Tree hydraulics: how sap rises

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Abstract
Trees transport water from roots to crown—a height that can exceed 100 m.
The physics of tree hydraulics can be conveyed with simple fluid dynamics
based upon the Hagen–Poiseuille equation and Murray's law. Here the
conduit structure is modelled as conical pipes and as branching pipes. The
force required to lift sap is generated mostly by transpiration or capillary
action; we investigate the effectiveness of both these forces for the two
conduit architectures considered. The level of analysis is appropriate for
undergraduates. The subject is of broad interest because it provides a naturally-
occurring example of an unusual metastable state of matter: liquid under
tension.

1. Introduction

The conduits which carry water from the roots to the crown of a tree are formed from dead
tissue known as *xylem*, unlike the transport of nutrients in the other direction via living *phloem*;
therefore, water is raised via a purely physical (not biophysical) process. The nature of this
process has been something of a mystery for over a century but, in the last two decades,
advances in experimental technique have settled some of the questions.

Biology is the last of the sciences to prove itself amenable to quantitative physical analysis,
for two reasons: because of the wide variability and interconnectedness of biological systems
(many variables and parameters) and because of the difficulty of making detailed observations.
An example of the first category is that of bird flight; it is only in the last 40 years that
aerodynamics has been applied quantitatively to the study of bird flight, though aerodynamics
itself has been well understood for over a century. (The changing wing shape of birds and
the changing wing position relative to the airflow, due to flapping flight, complicate the
analysis.) Tree hydraulics falls into both categories. Evolution has provided a wide variety
of water conduit designs among different types of plants; for a given type the rigid nature of
xylem conduits simplifies the theoretical analysis of water transport, but providing convincing
experimental confirmation of theoretical predictions has until recently proved difficult.

Tree hydraulics is not a subject familiar to most physicists or physics students and so we
provide references to articles written for non-specialist scientists [1–9] in addition to relevant

specialist research papers. We also avoid many technical terms and understate the variability of different water transport systems. Xylem conduits vary in diameter from several microns to several hundred microns; the variation is between species and, as we will see here, within a tree. The conduits can be several metres in length, and connect end to end to form a channel from root to leaf. In this paper, we will consider xylem conduits to be continuous pipes with circular cross sections, though in reality the pipes are not truly continuous and the cross sections are often not circles. True xylem has end caps separating pipe sections, and pits in the walls that permit water (and air) to pass from one conduit to another. Despite the messy realities, so typical of biophysics, it is fruitful to make a gross simplification by considering xylem as smooth circular pipes. The physics that is required to understand water transport through such pipes is accessible to undergraduates and provides insight into the real problem of how sap rises in trees.

In this paper we derive expressions for the pressure required to raise sap to a given height, and expressions for the maximum height attainable, assuming the idealized conduits just described.

2. The cohesion-tension theory, and embolism

Sap is essentially water, (more accurately a 10 mol m^{-3} aqueous solution of mineral and other nutrients [1]). For many years it was thought that the pressure required to move this water was generated in the roots: positive osmotic pressure pushed the water up the stem to the leaves. After all, it was a common observation to note how sap continued to rise once a stem had been cut. However, more detailed and systematic observation revealed that plants have variable root pressures, and some species exhibit no significant root pressure at all. Tall trees require larger pressures than small shrubs, and yet root pressure is not correlated strongly with tree height. Also, the energy cost of osmosis is significant, because mineral nutrient ions must be actively transported into the root xylem to generate osmotic pressure. In practice, while it may be important or even dominant for some small plants, root pressure is unimportant for the transport of water up to the leaves of tall trees. Its main significance for many trees is that it helps to refill empty xylem conduits in springtime.

We now know that the pressure that drives water up the xylem conduits is not a positive pressure at all, but a negative pressure (tension).[1] Water is not pushed from below by root pressure; it is pulled up the conduits from above, by tension that arises from the evaporation of water from the surfaces of leaves (transpiration) or by capillary action. This is a passive mechanism that requires no energy input from the tree: evaporation is powered by sunlight. The cohesion of water molecules in a conduit results in a concave meniscus with a high surface tension. As water evaporates, this meniscus is pulled by adhesion of water molecules to the hydrophilic conduit wall. (The same adhesion is responsible for the ready absorption of water by the cellulose fibres of paper towels.)

