New
Phytologist

Research

Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water

Michael L. Roderick and Sandra L. Berry

Ecosystem Dynamics Group and C. R. C. for Greenhouse Accounting, Research School of Biological Sciences, Institute of Advanced Studies, The Australian National University, Canberra ACT 0200, Australia

Author for correspondence:
M. L. Roderick
Tel: +61 261254020
Fax: +61 261255095
Email: Michael.Roderick@anu.edu.au

Received: *4 September 2000*
Accepted: *9 October 2000*

Summary

- An hydraulic model of a tree stem is presented to help understand how the carbon storage in ecosystems varies with changing environmental conditions.
- The model is based on the assumption that a tree stem is a collection of parallel pipes and was used to (qualitatively) predict how the mass concentration of dry matter ([*D*]) would vary with water temperature (via changes in viscosity), nitrogen supply and atmospheric CO_2.
- There was qualitative agreement between model predictions and observed gross trends. The model predicted that the flow rate would be relatively insensitive to variations in [*D*] in angiosperm stems; this was consistent with observations. It is concluded that other factors need to be considered to explain variations in [*D*] in angiosperm wood. The flow rate of water through gynmosperm stems was predicted to be very sensitive to variations in [*D*] and the model explained why [*D*]; decreases with decreases in water temperature, decreases with increases in nitrogen supply and increases with elevated CO_2.
- The model captured some of the important underlying relations linking water transport with wood density and environment and qualitative testing of the model is recommended.

Key words: elevated CO_2, nitrogen fertilization, tree hydraulics, viscosity, water temperature, wood density.

Introduction

Through practical experience, foresters and wood scientists have found that the basic density ([*D*], kg m^{-3}) of woody stems, defined as the ratio of dry mass to fresh volume, is correlated with a number of important mechanical properties and commercial attributes of wood (Desch, 1973; Zobel & van Buijenen, 1989). [*D*] is also important from a biological perspective because it is correlated with growth rates (Roderick, 2000). We became interested in variations in [*D*] following attempts to develop a generic plant growth and associated carbon balance model. [*D*] is critical in the latter case because the total mass of carbon (C, kg) in a stem (or a plant) is given by:

$$C = C_d[D]\ V \qquad \text{Eqn 1}$$

(C_d, the mass fraction of carbon in the dry matter; V(m^3), the stem volume.) C_d is usually relatively constant (*c.* 0.4–0.5 according to Schlesinger, 1997). It follows that the mass concentration of carbon in a plant is largely determined by [*D*] which typically varies from 0.1 to 1 g cm^{-3}. Because of that relatively large range, estimates of the mass of carbon contained in terrestrial vegetation are very sensitive to variations in [*D*] (Fearnside, 1997). Thus, to understand how the amount of carbon stored in terrestrial vegetation might respond to changes in atmospheric CO_2 and/or climate, it is necessary to understand how [*D*] varies with those factors. To do that, three questions need to be addressed: why is [*D*] so important?; what factor/s control [*D*]? and; can [*D*] be predicted?

The answer to the first question posed in the previous paragraph is well known and can be attributed to the fact that the density of material in dry cell walls is more or less constant at *c.* 1.5 g cm^{-3} (Desch, 1973; Siau, 1984; Skaar, 1988). Consequently, the volumetric fraction of the matrix of cell wall material (which we hereafter call the structure) within a tree increases with [*D*], and the volumetric fraction of the remaining space must therefore decline. Schniewind (1962) used that relationship to show that as [*D*] increases, a tree stem could be potentially taller per unit volume but noted that increases in [*D*] would lead to a decline in the amount of space available for the hydraulic network (transport and storage) per unit stem volume. Some other lines of evidence also suggest that there is a direct link between [*D*] and the hydraulic function of stems. For example, laboratory observations show that the permeability of *Pinus radiata* stems is negatively correlated with [*D*] (Booker & Kininmonth, 1978) and foresters have long been aware that variations in [*D*] were related to physiological activity within tree canopies (Lindstrom, 1996).

The idea that there is some level of hydraulic integration between stems and leaves (and roots) is not new (Shinozaki *et al.*, 1964; Zimmerman & Brown, 1971; Jarvis, 1975; Whitehead *et al.*, 1984; Tyree & Ewers, 1991) but we not aware of any studies which have developed theoretical expressions linking [*D*] with the hydraulic properties of stems. Nevertheless, some of the most basic principles are well known. In terms of flow mechanisms, calculations by numerous authors (Levitt, 1969) have demonstrated that observed flow rates exceed those that are possible by passive diffusion. Consequently, bulk flow, which is a function of the composition and geometric arrangement of the flow path, viscosity of the liquid and a pressure gradient is generally assumed to occur. Further, the flow of water through the xylem would usually be laminar because of the relatively slow speeds and very small vessel diameters involved (Leyton, 1975). The classical explanation for the source of the pressure gradient is the cohesion theory which proposes that water is pulled through the stem as a consequence of transpiration occurring at the leaves. Alternative explanations have been proposed (Canny, 1995, 1998) but have not been widely accepted (Milburn, 1996; Tyree, 1997; Comstock, 1999; Stiller & Sperry, 1999). For the purposes of this paper the source of the pressure gradient is not crucial and we just assume that a pressure gradient sufficient for bulk flow to occur exists.

In the case of water, viscosity is the only physical property of the liquid state that is particularly sensitive to variations in temperature (Table 1). Experimental tests have shown that most of the variation in the flow rate of water through a plant segment due to varying water temperature could be explained by variations in viscosity in general agreement with theoretical expectations (Yamamoto, 1995). The temperature–viscosity relationship should permit a link to be made between climate and the flow rate of water through a tree because the temperature of water, and hence the viscosity of water, will vary with climate.

