area from stem cross section, and is of some value in understanding tree growth, resource allocation, and biomechanics (Ewers & Zimmer-
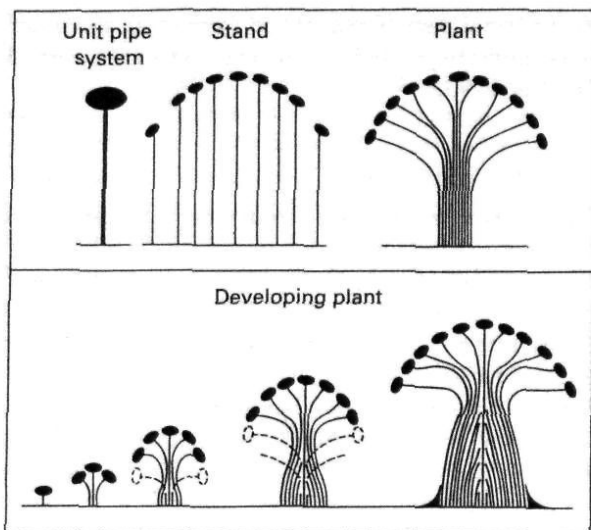

Figure 2. The unit pipe model of plant form; the tree is viewed as an assemblage of 'unit pipes' (from Ewers & Cruiziat, 1990).
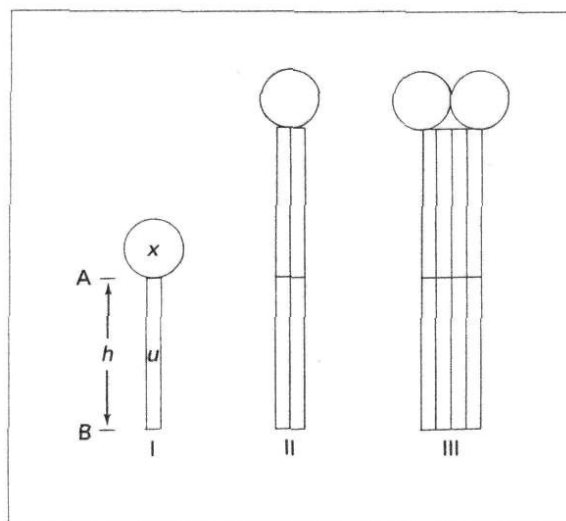
Figure 3. Three conditions showing the problem of maintaining constant conductivity in the unit pipe model as the pipe length and leaf area change. u, a unit pipe; x, leaf area; h, height. See text for details.

mann, 1984a, b). However, the model is of little value in understanding how trees are designed as a transport unit, because the stem cross-section allocated per unit leaf area and the vessel diameter in the stems vary widely within the crowns of many trees. Without that knowledge, the unit pipe model might suggest that large or small diameter stem segments are equally capable of supplying water to leaves distal to the segments. This is not so and parameters introduced below in section 3 will be used to prove the point.

Another failure of the pipe model is that it does not consider the varying lengths of the transport pathways to different leaves on a plant. Imagine a unit pipe of mass, u, supporting leaf area, x (Fig. 3). If the transport distance, h, were doubled with the same leaf area supplied (condition II in Fig. 3), four

unit pipes would be required to maintain the same k_{AB}. If the leaf area were doubled as the transport distance doubled (condition III in Fig. 3), eight unit pipes would be required to equally supply the leaves with water (Raven & Handley, 1987). Trees minimize this massive build up of unit pipes, as they age, by two methods. (i) Those that lack secondary growth (e.g. palm trees) initially are oversupplied with xylem and should attain considerable height before water transport limits. (ii) Trees with secondary growth normally produce wider and longer vessels or tracheids at their lower parts as they age, which helps to compensate for the increased transport distances (for examples and explanations for the control of conduit size see Aloni & Zimmermann, 1983; Aloni, 1987, 1991).

III. PARAMETERS AND CONCEPTS TO DESCRIBE HYDRAULIC ARCHITECTURE

1. *The hydraulic conductivity* (k_h)

The hydraulic conductivity per unit pressure gradient (k_h) is the most commonly measured parameter and equals the ratio between water flux $(F, \text{kg s}^{-1})$ through an excised stem segment and the pressure gradient $(dP/dx, \text{MPa m}^{-1})$ causing the flow.

$$k_h = F/(dP/dx). \tag{3}$$

This quantity has been described incorrectly as the conductance per unit length, in that k_h is obtained from conductance [eqn (1)] by multiplying by stem length (rather than by dividing by the length which is what is implied by the phrase 'per unit length'). Not surprisingly, k_h increases with stem diameter. To find out the relationship of k_h to the hydraulic architecture of trees, it can be divided by the cross section of the functional xylem (sapwood) in the segment or by the leaf area attached to plus distal to the segment.

2. *The specific conductivity* (k_s)

When k_h is divided by the sapwood cross-section, we obtain the specific conductivity, k_s, which is a measure of the porosity of the stem segment. Using the notation consistent with Poiseuille's law above and dividing by the sapwood cross-sectional area (A_w, m^2) we get

$$k_s = (\pi\rho/128\eta A_w) \sum_{i=1}^{n} (d_i^4). \tag{4}$$

From this, it is easy to see that k_s should increase if the number of conduits per unit-stem cross-section or the average conduit diameter increases. The k_s presumably will lessen with decreasing pit membrane porosity and decreasing conduit length, since the actual k_h will be less than predicted by Poiseuille's law.

3. *The leaf specific conductivity* (LSC)

When k_h is divided by the leaf area distal to the segment (A_L, m^2), we get the leaf specific conductivity (LSC). This is a useful measure of the hydraulic sufficiency of the stem to supply water to leaves distal to the stem. If we know the average evaporative flux density $(E, \text{kg s}^{-1} \text{m}^{-2})$ from the leaves supplied by the stem segment and if we can ignore the impact of water-storage capacitance, then the pressure gradient in the stem $(dP/dx) = E/LSC$. (This follows because $E = F/A_L$ and $LSC = k_h/A_L$ therefore $E/LSC = F/k_h = dP/dx$, which is the definition of k_h, eqn (3) solved for dP/dx.) So the higher the LSC the lower the dP/dx needed to supply water to the leaves fed by the stem.

4. *The Huber value* (HV)

The Huber value (HV) is defined as the sapwood cross-section (or sometimes the stem cross-section) divided by the leaf area distal to the stem. The number has units of m^2 of stem area per m^2 of leaf area and often is written without dimension. It measures the investment of stem tissue per unit leaf area fed. It also is a relational product between k_s and LSC since it follows from all the definitions above that $LSC = HV \times k_s$.