It has proved to be difficult to measure the pressure inside xylem, despite the large magnitude of this pressure; for many years the available experimental techniques provided only indirect estimations, and these techniques were open to question. Within the last 15 years, however, the measurement technique has improved and today most researchers consider that xylem conduits are under strong tension. This established fact raises an interesting question: why does the sap not boil? Cavitation should occur in a liquid under tension (i.e. it spontaneously vaporizes). We now know that cohesive forces between the polar water molecules are more than strong enough to hold the water column together (despite being

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[1] We shall follow the convention of treating tension as a positive quantity, though it is negative pressure.

subjected to a tension that may exceed 30 atmospheres) so that, inside the airtight xylem conduit, it exists in a metastable state.

This *cohesion-tension* (CT) theory, first proposed by Dixon and Joly at the end of the nineteenth century [10], drew early criticism because the strength of cohesion was not then appreciated: 'To believe that columns of water should . . . transmit downward the pull exerted on them at their upper ends by the transpiring leaves, is to some of us equivalent to believing in ropes of sand' [2]. Today it is possible to demonstrate the reality of water under tension via a simple classroom demonstration with a water pump, a porous membrane and plastic tubing [3–5]. Such demonstrations are inexpensive, are accessible to undergraduates and serve to provide an interesting application of physical principles to biology.

The reason why sap can exist in a metastable state is that it is confined to airtight conduits of small diameter. If cavitation occurs—if a bubble of water vapour appears in the liquid under tension—then the bubble radius is small because the conduit radius is small. The surface tension in small bubbles is enough to overcome the negative pressure, so that the bubble collapses and the water vapour is absorbed into the liquid. Above a critical radius, the surface tension is overwhelmed by the negative pressure and the bubble expands.

If air enters the conduit, as a result of damage or disease, the result is often embolism: an air bubble breaks the water column and the conduit is henceforth useless for transporting water. (Air entering the water column is a much more serious problem than water vapour because it is much less easily reabsorbed into the liquid.) Embolisms occur every spring after the xylem sap freezes and then thaws, which can result in damage to the thick conduit walls.[2] The tree does not necessarily die from such embolisms, because it grows new xylem conduits each year (these growth rings are readily observed) and because it is capable of reabsorbing gas that enters a conduit, so long as the bubble is not too large. As we have seen, if the bubble radius is small enough so that surface tension exceeds the tension of transpiration then the bubble will not expand, in which case the air can be extracted through pits in the xylem walls. Embolism will not occur if the bubble diameter is less than the conduit diameter. Embolisms can be confined to a short section of conduit, and sap is re-routed (the mechanism, and the sophisticated conduit design that permits this, is discussed in detail in [11]. In the simple models of this paper, however, embolism would render a conduit useless.) In practice embolisms are resisted successfully if the tension is less than a minimum value (which may be quite high—it has been measured at 19 atmospheres in *Sequoia sempervirens*) but for higher tensions the rate of embolism among conduits increases with tension [12].

The current experimental technique has progressed to the extent that the rate of embolisms can be quantified in *vulnerability curves* for different tree species. A vulnerability curve is a plot of loss of hydraulic conductivity (due to embolisms) versus negative pressure. Thus, the Eastern Cottonwood *Populus deltoides* suffers a 50% loss of conductivity at a pressure of −15 atmospheres whereas the Eastern Redcedar *Juniperus virginiana* loses less than 20% conductivity for pressures of −50 atmospheres [11]. These data suggest that, while important, the threat of embolism is not the crucial factor in determining the maximum height attainable by trees.