The aim of this paper is to develop a theoretical framework that links [*D*] with the hydraulic properties of tree stems. To do that, the flow rate is described using standard pipe flow equations that are modified to include the temperature dependence of the viscosity of water. Those expressions are then linked with [*D*] by developing a simple model of a tree stem which is used as the basis for estimating the total flow rate through a stem as a function of the flow rate through the individual pipes. It is not current practice to estimate [*D*] when measuring the flow rate through tree stems so it is not possible to quantitatively test the model using direct measurements from the literature. In addition, empirical studies usually report the hydraulic conductivity of stems instead of the permeability. The problem with hydraulic conductivity as a measure is that it is the ratio of permeability to viscosity (Leyton, 1975; Booker, 1977). Because the viscosity of water is sensitive to variations in temperature, it follows that reported measures of hydraulic conductivity must vary with water temperature and are very difficult to interpret. Consequently, the model is tested qualitatively (i.e. increase or decrease in [*D*]) against general trends that have been observed by foresters (Zobel & van Buijenen, 1989). The success, or otherwise, of the qualitative tests is used to decide whether it would be worthwhile to conduct quantitative testing of the model.

Table 1 Sensitivity of some physical properties of liquid water to variation in temperature. Data used in the calculations was from Slatyer (1967)

Property	$T = 0°C$	$T = 50°C$
Density	+0.3%	−0.9%
Surface tension	+1.5%	−5.6%
Viscosity	***+100.0%***	***−38.5%***
Heat of vaporization	+2.4%	−2.4%
Specific heat	+0.9%	+0.0%
Thermal conductivity	−8.0%	+5.5%

Sensitivity is calculated as $100(T_x - T_{25})/T_{25}\%$. T_x, value of the property at the indicated temperature; T_{25}, value at 25°C. Thus, the density of water is 0.3% higher at 0°C and 0.9% lower at 50°C than it is at 25°C.

Theory

Assumptions

As the basis of the model we make the following assumptions: that all of the dry matter is contained within the structural framework of a tree stem; a tree stem is a collection of rigid parallel pipes which occupy some of the space not occupied by the structural framework; and the flow rate through each pipe is described by the Hagen–Poisuelle law. (Throughout this paper, we call the xylem elements 'pipes', instead of more commonly accepted terms, vessels and tracheids, to remind readers of the basic assumption underlying the model.) The first assumption is a reasonable and widely used approximation because the cellular component is mostly water. However, the last two assumptions are more difficult to justify. In the case of the second assumption, the pipes cannot be entirely rigid because it is well known that the diameter of tree stems usually declines slightly during the day. We initially ignore those changes, but return to this issue in the discussion. In the case of the third assumption, the Hagen–Poisuelle law apparently over-estimates the flow rate through plant stems for a variety of reasons, for example obstructions along the flow path, lateral transport, cavitation and noncylindrical pipe cross-sections, amongst other factors (Zimmerman & Brown, 1971; Tyree & Ewers, 1991). However, as noted by Tyree & Ewers (1991), small errors in measuring the pipe radius can lead to large errors in the estimated flow rate so some of the disagreement could be due to measurement error. (Variability in pipe radius is also a major issue as will become apparent from our subsequent analysis.) The focus of this paper is on linking [*D*] with the potential to maintain a given flow rate. In that context, the actual flow rate will be proportional to the maximum flow rate which we assume is given by the Hagen–Poisuelle law.

Bulk flow

The laminar flow of liquid through a horizontal cylindrical pipe is given by the Hagen–Poisuelle law as:

$$q = \frac{\pi a^4 \Delta p_f}{8\eta l} \qquad \text{Eqn 2}$$

(q (m^3 s^{-1}), the flow rate; a (m), the pipe radius; Δp_f(N m^{-2}), the drop in pressure along the pipe segment due to friction; η (N s m^{-2}), the (dynamic) viscosity of the liquid; and l (m), the length of the pipe.) Note that in a pipe of fixed dimensions, Δp_f and η are the only factors that vary. Variations in η have not traditionally been considered in plant–water relations and for that reason are discussed briefly below.

The ratio of the viscosity of a solution (η) to that of the solvent (η_o) is known as the relative viscosity (η_{rel}). For the simplest possible case of noninteracting spherical molecules, where the solute molecules are large compared with the solvent molecules, Einstein showed that:

$$\eta_{rel} = 1 + \frac{5}{2}\phi \qquad \text{Eqn 3}$$

(ϕ, the volumetric fraction of solute molecules in the solution.) Analytical expressions for more general cases have not yet been developed. In those cases, for example when the solute and solvent molecules are roughly the same size and/or interact chemically/electrically, η_{rel} can be estimated as a function of solute concentration using empirical relationships. In general, η_{rel} usually, but not always, increases with solute concentration (Partington, 1951; Leyton, 1975; Atkins, 1994). The solution within the xylem of plants is usually dilute (Zimmerman & Brown, 1971) and calculations using the empirical relationship given by Leyton (1975) show that η_{rel} of the solution in the xylem would usually be close to unity.

The viscosity of liquid water varies with pressure at high pressures (> 200 atmospheres), but for pressures < *c*. 200 atmospheres it is more or less independent of pressure (Eisenberg & Kauzmann, 1969). The temperature (T) dependence of η for liquid water is shown in Fig. 1. A number of different relationships, for example Arrhenius type expressions or various other logarithmic or polynomial functions, have been proposed to describe that relationship (Partington, 1951). Over the complete range of temperature in which water is usually a liquid (273–373 K), a logarithmic equation (Fig. 1) can be used to represent the relationship. A more convenient relationship for the purpose of this analysis, derived for a T range of 273–323 K, is (Fig. 1):