5. *Water-storage capacitance* (Q)

The water storage capacity (C) of plant tissue was defined above as the mass of water (w) that can be extracted per MPa change in water potential (ψ) of the tissue $(C = \Delta w/\Delta\psi, \text{kg MPa}^{-1})$. Since the size of C is proportional to the size of the tissue in question, it is customary to define the tissue capacitance as C per unit tissue volume (V) or per unit tissue dry mass or, for leaves, per unit area (A):

$$Q_{\text{stem}} = \frac{\Delta w}{\Delta\psi}\frac{1}{V}, \tag{5a}$$

$$Q_{\text{leaf}} = \frac{\Delta w}{\Delta\psi}\frac{1}{A}. \tag{5b}$$

In leaves and in herbaceous stems and roots, the mechanism of water storage primarily is elastic, i.e. as tissue ψ increases or decreases, the volume of the tissue increases or decreases respectively. In the woody stems and roots the bark changes considerably in volume with changes in ψ, but the volume of the wood changes very little. Water storage and retrieval in wood involve two mechanisms in addition to elastic storage: (1) capillary storage and (2) cavitation release (Zimmermann, 1983). These mechanisms recently have been demonstrated by Tyree & Yang (1990). Capillary storage is highest at ψ_p values > -0.5 MPa and occurs only in wood cell lumina (vessels, tracheids, or wood fibres) containing air

bubbles because the lumina has cavitated previously (see below in subsection III.6). As the xylem pressure potential (ψ_p) changes, the size and shape of the bubbles change so that the surface tension at the air/water interfaces exactly balances the ψ_p. When ψ_p is > -0.5 MPa a substantial volume of water is left in the cell lumen, but the volume decreases with decreasing ψ_p, hence, capillary water becomes vanishingly small at $\psi_p < -0.5$. At much more negative ψ_p values, previously water-filled xylem lumina cavitate, releasing their water to the transpiration stream. The ψ_p at which cavitation starts releasing water to the stem varies between species. In some it can start at -0.5 MPa, whereas in others, it does not start until -4 or -5 MPa.

6. Vulnerability to xylem embolism

Water ascending trees usually does so under negative pressure down a gradient of increasingly negative pressure. The negative pressure is physically equivalent to a tension (a pulling force) transmitted to soil water via a continuous water column; any break in the column necessarily disrupts water flow. Xylem transport can occur under these extraordinary conditions because of the special properties of water and the structure of the xylem. Hydrogen bonding promotes cohesion between water molecules and allows water to remain liquid under tension. But if the continuity of the water in the xylem conduit should be broken by the nucleation of a micro-void, the void will expand explosively, or cavitate, to fill the conduit lumen. Surface tension usually makes the void/water interface stop at the pit membrane between adjacent conduits and prevents it from advancing to the adjacent conduits. The embolized conduit may be a tracheid (a single cell), or a vessel (many cells stacked end to end, connected by perforations). Upon cavitation, the lumen of the conduit initially will be close to vacuum conditions. However, the lumen soon will fill with air, coming out of solution from the surrounding water-filled tissues. From that point on, the lumen remains air-filled (embolized) until ψ_p returns to near-atmospheric pressures. At ψ_p near zero, surface tension can raise the pressure of the air bubble above atmospheric pressure, causing the embolism to dissolve over a period of days (Tyree & Sperry, 1989; Tyree & Yang, 1990). Embolisms are serious dysfunctions to be avoided by trees, because emboli reduce stem hydraulic conductivity, requiring increasingly negative pressures and steeper pressure gradients to keep up with transpiration thus making the stems even more likely to cavitate. It has been argued recently that this situation can lead to an unstable cycle of runaway embolism (Tyree & Sperry, 1988).

Each species appears to have a characteristic 'vulnerability curve', which is a plot of percent-loss hydraulic conductivity in stems versus the ψ_p needed to induce the loss (see section V and Fig. 6). Vulnerability curves usually are measured by dehydrating large excised branches to known water potentials. Stem segments are then cut under water from these dehydrated branches. The immersion in water releases the xylem tension, but does not dissolve the emboli immediately. An initial conductivity measurement can be made and compared to a maximum conductivity after all air bubbles have been dissolved (Sperry, Donnelly & Tyree, 1987). Measurements of the vulnerability curves of trees and of the hydraulic architecture can provide valuable insight into the probable drought resistance of trees and limitations imposed on the species by environmental stresses.

IV. PATTERNS OF HYDRAULIC ARCHITECTURE IN WOODY PLANTS
1. General features

The hydraulic architecture of 10 or more species of trees and other woody plants has been studied in varying degrees of detail and some patterns are beginning to emerge. In small plants the lowest conductance (main resistance) to water flow is in the living tissues of the roots and leaves (Huber, 1956; Kramer & Kozlowski, 1979; Boyer, 1985). In large woody plants, there are many instances documented in which stems are responsible for the lowest conductance to water flow from the roots to leaves (Hellkvist, Richards & Jarvis, 1974; Tyree, Caldwell & Dainty, 1975; Zimmermann, 1978; Tyree et al. 1983; Ewers & Zimmermann 1984a, b; Tyree, 1988; Ewers et al. 1989). However, there are some notable exceptions in the world of large woody plants. Liu et al. (1978) reported that for cultivated Vitis labrusca L. plants, the total conductance of the stem was much higher than that of the roots and leaves. However, how low stem conductances are may depend on the previous history of droughts; Schultz & Matthews (1988) found that in V. vinifera L., stem k_h dropped considerably in response to drought conditions. Tyree et al. (1991) found that adult Schefflera morototoni (Aublet) Maguire, Steyermark & Frodin (formerly Didymopanax morototoni a tropical, gap-specialist tree reaching heights of 20–25 m) has stem conductances higher than that of the leaves (see below).

2. Gymnosperms

The patterns of hydraulic architecture and the anatomical correlates have been documented more thoroughly in gymnosperms [Tsuga canadensis (L.) Carr., Abies balsamea (L.) Mill., and Thuja occidentalis L.] than in angiosperms. Stems of different branching order and of different diameter have been compared to boles (trunks) of different ages and diameters (Tyree et al., 1983; Ewers & Zimmer-
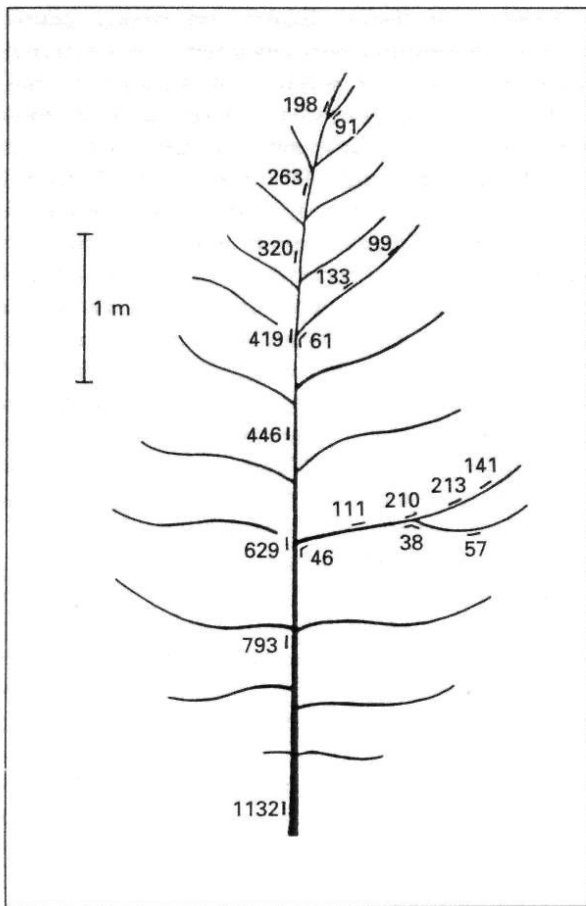
Figure 4. Pattern of LSC (leaf specific conductivity) in the crown of a *Tsuga canadensis*. LSC values are reported in 10^{-6} kg s^{-1} m^{-1} MPa^{-1}. Note that LSCs are higher in the trunk than in branches, and higher in first-order than in second-order branches. Branch junctions have hydraulic constrictions (modified from Ewers & Zimmermann, 1984 *a*).