There are two contenders for the source of strong negative pressure that pulls up the water column: leaf transpiration, as in the original version of the theory, and capillary action. Both may contribute, and the research community is divided upon this point. Here we will present simple calculations (simple because of our basic assumption that xylem conduits are rigid

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[2] The walls are thick to prevent air passing into the conduit and to prevent collapse due to the large tensions inside. The xylem does contract radially, however, and this is observed as a reduction in tree trunk diameters at midday, when transpiration (and hence the magnitude of tension it creates) is greatest. Embolisms also often occur following a prolonged period of drought, though the mechanism is different.

airtight pipes of circular cross section) assuming first transpiration pull and then capillary action as the sole source. We will consider single conduits initially, and then branching conduits.

We will see that the pressure inside a xylem conduit falls from about 1 atmosphere at the base of the trunk to a value of -20 or -30 atmospheres at the crown, depending upon tree height. Water flows in a direction that reduces the water free energy, i.e. the direction of lower *water potential*. Water potential is a concept fundamental to understanding tree hydraulics; it includes chemical potential as well as physical potential energy. The water potential of the atmosphere is much lower than that at the top of even the tallest tree; for example, if the atmospheric temperature is $10\,°C$ and the relative humidity 50%, then atmospheric water potential is -90 atmospheres. This is why water evaporates from the surface of leaves, even though the water within the tree crown is under strong negative pressure. Only when the relative humidity exceeds 98% is the atmospheric water potential high enough to prevent transpiration [15, 16]. Thus, even in humid rainforests (made humid by the transpiration of trees) and during rainfall, the atmospheric water potential is low enough to maintain tension in xylem.

CT theory is summarized for non-specialists in [2, 6, 7]; an extensive technical review is that of Cruiziat *et al* [11]. The considerable doubts about the theory prior to recent experimental developments are well expressed in [13]. The disagreements are aired in [14].

3. Conical conduits

We will assume that each xylem conduit in a tree is shaped like a section of a cone, as illustrated in figure 1. The force that lifts water up this conduit results from transpiration pressure or capillary action—we begin with transpiration pressure P (the magnitude of tension). This force is opposed by gravity acting upon the mass of water in the conduit, and by a viscous force f that resists flow:

$$P\pi r_1^2 = \rho g V + f. \tag{1}$$

(There are other terms that oppose transpiration pressure, such as atmospheric water vapour pressure, but these are here considered to be negligible.) In equation (1), ρ is the density of water and g is the acceleration due to gravity. V is the conduit volume; in the notation of figure 1 this is given by

$$V = \tfrac{1}{3}\pi \left(r_0^2 + r_0 r_1 + r_1^2\right)h. \tag{2}$$

The Hagen–Poiseuille equation describes the resistance to laminar flow of a fluid in a circular pipe. This equation is generally considered to apply quite well to sap rising in a xylem conduit (e.g. [2, 11, 17–19]—but see [20]). The pressure difference between positions x and $x + dx$ along the conduit, due to viscous drag, is

$$P(x + dx) - P(x) = -\frac{8\mu Q \, dx}{\pi r^4(x)}, \tag{3}$$

where μ is the dynamic viscosity of sap (assumed here to be water), Q is the (constant, for a given pressure) volumetric flow rate, and $r(x)$ is the conduit radius at position x. The force f of equation (1) is thus

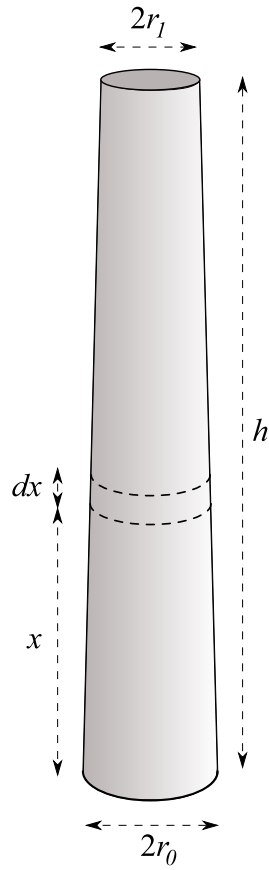$$f = \int_0^h dx \, \frac{8\mu Q}{r^2(x)} = \frac{8\mu Q h}{r_0 r_1}. \tag{4}$$

Figure 1. Xylem conduit shaped like a section of a cone. The radii $r_{0,1}$ are typically 5–100 μm whereas tree height h is 10–100 m.