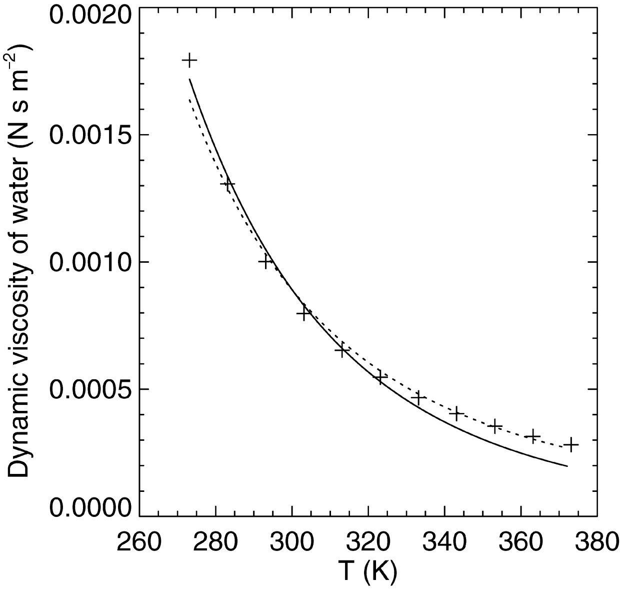

Fig. 1 Temperature–viscosity relationship for liquid water at atmospheric pressure. Data (+, $n = 11$) per Lide (1998). Equations fitted to those data are; $\ln\eta = 1856/T - 13.2$ is the dotted line and is fitted for T from 273 to 373 K ($n = 11$, $R^2 = 0.99$); $\eta = 1.95 \times 10^{14}\,T^7$ is the full line and is fitted to T from 273 to 323 K ($n = 6$, $R^2 = 0.99$). (Note: for the latter relation a least squares analysis gave the exponent as 6.96 instead of 7. We assumed 7 as the error involved is minor and then estimated the parameter, for example 1.95×10^{14}, using ordinary least squares).

$$\eta = \frac{1.95 \times 10^{14}}{T_w^7} \qquad \text{Eqn 4}$$

(T_w, the temperature of liquid water in K; η, in N s m^{-2}). Eqn 4 is accurate to better than 5% over the indicated range in T_w. Combining Eqns 2–4 gives:

$$q = 2.01 \times 10^{-15} a^4 \frac{\Delta p_f}{l} \frac{T_w^7}{\eta_{rel}} \qquad \text{Eqn 5}$$

for the (laminar) flow rate of an aqueous solution through a horizontal cylindrical pipe when SI units are used.

Segmenting woody stems

To simplify subsequent analysis, we briefly describe some of the basic principles of wood–water relations, as these are not usually discussed outside the wood science literature. The

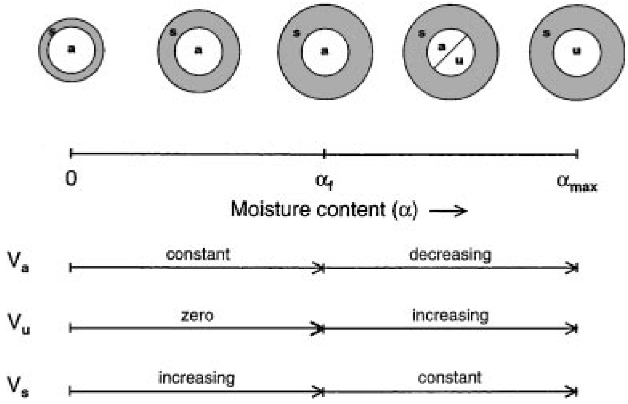

Fig. 2 Schema showing changes in the volumetric fraction of air space (*a*), solution (*u*) and structure (*s*) in a tree stem as a function of moisture content (*α*). α_f is the fibre saturation point. Note that $V_a + V_u$ is constant over the entire range and that swelling of the stem means that V_s increases with α for $\alpha < \alpha_f$.

following summary is derived from Siau (1984) and Skaar (1988).

When dry, the density of cell wall material is more or less constant at *c.* 1.5 g cm^{-3} although the composition (e.g. cellulose, hemi-cellulose, lignin, etc.) can, and does, vary. When exposed to water, wood behaves like a 'gel' and swells. That swelling may be anisotropic and can generate substantial pressures (*c.* 900 atmospheres). An important concept in wood science is the 'Fibre Saturation Point', denoted α_f (note that α is ratio of the mass of water to mass of dry matter, also see Appendix B). α_f was originally defined in 1906 by H. D. Tiemann as '… the moisture content at which the cell cavities contained no water, but the cells walls were fully saturated with water.' (Skaar, 1988). In practice, α_f is hard to measure. Nevertheless, the basic concept is of fundamental importance because many of the physical and chemical properties of wood change abruptly at α_f. For example, wood becomes stronger when $\alpha < \alpha_f$. Surprisingly, when wood swells the total volume of cavities apparently remains relatively constant. The relationships are summarized in Fig. 2 by separating the stem into three spatial components, air space (*a*), solution (*u*) and structure (*s*) after the *a-u-s-V* scheme (Roderick *et al.*, 1999).

From Fig. 2, the total volume (V, m^3) of a stem or stem segment is:

$$V = V_a + V_u + V_s \qquad \text{Eqn 6a}$$

The sum of the gaseous (V_a) and liquid (V_u) spaces within the stem represent the maximum available space which is available for the hydraulic network. From that, it is relatively easy to show (see Appendix B) that to a very good approximation, the volumetric fraction of a stem which is potentially available for the hydraulic network is:

$$\frac{V_a + V_u}{V} = 1 - 0.97[D] \approx 1 - [D] \qquad \text{Eqn 6b}$$

($[D]$, given in units of g cm^{-3}.) Eqn 6b is used to calculate the total flow through stems of varying $[D]$ in the following section.

Linking the stem and flow models

To calculate the flow through a stem we need to sum the flow through individual pipes of varying radius. For that purpose, we assume that in the stem segment of interest, all the pipes are capable of conducting solution. That is rarely the case in a real stem, but for the purpose of this paper there is no loss of generality in that assumption because the final expression (Eqn 15) is reduced to a proportionality. Thus, we assume that the stem segment of interest has a total cross-sectional area A (m^2) and length l (m) and contains N_p straight pipes having total cross-sectional area $\sum A_p$ (m^2) and total volume $\sum V_p$ (m^3). From those assumptions, the total volume of the stem segment is given by:

$$V = lA \qquad \text{Eqn 7a}$$

and the total volume of pipes is:

$$\sum V_p = l \sum A_p \qquad \text{Eqn 7b}$$

which is also given by:

$$\sum V_p = F_p(V_a + V_u) \qquad \text{Eqn 8}$$

(F_p, the volumetric fraction of the available space ($V_a + V_u$) which is occupied by the pipes.) It follows that:

$$\frac{\sum V_p}{V} = F_p \frac{(V_a + V_u)}{V} = \frac{\sum A_p}{A} \qquad \text{Eqn 9a}$$

and substituting from Eqn 6b gives:

$$\sum A_p \approx AF_p(1 - [D]) \qquad \text{Eqn 9b}$$

By definition, $\sum A_p$ is also given by:

$$\sum A_p = \overline{A_p} N_p \qquad \text{Eqn 9c}$$

from which it follows that the mean area of the pipes, $\overline{A_p}$, is:

$$\overline{A_p} \approx \frac{AF_p(1 - [D])}{N_p} \qquad \text{Eqn 9d}$$

Eqn 9d is used below to derive an expression for the flow through the stem.