Figure 5. Profiles of pressure potential of stems versus the distance (path length) water must travel from the base of the tree to a stem apex. The lower diagram shows *Schefflera* on an expanded scale of ψ_p. All values include the gravitational potential gradient (GPG) required to lift water up the tree. These curves are calculated from the hydraulic maps and representative evaporative flux density (E kg s^{-1} m^{-2}) for each species in the graph (modified from Tyree *et al.*, 1991).

mann, 1984 *a*, *b*). In all three species LSC increased with enlarging stem or bole diameter (Tyree *et al.*, 1991). The smallest diameter stems had LSCs 30–300 times less than the largest boles, i.e. LSCs of 0.3×10^{-5} kg s^{-1} m^{-1} MPa^{-1} for 1 mm diameter stems versus 30×10^{-5} kg s^{-1} m^{-1} MPa^{-1} for 300 mm diameter boles (Fig. 4). This means that the pressure gradient, dP/dx, needed to maintain water flux to transpiring leaves distal to the smallest stem segments, will be 30–300 times steeper than the corresponding gradients in the base of boles. For a typical $E = 1.5 \times 10^{-5}$ kg s^{-1} m^{-2}, we can calculate dP/dx from E/LSC; dP/dx will range from 5 to 0.05 MPa m^{-1} in the smallest diameter branch segments and the biggest diameter boles, respectively (excluding the dP/dx needed to overcome the gravitational potential gradient, 0.01 MPa m^{-1}, for vertically oriented segments). Large differences in dP/dx between large diameter boles and smaller diameter branches have been measured directly by a bagged shoot method (Hellkvist *et al.* 1974; Tyree *et al.*, 1983).
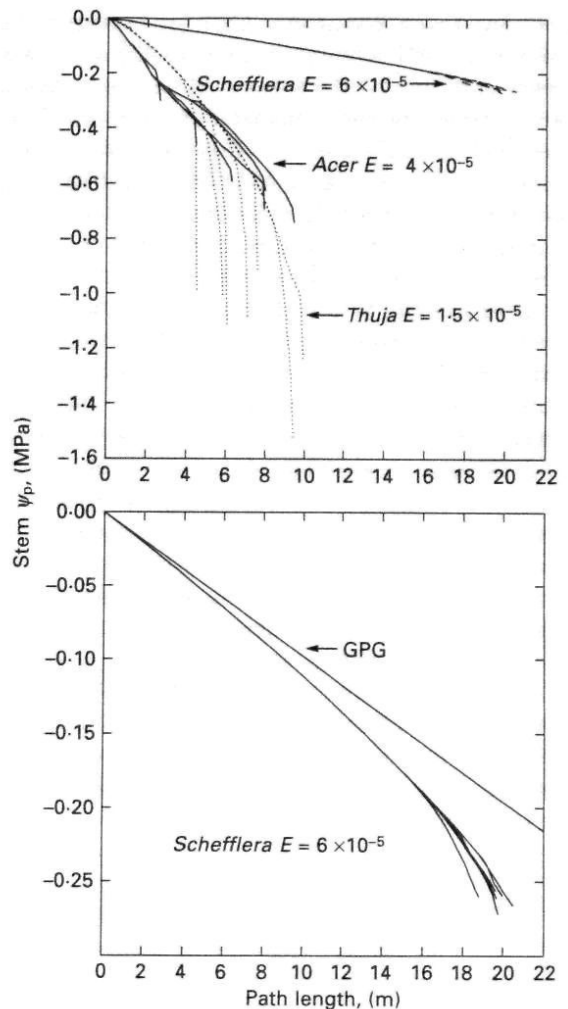
The effect of this pattern of LSC in a gymnosperm is to confine most of the resistance to water flow to the last metre, or less, of pathway from the base of the tree to the leaf-bearing branches (Fig. 5). Consequently, most small branches can compete for water on a more-or-less equal basis, i.e. each small branch behaves like an independent plant rooted in a common, highly conductive bole.

There is a correlation between 'apical control' and the pattern of LSCs in the bole. By apical control we mean that the dominant leader has greater elongation growth than lateral branches (Brown, McAlpine & Kormanik, 1967). This is not necessarily the same as apical dominance, which refers to the arrest of lateral buds. Of the three species studied, *Abies balsamea* has the highest level of apical control and a nearly constant LSC in the bole from base to dominant

apex. In *Tsuga canadensis* Carr. the plagiotropic leader frequently is replaced (Ewers & Zimmermann, 1984*b*) and the LSC values decline more rapidly with diminishing stem diameter in boles of *Tsuga*. The LSC of small-diameter *Tsuga canadensis* boles is about the same as that in branches of equal diameter. In contrast, in *Abies balsamea*, which has great apical control, the LSCs are much higher in boles than in branches of equal diameter.

It is of interest to correlate changes in LSC with changes in HV and k_s. Recall that LSC is equal to the product of HV and k_s. In *Tsuga canadensis* and *Abies balsamea*, with decreasing stem and bole diameters values of HV tend to increase whereas k_s decreases. In dominant shoots having apical control, the increase in HV, with decreasing diameter, is more than in shoots without strong apical control. The anatomical basis for the lowering in k_s with decreasing stem-diameter is that small diameter stems have smaller diameter tracheids than large diameter stems (Ewers & Zimmermann, 1984*a,b*; Aloni, 1987, 1991). In *Thuja occidentalis*, HV and k_s calculated on the basis of stem cross-section (rather than sapwood cross-section) both decrease with lessening stem diameter (based on the reanalysis of data published by Tyree, 1988).

3. Angiosperms

(*a*) *Trees*. The LSC of angiosperm trees tend to be higher than in gymnosperm stems of the same diameter; the values for *Acer saccharum* Marsh. range from 7×10^{-5} to 70×10^{-5} kg s^{-1} m^{-1} MPa^{-1} for stems of 3–100 mm diameter, respectively. The primary reason for differences in LSC of angiosperm stems is differences in k_s. The k_s of angiosperm stems tends to be 4–15 times that of gymnosperms (Tyree *et al.* 1991) because diameters of vessels generally exceed those of tracheids. Mean HV of *Acer saccharum* stems 2–10 mm diameter are about the same as (or perhaps slightly larger than) those of *Thuja occidentalis* of equal diameter. Angiosperm leaves tend to have higher evaporative flux densities than gymnosperms, so differences in dP/dx may not be as much as expected in accounting only for differences in LSC.