Substituting into equation (1) from equations (2)–(4) yields

$$\frac{P}{\rho g h} = \frac{1}{3}(s^2 + s + 1) + \frac{q}{s}, \tag{5}$$

where s and q are dimensionless quantities:

$$s \equiv \frac{r_0}{r_1}, \qquad q \equiv \frac{8\mu Q}{\pi \rho g r_1^4}. \tag{6}$$

If we regard the radius r_1 as being fixed, and consider s to be variable, then it is apparent that the pressure required to raise sap to a height h is minimized when s satisfies the following equation:

$$s^2(2s + 1) = 3q. \tag{7}$$

It is common for biophysics researchers to assume that organisms are optimally configured for the environment in which they live [19, 21]. Optimization improves survivability and so there exists selection pressure for, in our case, a tree to evolve so as to minimize the transpiration pull it must generate to lift water to its uppermost leaves. Equation (7) shows that there exists a relation between conduit radius and flow rate that is optimum. Substituting $s = 1$

Table 1. The optimization condition of equation (7) reduces to $r_{opt} = \sqrt{8\mu v_1/\rho g}$ for $s = 1$. We adopt a value for viscosity of $\mu = 0.0013$ N s m^{-2}, appropriate for a temperature of 10 °C. The measurement data of columns 2 and 3 are from [1]. Predicted radii (column 4) are compatible with measurements. We claim that this agreement shows that trees (and perhaps vines) minimize the pressure per unit height they must generate when raising water from roots to crowns.

Tree type	v_1	r_1	r_{opt}
Conifer	1–2 m hr^{-1}	5–20 μm	17–24 μm
Diffuse-porous angiosperm	1–6	3–75	17–42
Ring-porous angiosperm	4–44	5–300	34–114
Vine	150	300	210

and $Q = \pi r_1^2 v$, where v is the flow speed up the conduit, we predict the optimum radii for straight-sided conduits summarized in table 1. As shown in the table, these predicted radii fall among the range of radii observed in nature, and so we conclude that, for xylem conduits of fixed cross section along their length, xylem conduit radius is optimized for minimum pressure per unit height.

From equations (5) and (7) we find the minimum ratio of transpiration pressure to tree height:

$$\frac{P}{\rho g h} = s^2 + \frac{2}{3}s + \frac{1}{3}. \tag{8}$$

Thus for straight-sided conduits ($s = 1$) we see from equations (5) and (8) that half the pressure is needed to overcome viscous drag and half to overcome gravity. Equation (8) tells us that conduits which narrow from base to top ($s > 1$) require higher pressures, while those which flare out like a trumpet ($s < 1$) require less pressure. Although desirable for sap transport, flared conduits are not a good idea for mechanical strength because they imply a top-heavy tree. (Most of the wood in a tree trunk, and thus most of the weight, is xylem.) Assuming $s = 1$, we see that leaves in the crown of a very tall tree ($h = 100$ m) must generate a tension of about 20 atmospheres to raise sap from ground level—this magnitude is typical of real trees.

If sap is pulled up a conduit by capillary action, then the term $P\pi r_1^2$ in equation (1) is replaced by the capillary force $2\pi\gamma r_1 \cos\theta$, where γ is the sap surface tension and θ is the contact angle of the sap surface with the xylem wall (for sap in xylem the factor $\gamma \cos\theta$ equals 0.15 N m^{-1} [6]). Substituting the capillary force into equation (1) we obtain the following expression for the height attained by the rising sap:

$$h = \frac{2\gamma\cos\theta}{\rho g r_1} \frac{3s}{s^3 + s^2 + s + 3q}. \tag{9}$$