From Eqn 5, the flow rate through a given pipe (q_i) of radius a_i is:

$$q_i = Ba_i^4 \qquad \text{Eqn 10a}$$

where:

$$B = 2.01 \times 10^{-15} \frac{\Delta p_f}{l} \frac{T_w^7}{\eta_{rel}} \qquad \text{Eqn 10b}$$

which is assumed to be the same for each pipe. (This is not necessarily the case in a real stem and this assumption could be relaxed in future developments of this approach.) For a given pipe:

$$a_i^4 = \frac{A_{p,I}^2}{\pi^2} \qquad \text{Eqn 11}$$

($A_{p,i}$, the area of an individual pipe.) Substitution of that relation into Eqn 10a, and summing over all pipes in the stem gives the total flow rate through the pipes (q_p) as:

$$q_p = \frac{B}{\pi^2} \sum_{I=1}^{N_p} A_{p,i}^2 \qquad \text{Eqn 12a}$$

The sum of the squares (Eqn 12a) is equal to $N_p \overline{A_p^2}$, so Eqn 12a becomes:

$$q_p = \frac{B}{\pi^2} N_p \overline{A_p^2} \qquad \text{Eqn 12b}$$

($\overline{A_p^2}$, the mean square pipe radius.) By definition we have (see any statistics text):

$$\overline{A_p^2} = (\overline{A_p})^2 + \sigma_A^2 \qquad \text{Eqn 13a}$$

(σ_A, the standard deviation of the cross-sectional area of the individual pipes.) The coefficient of variation (ε) of the pipe cross-sectional area is defined as:

$$\varepsilon = \frac{\sigma_A}{\overline{A_p}} \qquad \text{Eqn 13b}$$

Combining Eqns 12b and 13a,b gives:

$$q_p = \frac{B}{\pi^2} N_p (\overline{A_p})^2 (1 + \varepsilon^2) \qquad \text{Eqn 13c}$$

Combining Eqns 9d, 10b and 13c gives the total flow rate as:

$$q_p \approx (2.04 \times 10^{-16}) \left(\frac{\Delta p_f T_w^7}{\eta_{rel}} \right) \left(\frac{A^2}{l} \right) ((1 - [D])^2) \left(\frac{F_p^2}{N_p} \right) (1 + \varepsilon^2) \qquad \text{Eqn 14}$$

($[D]$, in g cm^{-3}; all other nonfractional quantities are given in SI units and the approximation arises from Eqn 9d.) Eqn 14 is for the maximum flow rate, so it is more appropriate, based on the earlier discussion, to reduce it to a proportionality. Thus, dividing both sides of Eqn 14 by the volume of the stem segment ($V = lA$) we have:

$$\frac{q_p}{V} \approx \propto \left(\frac{\Delta p_f T_w^7}{\eta_{rel}} \right) \left(\frac{A}{l^2} \right) ((1 - [D])^2) \left(\frac{F_p^2}{N_p} \right) (1 + \varepsilon^2) \qquad \text{Eqn 15}$$

for the flow rate through a stem segment of unit volume. Predictions derived from Eqn 15 are tested below.

Application of the theory

Assessment of the model terms

Of the five bracketed terms in Eqn 15, the latter four describe the overall morphology of the stem, the available space within the stem and the internal subdivision of that space into pipes of various diameters. Those variables usually change slowly (if diurnal changes in stem diameter are ignored) and can be called 'growth' terms. By contrast, the first bracketed term contains variables which can potentially change rapidly. In this section, the significance of various terms in Eqn 15 are assessed.

The pressure gradient For the first term in Eqn 15, if we assume that η_{rel} is unity, it follows that the product, $\Delta p_f T_w^7$ must change over diurnal cycles because the flow rate through a stem usually changes over a diurnal cycle. Because the T of water would also presumably increase during daylight hours, it is difficult to independently estimate Δp_f. One way to do that is to use models which describe the pressure drop in flowing liquids. These models are based on a combination of mechanical (equations of motion and conditions of continuity) and thermodynamic (conservation of energy) considerations (Bird *et al.*, 1960). If the possibility of chemical reactions is ignored, and the fluid is assumed to be more or less incompressible, then these equations reduce to the well known Bernoulli's theorem. Here we used a modified form of that theorem to account for frictional losses (Widden, 1996):

$$p_1 + \tfrac{1}{2}\rho u_1^2 + \rho g z_1 = p_2 + \tfrac{1}{2}\rho u_2^2 + \rho g (z_1 + l\cos\theta) + \Delta p_f \qquad \text{Eqn 16}$$

(p (N m^{-2}), the pressure; ρ (kg m^{-3}), the density of the liquid; u (m s^{-1}), the average speed in the direction of flow; g (m s^{-2}), the gravitational acceleration; z (m), the height; l (m), the pipe length; θ, the zenith angle (i.e. angle from the vertical) of the pipe (where $z_2 = z_1 + l\cos\theta$); Δp_f (N m^{-2}), pressure loss due to friction (the same quantity as in Eqns 2, 5 and 15) and the subscripts denote the start (1) and end (2) of the pipe.) (Note that the total pressure drop ($\Delta p = p_1 - p_2$) in the pipe is not the same quantity as the pressure drop due to friction (Δp_f) in the pipe.)