An interesting extreme is *Schefflera morototoni*, a tropical tree with LSCs about 10 times that of *Acer saccharum* stems of similar diameter. The k_s of *S. morototoni* is less than twice that of *Acer saccharum*, so the main reason for the difference in LSC is that the HV is much larger. The computed ψ_p profiles of *S. morototoni*, *Acer saccharum*, and *Thuja occidentalis* are compared in Figure 5 for representative E values for each species. It can be seen that pressure–potential gradients in *S. morototoni* barely exceed that required to lift water against the gravitational potential gradient.

(*b*) *Shrubs and lianas*. Lianas are woody plants rooted in the ground but dependent upon external plants or objects for mechanical support. Lianas are thus, in a sense, mechanical parasites in competition with their host plants for light, water, and mineral nutrients (Putz, 1984; Stevens, 1987; Ewers & Fisher, 1991). Recall that the xylem has dual functions of mechanical support and water transport. In lianas the support functions are minimal and the transport functions accentuated. As a result, it should not be surprising that lianas tend to have low HV and high k_s (Ewers, 1985; Ewers, Fisher & Fichtner, 1991). A number of reports have shown that the vessels of lianas are wider than in closely related trees (Carlquist, 1975; Ewers, 1985; Ewers *et al.*, 1990). It appears that the wide vessels of lianas compensate for the narrow stem diameters.

Shrubs are an infrequently studied growth form in respect to hydraulic architecture. In shrubs the transport distances are not normally as large as in trees or lianas, but the branching system can be quite complex. The effect of branch junctions on conductive efficiency needs further study (see below in section IV.4).

Toxicodendron diversilobum (Terr & Gray) Greene can grow as either a shrub or a liana. Gartner (1991) found that vine forms had larger k_s values and vessel diameters but lower HV's than shrub forms. They found the same trends in externally supported (vine-like) versus self-supporting (shrub-like) branches of the same individuals of this species.

A comparative study of two tree, two shrub, and two liana species of the genus *Bauhinia* (Fabaceae) revealed some interesting comparisons between growth forms (Ewers *et al.*, 1991). The maximum transpiration rates, LSCs, and stem pressure gradients were quite similar in the three growth forms. Shrubs had the greatest HVs, lianas the lowest values, and trees were intermediate. In contrast, lianas had the highest k_s values and shrubs had the lowest values. As mentioned earlier for lianas in general, the *Bauhinia* lianas had the largest vessel lengths and diameters (Ewers *et al.*, 1990; Ewers & Fisher, 1991). Since LSCs were similar in the three growth forms, it was concluded that the wide vessels of lianas resulted in specific conductivities that were just big enough to compensate for the low HVs.

4. Junction constrictions

Hydraulic constrictions at branch junctions have been reported in gymnosperms (Tyree *et al.*, 1983; Ewers & Zimmermann, 1984*a, b*). The LSC values of branch junctions are most frequently documented in unequal junctions, i.e. where a small branch arises from a large bole or where one branch is much larger than the other. The LSC of the smaller branch generally is less than that of the larger branch or bole. The anatomical basis lies more in differences in

tracheid diameter, which influence k_s, than in differences in HV (Ewers & Zimmermann, 1984 *a*, *b*). The occurrence of circular tracheids might also contribute this (Lev-Yadun & Aloni, 1990). The tracheid diameters of the largest tracheids usually are less in the smaller-diameter branch. LSCs in stem segments distal to junctions usually are more than that of the junction measured through the lesser branch (e.g. Fig. 4). Similar patterns have been reported in several angiosperms (*Acer pensylvanicum* L., *A. rubrum* L., *A. saccharum*, *Betula papyrifera* Marsh. and *Populus grandidentata* Michx.), and the anatomical basis for the lower LSCs in the junctions is the same (Zimmermann, 1978) and might also be influenced by the presence of large circular non-functional vessels (Lev-Yadun & Aloni, 1990).

It is difficult to say whether these junction constrictions have much impact on the overall conductance and water relations of trees. To estimate the effect, we need to know the absolute conductance of a junction compared to that of the typical length of stem segment basal or distal to the junctions. LSC (or more rarely k_h) values often are given without specific reference to length of segments used in the measurements. What is the size of the junction constriction, measured in terms of equivalent length of stem segment basal to the junction? Let us consider two stem segments both of length L. If one contains a stem junction and the other does not and if their conductances [eqn (1)] are x_j and x, respectively, then $L_n = L(x - x_j)/x_j$ should equal the length of the stem segment without junction, having a conductance equal to that of the junction constriction.

In an attempt to estimate L_n, Tyree & Yang (unpublished) compared the conductance of stem junctions and stem segments contiguous with, and immediately distal or basal to the junction. Y-shaped junctions with nearly equal or unequal branches were cut from 8 to 15 mm diameter stems of *Acer saccharum* and of 20–40 mm diameter *S. morototoni*

(which have more-or-less equal dichotomous branches). The junction was located in the middle of each Y and contiguous segments distal and basal to the Y segments were cut to the same length as the path length through the Y (usually 0·14–0·21 m for *Acer saccharum* and 0·25–0·30 m for *S. morototoni*). The results are summarized in Table 1. In *Acer saccharum* the conductances of the contiguous segments distal to the Y tended to be less than that of the left or right arm of the Y, but in only one case was this difference significantly different ($P < 0.05$); the conductances of the contiguous segments basal to the Y tended to be about 1·3 times that of the conductance summed for the left and right arms. The net effect is that the Y junctions tended to have a conductance of about 0·04 m of stem below the Y. More research is needed to determine if the ratio of junction conductances of 8–15 mm diameter *Acer saccharum* branches are similar to that in larger or smaller diameter junctions. But we might tentatively conclude that the combined effect of the 5–8 junctions that water must pass through from the base of a tree to small twig of a 10 m tall tree might be the equivalent of adding just 0·04 m extra stem length at each junction for a total of just 0·2–0·3 m; this does not seem like much of a hydraulic constriction in a 10 m tree.

In *S. morototoni* there were no significant junction constrictions, which is not surprising for a tree with equal bifurcations. An equal dichotomy would result in two stems with similar transport distances and similar leaf areas to supply. (Strictly speaking this species has a pseudodichotomy since the apex itself does not dichotomize.) The effect of a hydraulic constriction presumably is to favour one pathway over the other (e.g. the main stem over the lateral branch). In an equally bifurcating branching system, the hydraulic pathways remain equal to one another and constrictions, if they occur, would be equally deleterious to each of the two shoots.