Without viscous drag and for parallel conduits ($q = 0$, $s = 1$) equation (9) reduces to the usual expression for height attained by capillary action. For the narrowest xylem conduit (say $r_1 = 5$ μm) this height is about 6 m. From equation (9) we see that there exists an optimum value for s, in the sense of producing maximum height for a given capillary force. This optimum value is given by equation (7), and reduces the maximum height attainable by parallel-sided conduits by half, to 3 m. This height is much less than the maximum height attainable by trees. However, some researchers claim that the relevant capillary dimensions are not those of the xylem conduits but rather are determined by the microfibril matrix at the air–water interface of leaves, with spacings that are something like 5–10 nm; this small size is sufficient to raise water to a height of 3 km [6]. The optimum value of q leads, from equations (6) and (7), to the predicted speed at which sap rises due to capillary action: $v_1 = \rho g r_1^2/8\mu$, for $s = 1$.

Substituting $r_1 = 5 \, \mu$m leads to $v_1 = 0.08$ m hr^{-1}; this is much slower than speeds observed in nature (see table 1). Reducing r_1 to 5 nm may help to raise the height to which capillary action raises sap, but it also slows down the speed by a further six orders of magnitude.

4. Branching conduits

We have so far considered conduits that run continuously from root to leaf; for parallel-sided conduits this model of tree hydraulics is well known and is called the *pipe model*. We have seen that transpiration pull may work for the pipe model (by making water transport predictions that are consistent with observation), but that capillary action does not. In some ways the pipe model does not reflect the true nature of tree hydraulics; the most important of these is the observation that real xylem conduits branch, as suggested in figure 2(a).

In the vascular system of animals, conduits such as arteries and veins bifurcate, i.e. one pipe splits into two pipes. Derived in the 1920s, Murray's law describes how the pipe radii on either side of the split are related. Hydraulic conductance is maximized if the radius cubed of the input pipe equals the sum of the cubes of the radii of the output pipes. In the 1990s it was realized that Murray's law also applies to the conduits of plants [17–19, 22, 23]. Thus if a xylem conduit of radius r_0 splits into two conduits, each of radii r_1, then we expect natural selection to have optimized these radii to maximize hydraulic conductance so that $r_0^3 = 2r_1^3$. There are a number of major differences between plant and animal plumbing, however, and one of them is the *conduit furcation number*, here denoted F. This number is 2 in the case of bifurcation, but for trees it is usually in the range $1.0 < F < 1.3$. We can visualize such fractional furcation numbers as in figure 2(a). In this example one of three pipes bifurcates so that, over some characteristic distance, the number of conduits increases from 3 to 4, so that $F = 4/3$. In what follows, we will assume fractional conduit number in this sense. The reader may question the validity of working with non-integer F. Given that the Hagen–Poiseuille law shows how sensitively flow rate depends upon radius, then the flow rates in the two smaller pipes at the top of figure 2(a) will be very much lower than those in the two larger pipes at the same level, so how can we meaningfully discuss 'flow rate' or 'pipe radius' given that both quantities are not uniquely defined for non-integer F? In the appendix we show for the configuration of figure 2(a) that it is sensible to consider fractional furcation number: the radii of the input and output pipes (for a single conduit that branches into 1.333 conduits) is very close to the mean values obtained directly from figure 2(a). Also in the appendix we show that the viscous resistance of the pipes in figure 2(a) changes from bottom to top as for a single pipe with furcation number 1.31, which is very close to the actual value of 4/3.

The microscopic branching of xylem conduits in a tree is independent of the macroscopic branching of trunk into branches and twigs. We need therefore consider only a single conduit at the base of our tree, and assume that it splits N times so that, in the tree crown, the number of conduits is F^N. The radius of each conduit at level n (where $0 < n < N$) is given by $r_n = F^{-n/3}r_0$, assuming Murray's law. The total cross-sectional area of the conduits increases with n: $A_n = F^{n/3}A_0$. In this sense, the branching conduit behaves like the conical conduit of the last section, with $s < 1$. On the other hand, here each conduit radius decreases with increasing distance from the tree base, whereas it increased for our conical conduit with $s < 1$. We will see that this geometry makes it easier for a branching conduit, compared to one that does not branch, to raise water to a given height.