Estimates of u and a (pipe radius) are needed to estimate q ($= u\pi a^2$), which can then be substituted into Eqn 2 to estimate Δp_f per unit length assuming laminar flow. However, accurate estimates of u are difficult to make because the speed changes in a parabolic manner across the pipe cross-section (Zimmerman & Brown, 1971; Zimmerman, 1983). In addition, many estimates of u are made using the so-called heat-pulse technique. The application of heat to a stem would increase the water T, and hence decrease the viscosity, which would usually lead to an increased speed in the centre of the pipe and an increased flow rate. Because of that, many published estimates of u are likely to be larger than the actual values. Consequently,

Table 2 Estimates of the maximum pressure gradient due to friction ($\Delta p_f / l^{-1}$) and the Reynolds number (*Re* = 2apu/n) in a single xylem vessel or tracheid of tree species having fast (Oak) and slow (Conifer) flow speeds. The data on pipe radius (*a*) and maximum speed of flow (u_{max}) are from Zimmerman (1983)

	a (m)	u_{max} (m s^{-1})	q_{max} (m^3 s^{-1})	$\Delta p_f \, l^{-1}$ (Pa m^{-1})	*Re*
Oak	130×10^{-6}	1.4×10^{-2}	7.4×10^{-10}	6600	*c.* 4
Conifer	20×10^{-6}	2.8×10^{-4}	3.5×10^{-13}	5600	*c.* 0.01

q_{max} ($= u_{max}\Pi a^2$), estimated max flow rate which is substituted into Eqn 2 to yield the estimate of $\Delta p_f / l^{-1}$. For the calculations, η was set at 1×10^{-3} N s m^{-2} (i.e. *T c.* 293 K). Note that $\Delta p_f / l^{-1}$ will vary with η, and is therefore sensitive to the assumed value of *T*. *Re* is a dimensionless ratio that measures the importance of inertial forces relative to viscous (i.e. frictional) forces. When $Re < 2000$ the flow is dominated by viscous forces and is usually laminar while if $Re > 2000$ the flow is usually turbulent. The computed values of *Re* are very small by conventional engineering standards because of the slow speeds and very small pipe radii, and highlight the dominance of viscous forces in determining the flow rate through the xylem of trees. (We also estimated $\Delta p_f / l^{-1}$ and *Re* using data for trees from a variety of other sources and found values of a similar order of magnitude to those shown in the table.)

the estimates of Δp_f per unit length calculated using the above technique would most likely exceed the actual values.

With the above problems in mind, observations show that the maximum average flow velocity often increases in tree stems which have wider pipes (Zimmerman & Brown, 1971; Zimmerman, 1983). Consequently, the maximum value of Δp_f per unit length appears to be relatively conservative (Table 2). For the typical average flow velocity in the xylem of trees of *c.* 0.1–50 m h^{-1} (Zimmerman (1983), the kinetic component of Eqn 16 ($\frac{1}{2}\rho u^2$) is minor and can be ignored. (Note that this approximation would not hold for herbaceous plants given the much larger flow speeds noted by Zimmerman (1983).) If the stem is vertical, the hydrostatic gradient (*c.* 0.01 MPa m^{-1}) must be added to the frictional gradient to yield a typical pressure gradient in a vertical stem of between *c.* 0.01 MPa m^{-1} if the liquid is stationary, up to *c.* 0.016 MPa m^{-1} at maximum flow rates, which as previously noted is likely to be larger than the actual pressure drop. Those estimates are generally consistent with measurements showing that the pressure gradient in the xylem of trees is often reasonably close to the hydrostatic gradient (Zimmerman, 1983). (Canny (1995, 1998) has noted examples where the pressure gradients were apparently less than the hydrostatic gradient. In the above analysis, continuity of the liquid is assumed and where that is the case, the pressure gradient is very unlikely to be less than the hydrostatic gradient for the typical flow speeds involved. However, if embolisms occurred, which appears to be a common occurrence (McCully *et al.*, 1998), then the liquid phase would not be continuous. In that situation, one can imagine there could be pipes containing segments of liquid which are separated by gaseous spaces along the xylem, and the pressure gradient would almost certainly be less than hydrostatic gradient. That may explain those observations. Note that slippage along the direction of flow at the pipe wall, if it occurred, would also reduce the pressure gradient.)

The above analysis suggests that pressure gradients in the xylem of trees may be relatively conservative. A conservative pressure gradient would result from the assumption that the vascular system has evolved in a way which minimizes the resistance to flow (West *et al.*, 1997, 1999). For the purpose of this analysis, we are primarily interested in linking the hydraulic properties of stems with observed variations in [*D*]. To do that, we assume, based on the above analysis, that the pressure gradient is relatively conservative, and focus on the interaction between stem morphology, geometry of the flow path and water *T* in subsequent analysis.

Variability in pipe geometry The range of possible values of most of the morphological variables in Eqn 15 is self-evident. Exceptions are F_p (fraction of the available space within the stem which is occupied by pipes) and ε (coefficient of variation of cross-sectional area of the pipes) and in this section we estimate the likely range in F_p and ε.

Inspection of anatomical cross-sections of the wood from a variety of species (Miles, 1978) suggests that F_p would typically be within the range of 0.5–0.9, but for most wood it would be *c.* 0.6–0.8 (see examples in Table 3). By contrast, there are substantial variations in ε. In general, wood from angiosperms (Carlquist, 1988) is composed of relatively few large vessels and more numerous tracheids having smaller radii. Thus, for angiosperms, the frequency distributions of pipe cross-sectional area are markedly bimodal, and ε is generally large. Estimates of ε are listed in Table 3 for two angiosperm species, which represent typical small and large values of ε. We have no doubt that there are smaller and larger values of ε. However, what interests us here is the typical range, rather than establishing the extreme values of that range. Based on the estimates of ε in Table 3, it follows that for angiosperm species, the ($1 + \varepsilon^2$) term in Eqn 15 would at least vary over a typical range from 5 to 200. By contrast, [*D*] typically varies from 0.1 to 1 g cm^{-3}, so the ($1 - [D])^2$ would vary from near zero to unity. Consequently, for angiosperms, variation in the ($1 + \varepsilon^2$) term will be much greater than the ($1 - [D])^2$ term, and the flow rate through the stems of angiosperms should be relatively insensitive to variations in [*D*].