Ewers *et al.* (1989) calculated the impact of

Table 1. *Ratio of conductances of* Y *junctions and of contiguous stem segments of equal length basal and distal to the* Y *junction. All results are reported as ratios of conductances calculated from flux* ($kg\ s^{-1}$) *divided by pressure drop* (*MPa*). *The area ratio is the cross-sectional area of the smaller branch* (*right arm*) *to that of the larger branch*

Species	Area ratio	$A/(B+C)$	D/B	E/C
A. saccharum	0·87 ± 0·09	1·29 ± 0·10	0·737 ± 0·175	0·941 ± 0·187
A. saccharum	0·44 ± 0·10	1·28 ± 0·12	0·919 ± 0·156	0·881 ± 0·175
S. morototoni	0·93 ± 0·07	1·02 ± 0·05	0·95 ± 0·06	0·95 ± 0·07

A, conductance of contiguous segment basal to Y; *B*, conductance of left arm of Y with flow permitted through right arm; *C*, conductance of right arm of Y (the smaller branch) with flow permitted through left arm; *D*, conductance of contiguous segment distal to left arm of Y; *E*, conductance of contiguous segment distal to right arm of Y. All errors are standard deviations $n = 9$ for *Acer saccharum* and $n = 4$ for *Schefflera morototoni*.

unequal branch junctions in the liana *Bauhinia fassoglensis* Kotschy ex Schweinf., where LSCs entering branches were about 20 % of that along the main axis. LSCs were similar along the axes of the main stem and branches except for the constriction entering the branch. At maximum transpiration rates the measured drop in water potential was about 0·08 MPa m^{-1} along the stems and about 0·27 MPa in moving from stem to leaf. There was a drop of about 0·20 MPa at branch junctions as predicted by E/LSC. Therefore, a single junction from stem to leaf or from stem to branch had the same drop in water potential as, respectively, 3·4 or 2·5 m stem length. Sampled stems of this species were up to about 16 m in length. The stomates closed in this species at about −1·1 MPa so, if water had to pass through several junctions, the junctions would begin to have considerable negative impact on gas exchange. Thus it is not surprising that this species is very sparsely branched. It may be that a species with severe hydraulic constrictions can support fewer orders of branches than those with mild or non-existent constrictions.

V. VULNERABILITY TO CAVITATION: RELATION TO HYDRAULIC ARCHITECTURE AND DROUGHT RESISTANCE

Drought generally reduces the growth rate of plants (Hsaio *et al.*, 1976) and reduces stomatal conductance to gas exchange. Net assimilation is reduced by drought because of a reduction in stomatal conductance and because of a direct effect of water stress on growth and on the enzymes involved in photosynthesis. Although the latter mechanism has been demonstrated (Boyer, 1976), it is not clear if it is of primary importance. Drought resistance has been ascribed to a suite of measurable properties such as high root-to-shoot ratios, low solute potentials, differences in cell wall elastic modulus (both high and low!), and 'osmo-regulation', i.e. increases in solute concentration apparently induced by drought. Until recently, the most commonly held view was that stomatal closure occurs in order to avoid damage by water stress to the biochemical machinery of plants.

It is now becoming clear that xylem dysfunction induced by drought is a serious problem to plants. Therefore, resistance of xylem to cavitation events is an important (perhaps the most important) parameter that determines drought resistance. Vulnerability curves have been measured on 11 species (5 gymnosperms and 6 angiosperms, see Fig. 6) and so far there appears to be an approximate correspondence between the vulnerability curves and our general perception of the drought resistance of the species.

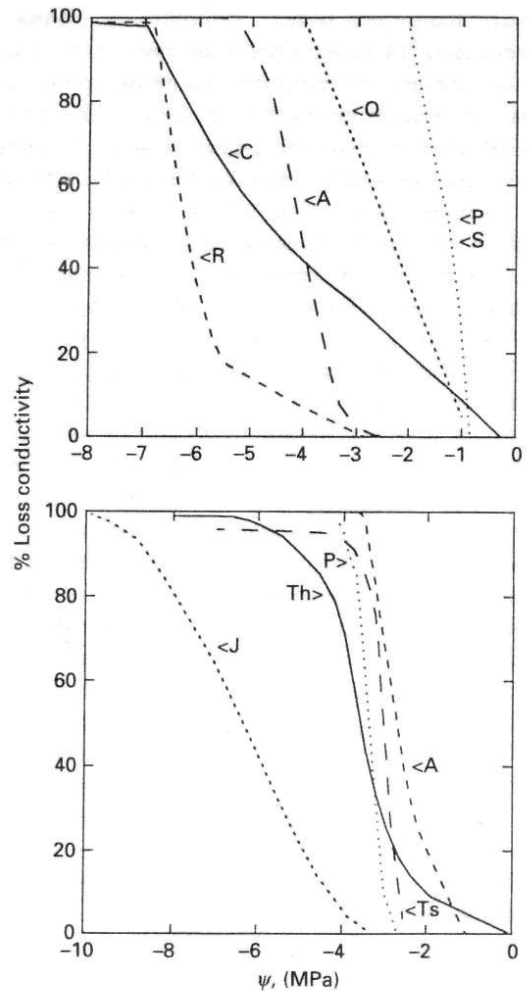Among the least vulnerable taxa are *Juniperus virginiana* and *Rhizophora mangle* L.; the ψ for just

Figure 6. Vulnerability of various species to embolism measured as the percentage loss hydraulic conductivity versus water potential. Upper panel are angiosperms: R, *Rhizophora mangle*; A, *Acer saccharum*; C, *Cassipourea elliptica* (Sw.) Poir.; Q, *Quercus rubra* L.; P, *Populus deltoides*; S, *Schefflera morotoni*. Lower panel are gymnosperms: J, *Juniperus virginiana*; Th, *Thuja occidentalis*; Ts, *Tsuga canadensis*; A, *Abies balsamea*; P, *Picea rubens* Sarg.

20 % loss of hydraulic conductivity occurs at −5 to −6 MPa. *J. virginiana* L. is a widely distributed conifer capable of growing on both mesic and xeric sites. *R. mangle* is a mangrove growing in saline coastal marshes, but its roots exclude salts from the xylem stream. This means that the maximum ψ_p equals the maximum ψ_{soil} that it experiences, which is approximately that of 0·5–1·5 times sea water ($\psi = -1·1$ to $-3·3$ MPa). At the other extreme of vulnerability are *Populus deltoides* Bartr. ex Marsh. and *S. morototoni*, which lose 50 % of their hydraulic conductivity by $\psi = -1·5$ MPa! *S. morototoni* grows in rain forest gaps where ψ_{soil} tends to be higher than in old forests and it reduces the impact of short-term droughts by having very high stem hydraulic conductivity and deep tap roots. *Populus deltoides* is a temperate mesic species that grows near lakes and streams or where water tables are high. During

droughts many species of poplar tend to close their stomata early and shed their leaves to reduce water stress (Kozlowski, Kramer & Pallardy, 1991, p. 147).