First, consider a tree that raises sap via transpiration pressure. Equation (1) becomes

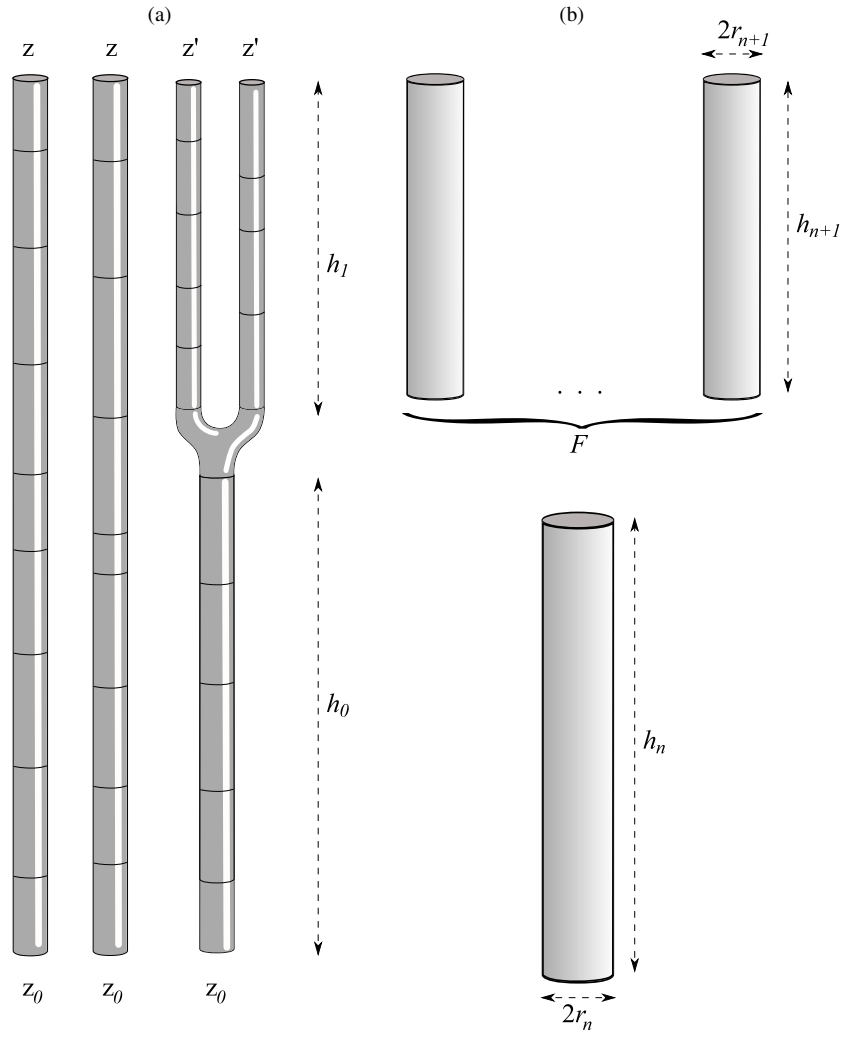$$PA_N = \rho g \sum_{n=0}^{N} V_n + \sum_{n=0}^{N} f_n. \tag{10}$$

Figure 2. Fractional conduit furcation number F. (a) For this configuration, $F = 4/3$. The length scale h_0 can vary from millimetres to metres, depending upon tree species. z refers to conduit hydraulic resistance to flow, discussed in the appendix. (b) Notation for the calculation of section 4.