A very different situation emerges for wood in gymnosperm species. That wood is typically relatively uniform, and most of the variation in pipe cross-sectional area is due to changes in the proportion of the so-called latewood, which has pipes of smaller radius and hence smaller pipe cross-sectional area, within a single growth ring. We estimated ε from photographs of the wood from numerous gymnosperm species (Miles, 1978), and found that it is very conservative at *c.* 0.4–0.6. Some examples are listed in Table 3. Based on that finding, we

Table 3 Estimates of the variability in pipe cross-sectional area within woody stems. The estimates are derived from photomicrographs (Miles, 1978) where Ref. gives the page number in that reference. Thus, the estimates of A_{min}, A_{max}, $\overline{A_p}$ and σ_A are specific to the particular photomicrographs, but the estimates of ε and F_p are generally applicable

Species	Ref.	A_{min}–A_{max} (x 10^{-12} m^2)	$\overline{A_p}$ (x 10^{-12} m^2)	σ_A (x 10^{-12} m^2)	ε	ε^2	F_p (x 10^{-12} m^2)
Gymnosperms							
Abies alba	p. 207	50–1500	500	300	*c.* 0.6	*c.* 0.4	*c.* 0.8
Juniperus procera	p. 216	150–2500	1000	500	*c.* 0.5	*c.* 0.3	*c.* 0.8
Picea abies	p. 218	10–1800	800	350	*c.* 0.4	*c.* 0.2	*c.* 0.9
Angiosperms							
Eucalyptus pilularis	p. 157	10–60000	150	2000	*c.* 13.3	*c.* 188	*c.* 0.6
Sorbus aucuparia	p. 171	10–5000	250	550	*c.* 2.2	*c.* 5	*c.* 0.6

Table 4 General trends in mass concentration of dry matter ([*D*]) as a function of water temperature and nitrogen fertilization as summarized by Zobel & van Buijenen (1989). The page numbers noted in the table are those in the citation on which general summaries can be found

Factor	Gymnosperms	Angiosperms
Water temperature[1]	As elevation increases, [*D*] and tracheid length decline (pp. 46–47) As latitude increases, [*D*] and tracheid length decline (pp. 46–47)	Sometimes similar to trends for gymnosperms, but no general trend emerges (pp. 46–47)
Nitrogen (N) fertilization[2]	Substantial decrease in [*D*] following application of N. After 5–10 yr, [*D*] returns to value it would have had if no fertilizer had been applied. In some instances, [*D*] does not respond to N fertilization (pp. 227–228)	Sometimes similar to trends for gymnosperms, but no general trend emerges. Very divergent results for species with diffuse-porous wood (pp. 229–230)

[1] We have assumed that the trends along elevation and latitude gradients are correlated with water temperature (see main text). [2] Zobel & van Buijenen (1989) noted that on some occasions, other minerals can have effects on [*D*], but nitrogen fertilization has the major effect.

conclude that for gymnosperms, variation in the $(1 + \varepsilon^2)$ term will be minor and will not have a major influence on the flow rate. Because F_p and ε are both less than one and are roughly the same magnitude, it follows that $F_p^2(1 + \varepsilon^2)$ can be crudely approximated as F_p. Thus, for gymnosperms, Eqn 15 becomes:

$$\frac{q_p}{V}\,(gymnosperms) \approx \propto \left(\frac{\Delta p_f T_w^7}{\eta_{rel}}\right)\left(\frac{A}{l^2}\right)((1-[D])^2)\left(\frac{F_p}{N_p}\right) \qquad \text{Eqn 17}$$

In summary, the flow rate per unit stem volume through gymnosperm species can be approximated using Eqn 17, and should be sensitive to differences in [*D*]. For angiosperm species, $(1 + \varepsilon^2)$ will be much larger than $(1 - [D])^2$, and the flow rate should be relatively insensitive to variations in [*D*].

Model predictions

Observed trends in [*D*] Zobel & van Buijenen (1989) have conducted an extremely thorough review of the relation between [*D*] and various environmental factors and we have summarized the most important trends of relevance to the current study in Table 4. However, we emphasize that the original source material contains much more detailed information about trends in [*D*] than we can reproduce here.

The lack of any clear trend between either water *T* or N fertilization and [*D*] in angiosperms (Table 4) is consistent with our previous conclusion that the flow rate would be relatively insensitive to variations in [*D*] in angiosperms. For that reason, we focus on predicting the response in gymnosperms in subsequent analysis.

Predicted relation between [*D*] and environmental temperature The *T* of water flowing through a plant is determined by a number of factors. For example, the water *T* would depend on the time of the year and the depth from which it was extracted from the soil (Monteith & Unsworth, 1990), metabolic activity within the stem which will generate heat, as well as the *T* and thermal conductivity of materials in the surroundings. Despite the many complexities, the water *T* will generally be lower in cold climates and should decline with increasing latitude (as a consequence of decreased solar radiation) and elevation (as

Table 5 Summary of studies investigating the effect of increasing [CO_2] on mass concentration of dry matter ([*D*]). This is an update of Table 1 in Telewski *et al*. (1999)

Species	Change	Reference
Gymnosperms		
Pinus taeda	0	Rogers *et al*. (1983)
	0	Telewski & Strain (1987, 1994)
	+	Doyle (1987)
	0	Telewski *et al*. (1999)
Pinus radiata	+	Conroy *et al*. (1990)
Picea abies	+	Hättenschwiler *et al*. (1996)
Angiosperms		
Liquidambar	+	Rogers *et al*. (1983)
styraciflua	0	Telewski & Strain (1987)
	+	Doyle (1987)
Quercus alba	0	Norby *et al*. (1995)

Changes are coded as; 0, no change in [*D*]; +, increase in [*D*].

a consequence of the earth's gravitational field). Consequently, the trends observed along elevation and latitudinal gradients (Table 4) would be correlated with water *T* and show that [*D*] generally declines as water *T* declines in gymnosperms.

For gymnosperms, Eqn 17 predicts that the flow rate per unit stem volume can be maintained as water *T* declines by decreasing [*D*], N_p and/or *l*, and/or increasing *A* and/or F_p. Therefore, for gymnosperm species, [*D*] should decline with environmental temperatures. That prediction is consistent with observations (Table 4).