The most likely limitation on long-lived species like trees, is the minimum ψ_{soil} reached during severe drought that occurs once every 20–40 yr, which are likely to kill trees and reduce reproductive success. During extreme droughts, the stomata are likely to remain closed for most of the day and the water potential of the trees will approximately track that of the soil. Vulnerability to cavitation must put an evolutionary limit on the water potential at which stomates close. In species with high vulnerability to cavitation, stomatal closure must occur before a substantial fraction of the hydraulic conductivity of the stems is lost by cavitation events. In highly vulnerable species stomatal closure will reduce net carbon gain and competitive ability.

VI. DYNAMIC AND STEADY STATE MODELS OF WATER FLOW IN TREES

1. *Rationale for models*

In order to understand how the pattern of LSC in the crown of trees effects water distribution to leaf-bearing branches, it is necessary to map the stem and leaf distribution in representative trees or large branches of each species. The data base derived from this hydraulic map is used in computer programs to simulate water-flow patterns through the branch in steady-state models (water-storage capacitance is of no effect) or in dynamic models (capacitance taken into account).

2. *Hydraulic maps*

A tree or large branch is cut into numbered segments as illustrated in Figure 7. Economy in program writing and execution is achieved by numbering the segment starting at the base (segment number 1) and proceeding to side branch segments before numbering continuation segments. Data collected for each numbered segment is: (*a*) a connecting segment code number. This was the number (N) of the next most basal segment. This was written as $+N$ if two segments were on the same branch, and was written as $-N$ if the next most basal segment was a separate branch. The numbering system on an 11-segment branch is illustrated in Figure 7. (*b*) The basal diameter of the segment. (*c*) The length of the segment. Segment lengths were adjusted to fit the degree of resolution desired and the scale of dimensions between stem junctions. (*d*) The surface area of all 'leaves' attached to the segment. Where a fine mapping scale is not needed then leaves attached might include leaves from minor branches attached to the numbered segment.
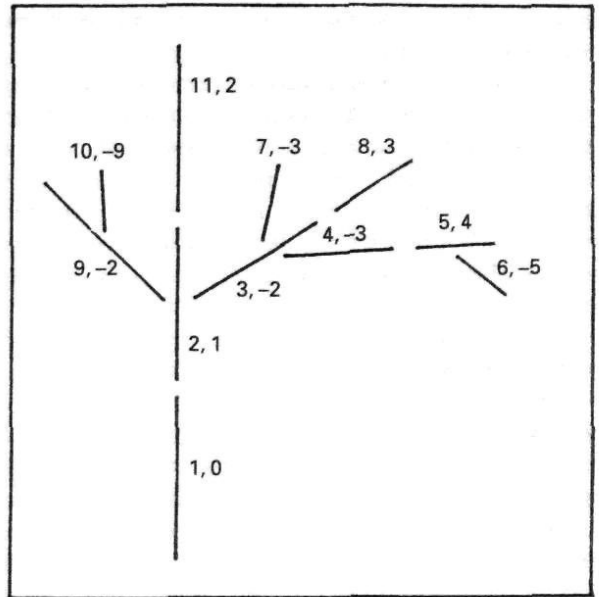

Figure 7. The numbering system used in an 11-segment branch. Gaps indicate locations of branch cuts. The first number beside each segment is the segment number, the second is the connecting segment number (from Tyree & Sperry, 1988).

3. *Steady state profiles of ψ*

A steady state solution of stem ψ_p versus path length is illustrated in Figure 5. Every leaf in the hydraulic map was allowed to have the same evaporative flux density, E, and the profiles of ψ_p versus path length were calculated from the base of the tree to representative apices. The 'droopy' plot for *Thuja occidentalis* shows that the lowest conductance to water flow resides in the minor branches of the crown, putting each minor branch on more-or-less equal competitive status for water resources, which may be necessary for species having strong apical control. The relatively flat plot of *S. morototoni* shows that hydraulic conductances for the stems are very high; the dichotomous branching of this species places each leaf approximately equidistant from the ground so no hydraulic compensation is needed to protect the access of water to growing apices. *Acer saccharum* is intermediate in apical control and is reflected in the intermediate ψ_p profiles.

4. *Dynamic water flow and stored water*

Dynamic mathematical solutions are useful in assessing the relative contribution of stored water to the transpiration stream in trees. A description of how to develop dynamic models can be found in Tyree (1988 & 1989) and Tyree & Sperry (1988). In order for a tree to extract usable water from a structure (e.g. leaf or stem segment), the ψ of the structure must decline. A hydraulic map and data on E are needed to compute the changes in ψ and thus the

diurnal or seasonal changes in water content of leaf and stem segments.

The hydraulic architecture of very large trees has yet to be quantified, but could be quite fascinating. As an extreme example, how do stems of *Sequoia sempervirens* Endl. (coast redwood), the world's tallest tree, with individuals up to 111·6 m in height, supply their leaves with water, even though, being a conifer, their wood lacks vessels? Part of the answer may be that the tracheids, although narrow compared to vessels of many dicotyledonous trees, are perhaps the widest of extant conifers (up to 80 μm; Panshin & De Zeeuw, 1980). Perhaps redwoods have enormous HVs to allow for extremely efficient water transport. Is water storage in the massive trunks crucial to their survival? Is seasonal, as well as diurnal, water storage important in this species since most of the precipitation occurs in winter under suboptimal photosynthetic conditions? Why is the natural distribution of the trees limited to fog banks along the Pacific coast? Only with quantitative dynamic models of water transport can we answer some of these questions.

In moist environments, water stored by capillary forces (see above) could be a substantial source of stored water for the transpiration stream. For example, Waring & Running (1978) have estimated that stored water in the boles of 50–60 m tall Douglas fir forests in Oregon could contribute water equivalent to 1·7 mm d^{-1} for much of the growth season. In Scotland, where soils are wet and evaporative demand is low, stored water may account for 30–50 % of the seasonal water use (Waring, Whitehead & Jarvis, 1979). Similar relationships might hold for many temperate trees in early spring when soil water reserves are high and evaporative demand is low. However, the adaptive advantage of such stored water is not so clear since water is not limiting in soils. Large quantities of stored water in very moist environments could be an advantage if the species can gain by investing less carbon in wood for hydraulic conductance, but if the wood is needed more for mechanical stability than for hydraulic architecture, then the advantage of stored water is more questionable.

In less wet environments, when ψ_{soil} might be around $-0·2$ to $-0·4$ MPa for much of the growth season, then capillary water will be minimal and the contribution of stored water to the transpiration stream might be quite small (Tyree & Yang, 1990). Large leaf and stem-water capacitances would substantially reduce the maximum rate of water uptake from the roots below the transpiration flux (leaf area times E, kg s^{-1}) at midday and will spread out the period of water uptake by the roots over more hours in the diurnal cycle. There would be an adaptive advantage to trees if they could make use of diurnal stored water in exchange for investing less in roots. To test this hypothesis, diurnal calculations of water storage and release have now been done in detail from hydraulic maps for *Thuja*, *Acer* and *Schefflera*. Table 2 shows the water-storage capacity of stems and leaves and the contribution of water released from these structures from predawn to the time of minimum water potential. The contribution of stored water to the transpiration stream is expressed as a percentage of the total water transpired in a 24 h period. The contribution of stored water would be maximal if it contributed 50 % to the transpiration stream over a 24 h period; in such case, for half the diurnal cycle water would be released from stores and for the other half of the diurnal cycle (i.e. mostly during the night) the water would be returned to the storage areas. It can be seen that the contribution of stored water to transpiration is most in *Thuja* and least in *Schefflera*. This happens even though the water storage capacitance is most in *Schefflera* and least in *Thuja*. The stored water in *Schefflera* can not be tapped diurnally because the LSCs of *Schefflera* stems are so high that ψ_{stem} never gets very negative; the stored water can not be extracted by diurnal variations in dynamic water stress.