Here V_n is the volume of the nth level (of all the conduits at that level), and f_n is the viscous drag contribution of the nth level. If the length of the nth level, between branchings, is related to the length of the lower contiguous level via $h_n = \lambda h_{n-1}$ (see figure 2(b) for notation) then

$$V_n = \pi r_0^2 h_0 (\lambda F^{1/3})^n, \tag{11}$$

$$f_n = \frac{8\mu Q h_0}{r_0^2} (\lambda F^{2/3})^n. \tag{12}$$

In deriving equation (12) it must be recalled that the resistance to flow of fluid in parallel pipes adds like that of electrical resistors in parallel. Substituting equations (11) and (12) into (10) yields

$$\frac{P}{\rho g h} = F^{-N/3} \left(\frac{1-\lambda}{1-\lambda^{N+1}} \right) \left[\frac{1-(\lambda F^{1/3})^{N+1}}{1-(\lambda F^{1/3})} + q \frac{1-(\lambda F^{2/3})^{N+1}}{1-(\lambda F^{2/3})} \right]. \qquad (13)$$

In equation (13) we have made use of the equation

$$h = h_0 \sum_{n=0}^{N} \lambda^n. \qquad (14)$$

We have also assumed that the volume of the curved section of conduits, close to the branch points (see figure 2(a)), is negligible compared with the volume of straight sections. Note that for $F = 1$ the right side of equation (13) reduces to $1 + q$, as we expect from equation (5) with $s = 1$.

Equation (13) is plotted in figure 3(a). Note that, over a wide range of λ values, the required pressure to raise sap to height h is reduced by a factor of A_N/A_0 which, as we have seen, increases with both F and N. Thus branching conduits with an initial radius r_0 perform better than do single pipes of the same radius. Given this result, it is natural to ask why F is not higher—this would result in a larger increase in terminal cross-sectional area A_N, and so would reduce the required pressure per unit height. The answer is that such a proliferation of conduits would require more xylem higher up the tree. The tree would become top-heavy and mechanically unstable. Thus, the furcation number adopted by trees is a trade-off between hydraulic efficiency and mechanical safety.

To determine how high capillary action can draw sap up a branching conduit, we replace PA_N in equation (10) with $2\pi r_N \gamma \cos\theta \cdot F^N$. This is the force acting on the sap in a single conduit of radius r_N, multiplied by the number of such conduits. Again we obtain an expression for the height to which sap is raised; there is an optimum radius, for which we obtain the maximum height:

$$h_{\max} = \frac{\gamma \cos\theta}{\sqrt{8\rho g \mu v_0}} F^{2N/3} \frac{1-\lambda^{N+1}}{1-\lambda} \sqrt{\frac{1-\lambda F^{1/3}}{1-(\lambda F^{1/3})^{N+1}} \frac{1-\lambda F^{2/3}}{1-(\lambda F^{2/3})^{N+1}}}. \qquad (15)$$

For $F = 1$ equation (15) reduces to equation (9), with $s = 1$, $q = 1$, as it should. Again, the optimum choice for conduit radius r_0 leads to maximum sap ascent speeds that are much lower than those observed in nature. The maximum speed occurs near the ground ($n = 0$); higher up, sap speed falls as $v_n = F^{-n/3} v_0$.