Predicted change in [*D*] with changes in nitrogen and carbon dioxide supply When the availability of nitrogen (N) increases, the surface area : volume ratio of leaves usually increases and the rates of photosynthesis and transpiration per unit leaf volume should increase (Roderick *et al.*, 2000). Thus, for a fixed leaf volume the flow rate through the stem would have to increase and in a constant thermal regime, it follows from our previous analysis (for gymnosperms) that [*D*] should decrease. The observed trends (Table 4) indicate that [*D*] either declines or remains constant in response to increasing N fertilization (Table 4). Thus, when a response occurs, it is in the predicted direction.

The observed trends linking [*D*] with water *T* and N fertilization (Table 4) have been derived from numerous observations in a wide variety of climates over many years. By contrast, there are only a few empirical studies which have assessed the effect of elevated [CO_2] on [*D*]. Despite that, it is important to consider the effect of atmospheric [CO_2] because it is currently increasing. To that purpose, as atmospheric [CO_2] increases the amount of water transpired by a leaf per unit CO_2 fixed generally decreases (Drake *et al.*, 1997). Assuming a fixed leaf volume and surface area and a constant thermal regime, the flow rate through the stem should decrease and [*D*] should increase. The available data (Table 5), show that [*D*] either increases or remains constant in response to increasing [CO_2]. Thus, once more, when a response occurs, it is in the predicted direction.

Comment on the predictions The above analysis assumed that a plant could freely adjust and that all other things were constant. However, it may be the case that an individual plant already had the lowest (or highest) [*D*] which is genetically possible and therefore a further reduction (or increase) in [*D*] would be unlikely. Therefore, the response would be context dependent. It must also be remembered that all other things are unlikely to be constant. For example, the leaf volume, leaf surface area or thermal regime may not be constant. Similarly, the morphology of plants can also change in response to changed conditions. For example, changes in the distribution of leaves within a canopy have been noted with changes in the supply of nitrogen (Fahey *et al.*, 1998) and CO_2 (Reekie & Bazzaz, 1989; Hättenschwiler *et al.*, 1997). Despite these qualifications, the qualitative agreement between the predictions and observations is encouraging.

Discussion

Assessment of the model

In general, the predictions derived from the model agreed in a qualitative manner with the gross trends that have been observed. For example, the model predicted that the flow rate would be relatively insensitive to variations in [*D*] in angiosperms which was consistent with observations. Similarly, the model predicted that the flow rate would be sensitive to variations in [*D*] in gymnosperms. In qualitative tests for gymnosperms, the model predicted the correct direction of change in [*D*] as a function of changes in water temperature, nitrogen availability and elevated [CO_2]. On that basis, we conclude that the model captures at least some of the important underlying relationships and the above-noted agreement is sufficient to justify quantitative testing of the model (see later for angiosperms).

As well as testing the description of flow, some other factors that need to be considered are as follows.

- The changes in [*D*] with position within the stem (Zobel & van Buijenen, 1989) and their interrelationship with stem taper. In that latter case, it seems likely that stem taper should be related to the pressure drop due to friction along the flow path (West *et al.*, 1997, 1999).
- The generation of heat by metabolic activity in the cells adjacent to the xylem because it would alter the temperature, and hence the viscosity, of the solution.
- The formation of embolisms and their effect on stem permeability (Booker, 1977; Booker & Kininmonth, 1978; Tyree & Sperry, 1989).
- The motion of the structure (i.e. wood) is also likely to be very important. In particular, because water is more or less incompressible, but much less viscous than the structure, it follows that any motion of the structure would usually result in motion

of the solution, and the amount of swelling and shrinkage in wood largely depends on [*D*] (Fig. C2 in Appendix C). To incorporate this in future work, Eqn B6b (Appendix B) in our analysis will need to be examined in some detail to develop an accurate relation between the volume of a water–cell wall mixture and the relative proportions of the components (Siau, 1984).

As well as testing the model using flow measurements, the theoretical framework can also be tested using experimental approaches. For example, the model would predict that growing trees in water (or soil) of different temperatures should lead to differences in the geometry of the vascular system. Field observations partly confirm that this does occur. For example, in gymnosperms there is a larger volume fraction of pipes in early wood (i.e. lower [*D*]) compared with late-wood. The model would predict this trend because early wood is formed in spring when the soil water is cool, but late-wood is formed in autumn when the soil water is warmer. It should be relatively simple to design experiments to test these and other predictions derived from the model.

Angiosperms

Observations show that there is not a strong link between [*D*] and environmental conditions in angiosperms. Our model also predicted this trend, but even if our model is wrong, the observations still stand. Consequently, other factors will have to be considered to understand how and why [*D*] varies spatially and temporally in forests dominated by angiosperms.

One possible approach which may be useful in forest environments is to assume that [*D*] is related to competition for light. For example, Wiemann & Williamson (1989) noted that early successional species often have a low [*D*]. That makes sense because a low [*D*] would usually imply a fast growth rate (Roderick, 2000). Thus, as succession proceeds at a site, the increased competition for light would mean that trees which can be taller per unit stem volume (i.e. those with a higher [*D*] (Schniewind, 1962)), would gradually replace the more squat profiles. That would lead to interesting dynamics, because while trees with a high [*D*] may be potentially taller per unit volume, they are not necessarily taller (Thomas, 1996) (Fig. 3). Whilst speculative, the above approach may be worth further investigation.