Most water extraction from stems will occur when ψ_{soil} becomes progressively negative during a drought. This is because most of the mass of a tree is contained in the bole, which is in close hydraulic contact with the ground, so the bole is going to track changes in ψ_{soil} more closely than ψ_{leaf}. Under conditions of severe drought, stomata are likely to remain closed for most of the day, and E, averaged

Table 2. *Stem and leaf water-storage capacitances (Q_{leaf} in kg m^{-2} MPa^{-1}, Q_{stem} in kg l^{-1} MPa^{-1}) and the contribution of stored water to the diurnal transpiration of water in trees*

Species	Q_{leaf}	Q_{stem}	% T_{leaf}	% T_{stem}
Acer saccharum	0·006	0·02	14	3
Thuja occidentalis	0·04	0·02	16	5·5
Schefflera morotoni	0·01	0·03 to 0·2	< 0·5	2

% T is the percentage of the total daily transpiration derived from storage in the leaf and stem (depending on subscript) based on the calculated maximum change of ψ_{leaf} and ψ_{stem} from predawn until midday.

Table 3. *Contribution of stored water to transpiration during severe drought expressed as days of transpiration (stomates closed) for changes in soil water potential (ψ_{soil}), starting with ψ_{soil} likely to cause stomatal closure until ψ_{soil} likely to cause 50% loss of hydraulic conductivity in the stems of each species*

Species	Range of ψ_{soil} (MPa)	Transpiration (d)	V/A (l m^{-2})
Acer saccharum	−1·8 to −2·8	< 0·2	1·3
Thuja occidentalis	−1·5 to −3·5	1·7	1·8
Schefflera morotoni	−0·7 to −1·5	16	17·6

V/A, stem volume per unit leaf area, l m^{-2}.

over 24 h periods, is likely to be 0·05 or 0·02 times that during midday under mesic conditions. Table 3 shows the calculation of the contribution of stored water to transpiration in terms of the number of days of transpiration that stored water can contribute, assuming no water is extracted from the soil and when ψ_{soil} changes from the value likely to cause stomatal closure until half the hydraulic conductance of the bole has been lost by cavitation events. Under these conditions, the contribution of stored water is likely to be most important in *Schefflera*, where the water storage capacitance of stems is most and where the stem volume per unit leaf area is most, and is least in *Acer*, where stem capacitance and stem volume per unit leaf area are least.

VII. THE SEGMENTATION HYPOTHESIS

1. *Hydraulic segmentation*

Zimmermann (1983) was fascinated by plant segmentation, which can be defined as any structural feature of a plant that confines cavitations to small, distal, expendable organs in favour of larger organs representing years of growth and carbohydrate investment. Among these features, Zimmermann recognized the value of the decline of LSC with lessening stem diameter and the presence of hydraulic constrictions at stem and leaf junctions.

Zimmermann argued that plant segmentation is vital in arborescent monocotyledons, such as a palm tree. Palms tend to have unbranched stems with no vascular cambium. A palm stem, once formed, can never add new vascular tissue, whereas dicotyledonous and coniferous trees can form new vascular tissue by stem diameter enlargement each year. A coconut palm, with approximately 20–30 mature leaves, retains that number of leaves for its life. Old leaves die and are shed at about the same rate that new leaves mature (Zimmermann, 1983). The primary vascular tissue of the stem is probably over efficient when the palm is short but perhaps limits growth by water stress as the palm gains height; the

same transpiration rate requires an ever-increasing total pressure drop to lift water to the top.

The palm stem represents many years of carbohydrate investment and the functionality of the xylem must be maintained at all costs. In palms there appear to be substantial hydraulic constriction at the level of the leaf junction (Sperry, 1986). Zimmermann (1983) argues that this is an essential architectural feature needed to confine embolisms to palm leaves during drought. Leaves are expendable, but if the stem is embolized, then the tree may never recover.

Zimmermann argued that similar relationships apply to dicotyledonous trees where small branches and leaves are more expendable than the bole, which represents a considerable carbohydrate investment. Stem and leaf junction segmentation is caused by a decline in conduit diameter and by proportionately more vessel ends in junctions than in the rest of stems (e.g. Isebrands & Larson, 1977; Salleo, Rosso & LoGullo, 1982). Considering the high vulnerability of *Populus deltoides* stems to cavitation (Fig. 6) the hydraulic constriction of the leaf insertion discovered some years ago (Larson & Isebrands, 1978) may be very important in the context of Zimmermann's segmentation hypothesis.

2. *Vulnerability segmentation*

We feel that Zimmermann's segmentation hypothesis needs to be generalized to include vulnerability segmentation. By vulnerability segmentation we mean the vulnerability of leaves, petioles, or minor twigs compared to the vulnerability of larger stems. If expendable organs are more vulnerable than nonexpendable organs, then hydraulic segmentation is really unnecessary. Even if there were no junction constrictions and even if LSC *increased* with *decreasing* stem diameter, the distal portions of plants would still be at more negative ψ_p than proximal portions. This is because water must always flow in the direction of declining ψ. This, alone, would

ensure a large measure of segmentation of cavitation. But if large stems are *more* vulnerable than small stems, then large stems could cavitate before small stems in spite of hydraulic segmentation. Does vulnerability segmentation exist? We have only one example to date. Minor twigs of *Acer* (< 6 mm diameter) are more vulnerable to cavitation than larger stems (> 6 mm diameter). The percentage loss of conductivity in minor stems reaches 50% at $\psi = -3$ MPa, whereas only a few % loss has occurred in larger stems at the same ψ (Fig. 8). Both hydraulic and vulnerability segmentation probably are necessary to make trees work. Without hydraulic segmentation, distant, rapidly-growing leader stems might cavitate before minor stems nearer the ground. That could be a disadvantage to a tree.