5. Summary and discussion

By considering the pipe model generalized to conical conduits, we can show that transpiration pull is optimized for a particular choice of conduit radius and ascent speed. For the common case of parallel-sided conduits, this optimization yields conduit radii that correlate well with observations. A branching conduit requires a lower pressure than does a single pipe to lift sap to a given height. If the force driving sap ascent is considered to be capillary action alone, then we find that the sap ascent speed is at least one order of magnitude lower than those observed in nature, for both conical and branching conduits. Our simple models show that hydraulic considerations limit the maximum height of trees. (This hydraulic limit hypothesis is discussed in more detail in [23, 24].)
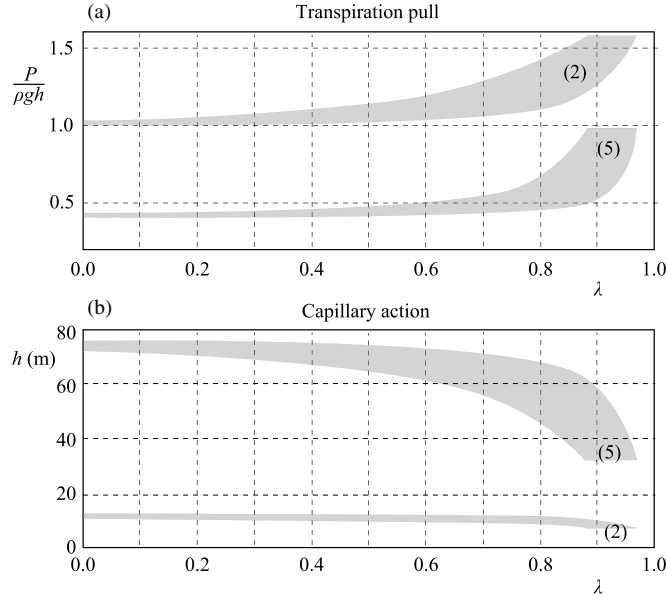
Figure 3. Branching conduits perform better than pipes. These plots are for the case $q = 1$. (a) If leaf pressure is supplied by transpiration pull, the shaded areas show the required value of $P/\rho gh$ versus branching parameter λ. The shaded areas are bounded by the curves for $(F, N) = (1.05, 43)$ and $(F, N) = (1.20, 11)$, both of which correspond to $A_N/A_0 = 2$, and by $(F, N) = (1.05, 99)$, $(F, N) = (1.20, 26)$, which correspond to $A_N/A_0 = 5$. Note that $P/\rho gh = 2$ for non-branching pipes (equation (8) with $s = 1$). (b) If capillary action is responsible for raising sap, then for $r_0 = 5\ \mu$m the maximum height is $h = 3$ m if the conduit does not branch; here are the maximum heights for a branching conduit. Again, we have adopted (F, N) values that yield $A_N/A_0 = 2$ and $A_N/A_0 = 5$.

Acknowledgment

Appendix

Here we demonstrate that a conduit furcation number of $F = 4/3$ accurately describes the configuration of conduits shown in figure 2(a). The Hagen–Poiseuille law tells us that the pressure difference due to viscous drag over the distance h_0 is given by

$$\Delta P = \frac{1}{3} Q z_0, \qquad z_0 \equiv \frac{8\mu h_0}{\pi r_0^4}. \tag{A.1}$$

(The radius of each of the three input pipes of figure 2(a) is the same, and so the flow Q divides equally between them.) At the output we write

$$\Delta P \equiv \tfrac{1}{4} Q z_1, \tag{A.2}$$

where Q is the sum of contributions from the four output pipes:

$$Q = 2\frac{\Delta P}{z} + 2\frac{\Delta P}{z'}. \tag{A.3}$$

From equations (A.1)–(A.3) we thus find that

$$1 = \frac{1}{2} z_1 \left(\frac{1}{z} + \frac{1}{z'} \right), \tag{A.4}$$

where

$$z_1 = \frac{8\mu h_1}{\pi r_1^4} = \lambda F^{4/3} z_0, \qquad z = \frac{8\mu h_1}{\pi r_0^4} = \lambda z_0, \qquad z' = \frac{8\mu h_1}{\pi (2^{-1/3} r_0)^4} = 2^{4/3} \lambda z_0. \quad (A.5)$$

Here we have applied Murray's law, which tells us that $r_1 = 2^{-1/3} r_0$. We also see that the hydraulic resistances of pipes in parallel add like electrical resistors in parallel. From equations (A.4) and (A.5) we have

$$F = \left(\frac{4}{2 + 2^{-1/3}} \right)^{3/4} = 1.31. \quad (A.6)$$

Thus, by considering the hydraulic resistance of the configuration of pipes we deduce an effective furcation number that is very close to the 4/3 value defined by the ratio of output to input pipes.

The mean radius of the output pipes is $\bar{r}_1 = \frac{1}{2} r_0 (1 + 2^{-1/3}) = 0.90 r_0$. The value obtained from the calculation of section 4 is $r_1 = F^{-1/3} r_0 = 0.91 r_0$ for $F = 4/3$. Again, the two values are close.

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