3. Runaway embolism and ecological strategies

In section VI.4 we discussed the dynamics of water flow in trees and the extraction of water stores under severe drought conditions. Our concern about the vulnerability of the stem to cavitation was only incidental, i.e. how much water can be extracted from stems until the soil becomes dry enough to cause a 50% loss of hydraulic conductivity by cavitation events. During severe droughts the water flux through trees is minimal because stomata are closed. Therefore, ψ_{stem} is nearly the same everywhere throughout the tree and close to that of the soil. This represents a static stress, i.e. water stress that persists almost without water flow. Dynamic (frictional) water stress is that decline in water potential needed to move water through the plant. Usually, trees experience a combination of static and dynamic water stresses, but at times one component can dominate. Well-watered, elevated light condi-
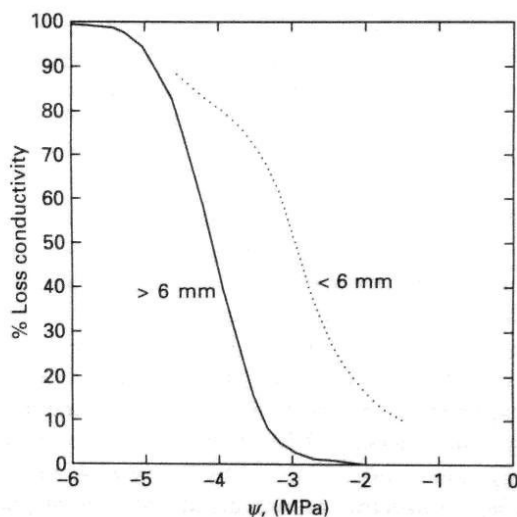
tions result in more dynamic water stress; drought conditions result in more static water stress.

If we examine the vulnerability curves in Figure 6 and consider only static stresses, then we might conclude that cavitation is not a threat to many species. Rarely, if ever, would the ψ_{soil} become negative enough to cause > 50% loss of hydraulic conductance in *J. virginiana* or *R. mangle*. However, if we consider the dynamic situation, we might predict that these species are much more at risk. Loss of hydraulic conductance from embolism could enhance dynamic water stress by causing a faster flow and thus steeper ψ_p gradients in the remaining conduits. If total transpiration (and thus total water flux) were constant while cavitations were occurring, the blockage of xylem conduits would force faster transport in the remainder, causing yet more xylem vessels to be blocked by cavitation in a runaway vicious cycle of embolism. We call this cycle of dynamic stress leading to reduced conductance and further dynamic stress an 'embolism cycle'. The embolism cycle inherently is unstable (Tyree & Sperry, 1988); theoretical calculations reveal that, once started, the cycle will lead to runaway embolism unless stomatal closure reduces the transpiration flux. If emboli do not disappear after formation, then gas exchange must remain permanently below the theoretical maximum rate in order to prevent runaway embolism, which reduces the net carbon gain in a tree. So embolisms can have a long-term effect on the physiology, and perhaps even the reproductive success, of a tree.

Normally, stems harvested from trees have a 'native' state of embolism causing a 5–20% loss of hydraulic conductance. Tyree (1989) has demonstrated that in *Thuja occidentalis* this native level of embolism is approximately the level that would be expected to arise from normal transpiration rates. This conclusion was reached by running dynamic models of *Thuja* in which all the minor branches (< 8 mm diameter) were assigned a hydraulic conductance 5–15% higher than the native state to compensate for the loss. The dynamics of water stress in the crown were then calculated for successive days of transpiration with increasing peak transpiration rates for each successive day. After each cycle of calculation the ψ_{stem} was examined in each stem segment to see if it had reached a new minimum and, if it had, its conductance was reduced by an amount equivalent to the vulnerability curve (Fig. 6). Once normal levels of transpiration were reached, the predicted percent loss conductivities of the small branches approximately equalled that found in the native state. Higher levels of transpiration than occur in nature caused even more embolism and loss of hydraulic conductance.

Trees can accommodate 5–20% loss of hydraulic conductance before approaching a state of unstable runaway embolism (Tyree & Sperry, 1988). The

Figure 8. Similar to Figure 6 but shows vulnerability of *Acer saccharum* stems > 6 mm in diameter versus < 6 mm diameter (modified from Tyree *et al.* 1991).

conditions under which the threat of embolism reaches an unstable runaway state depends on several factors: (1) the vulnerability of stems to embolism, (2) the magnitude of the LSCs and their pattern in the crown, i.e. the hydraulic architecture, (3) ψ_{soil}, and (4) the transpiration flux through the stems. High vulnerability (i.e., vulnerability curves shifted toward the right in Fig. 6), low LSC, and low ψ_{soil}, all make runaway embolism start at a lower transpiration flux in the stems. The transpiration flux, itself, is determined by stomatal conductance of leaves and by the amount of stem cross section servicing a unit of leaf area, i.e. the HV.

It seems probable that the physiology of stomatal regulation in each species has evolved to maximize gas exchange in order to bring each species to the brink of runaway embolism. There must be fascinating ecological tradeoffs and cost benefits for different strategies, but we know virtually nothing about them. For example, high LSC and low vulnerability to cavitation may be mutually exclusive goals. In terms of carbon investment, high LSC can be achieved in a cost-free way by producing larger vessels or by producing greater vessel density (more vessels per transverse wood area). But there are potential hidden costs; most of the mechanical strength of dicotyledonous trees resides in the small wood fibre cells so more or wider vessels would mean less strength and perhaps fewer living cells in which to store carbohydrate reserves or by which to fight off pathogens. Strength could be preserved by having fewer but larger vessels, but this is at a cost of loss of redundancy. If there are only a few large vessels, then an embolism in any one will interrupt flow to a larger fraction of the leaf area. It also is possible that low vulnerability is achieved at the cost of low LSC. There is increasing evidence that vulnerability to cavitation induced by water stress is determined most by pit membrane porosity (Crombie, Hipkins & Milburn, 1985; Sperry & Tyree, 1988, 1990). Conduits having pit membranes with smaller pores are less vulnerable to embolism because surface tension makes difficult the passage of air-bubbles through small pores, but conduits with small pores will have low hydraulic conductivity.

In other than tropical environments, we have to consider, also, the impact of freezing-induced embolism on xylem conductance. Freezing in the xylem causes air to come out of solution, which can result in permanent embolisms. Wide diameter vessels, as in ring-porous trees, appear to be more vulnerable to freezing-induced embolism than are narrow conduits (Ewers, 1985; Ellmore & Ewers, 1986; Cochard & Tyree, 1990). Long and wide vessels also may be less able to recover from embolism once it occurs (Tyree & Yang, 1990). Given these considerations, colder environments would seem to favour smaller conduits, which are limited in their size by their environment (see Aloni, 1987).

There must be more than one successful ecological strategy. For example, *S. morototoni* trees are extremely vulnerable to cavitation, but they cope by investing more in stems per unit leaf area, which gives them high LSC and high water storage capacities. *S. morototoni* is an early successional species in newly formed gaps, where rapid growth rates might be particularly well favoured. The suite of wood characteristics (wide vessels, high vessel density, high LSCs, high water-storage capacity), may reduce dynamic water stress permitting high photosynthetic rates and high growth rates. At the other extreme we might cite *J. virginiana*; a species with low vulnerability to cavitation at the cost of very low LSC. This species can grow on very dry and cold sites, including Lake Michigan sand dunes. Presumably, the price paid for this suite of characteristics is a reduced theoretical maximum gas exchange rate.

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