Epilogue

In many areas of the biological sciences, variations in viscosity are rarely considered when trying to understand the temperature sensitivity of many processes. However, many important properties of solutions are known to depend on solvent viscosity. For example, Einstein (1956) showed how the rate of diffusion of solutes through a solution was (approximately) inversely proportional to solvent viscosity, which was in turn linked with the osmotic pressure in the solution. In a similar manner, physical chemists have long been aware that the rate of many chemical reactions must somehow depend on the viscosity of the solvent (Barrow, 1973; Swiss & Firestone, 1999), particularly in diffusion-controlled reactions (Atkins, 1994). A general theory has not yet been developed to accurately describe that relationship. Nevertheless, as pointed out by Thornley & Johnson (1990), the temperature dependence of the rate of many biochemical reactions is of a similar magnitude to the temperature dependence of the viscosity of water. Presumably, that is not a coincidence. However, the significance of viscosity in understanding the temperature dependence which has been observed in many biological processes has not always been neglected:

> *… Van't Hoff suggested a viscosity-correction for the temperature-coefficient even of an ordinary chemical reaction; the viscosity of protoplasm varies in a marked degree, inversely with temperature, and the viscosity-factor goes, perhaps, a long way to account for the aberrations of the temperature-coefficient. It has even been suggested (by Belehradek) that the temperature-coefficients of the biologist are merely those of protoplasmic viscosity. For instance, the temperature-coefficients of mitotic cell-division have been shewn to alter from one phase to another of the mitotic process, being much greater at the start than the end; and so, precisely, has it been shewn that protoplasmic viscosity is high at the beginning and low at the end of the mitotic process.* (Thompson, 1942).

Acknowledgements

We thank Dr R. J. Norby and three anonymous reviewers for helpful comments on earlier versions of this manuscript. We also thank Dr Phil Evans of the Forestry Department at The Australian National University for pointing out to us some trends linking wood density with growth and environment which are apparently common knowledge amongst wood scientists. Those relationships are best described as very uncommon knowledge outside the wood science discipline.

References

Atkins PW. 1994. *Physical chemistry, 5th edn.* New York, USA: W. H. Freeman.

Barrow GM. 1973. *Physical chemistry, 3rd edn.* Tokyo, Japan: McGraw-Hill Kogakusha.

Bird RB, Stewart WE, Lightfoot EN. 1960. *Transport phenomena.* New York, USA: John Wiley and Sons.

Booker RE. 1977. Problems in the measurement of longitudinal sapwood permeability and hydraulic conductivity. *New Zealand Journal of Forest Science* 7: 297–306.

Booker RE, Kininmonth JA. 1978. Variation in longitudinal permeability of green radiata pine wood. *New Zealand Journal of Forest Science* **8**: 295–308.

Canny MJ. 1995. A new theory for the ascent of sap – cohesion supported by tissue pressure. *Annals of Botany* 75: 343–357.

Canny MJ. 1998. Applications of the compensating pressure theory of water transport. *American Journal of Botany* **85**: 897–909.

Carlquist S. 1988. *Comparative wood anatomy.* Berlin, Germany: Springer Verlag.

Comstock JP. 1999. Why Canny's theory doesn't hold water. *American Journal of Botany* **86**: 1077–1081.

Conroy JP, Milham PJ, Mazur M, Barlow EWR. 1990. Growth, dry weight partitioning and wood properties of *Pinus radiata* D. Don after 2 years of CO_2 enrichment. *Plant, Cell & Environment* **13**: 329–337.

Desch HE. 1973. *Timber: its structure and properties, 5th edn.* London, UK: The Macmillan Press.

Doyle TW. 1987. Seedling response to CO_2 enrichment under stressed and non-stressed conditions. In: Jacoby GC Jr, Hornbeck JW, eds. *Proceedings of the international symposium on ecological aspects of tree ring analysis.* National Technical Information Service, 501–506.

Drake BG, Gonzalez-Meler MA, Long SP. 1997. More efficient plants: a consequence of rising atmospheric CO_2. *Annual Review of Plant Physiology and Plant Molecular Biology* **48**: 609–639.

Einstein A. 1956. *Investigations on the theory of the brownian movement.* New York, USA: Dover Publications.

Eisenberg D, Kauzmann W. 1969. *The structure and properties of liquid water.* Oxford, UK: Clarendon Press.

Fahey TJ, Battles JJ, Wilson GF. 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs* **68**: 183–212.

Fearnside PM. 1997. Wood density for estimating forest biomass in Brazilian amazonia. *Forest Ecology and Management* **90**: 59–87.

Hättenschwiler S, Miglietta F, Raschi A, Körner C. 1997. Morphological adjustments of mature *Quercus ilex* trees to elevated CO_2. *Acta Ecologica* **18**: 361–365.

Hättenschwiler S, Schweingruber FH, Körner C. 1996. Tree ring responses to elevated [CO_2] and increased N deposition in *Picea abies. Plant, Cell & Environment* **19**: 1369–1378.

Jarvis PG. 1975. Water transfer in plants. In: De Vries DA, Afgan NH, eds. *Heat and mass transfer in the atmosphere.* New York, USA: John Wiley and Sons, 369–394.

Levitt J. 1969. *Introduction to plant physiology.* Saint Louis, MO, USA: The C.V. Mosby Co.

Leyton L. 1975. *Fluid behaviour in biological systems.* Oxford, UK: Clarendon Press.

Lindstrom H. 1996. Basic density in norway spruce 1. A literature review. *Wood and Fiber Science* **28**: 15–27.

McCully ME, Huang CX, Ling LEC. 1998. Daily embolism and refilling of xylem vessels in the roots of field-grown maize. *New Phytologist* **138**: 327–342.

Milburn JA. 1996. Sap ascent in vascular plants: challengers to the cohesion theory ignore the significance of immature xylem and the recycling of munch water. *Annals of Botany* **78**: 399–407.

Miles A. 1978. *Photomicrographs of world woods.* London, UK: HMSO.

Monteith JL, Unsworth M. 1990. *Principles of environmental physics, 2nd edn.* London, UK: Edward Arnold.

Norby RJ, Wullschleger SD, Gunderson CA, Nietch CT. 1995. Increased growth efficiency of *Quercus alba* trees in a CO_2 enriched atmosphere. *New Phytologist* **131**: 91–97.

Partington JR. 1951. *An advanced treatise on physical chemistry, Vol. II. The properties of liquids.* London, UK: Longmans, Green and Co.

Reekie EG, Bazzaz FA. 1989. Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO_2. *Oecologia* **79**: 212–222.

Roderick ML. 2000. On the measurement of growth with applications to the modelling and analysis of plant growth. *Functional Ecology* **14**: 244–251.

Roderick ML, Berry SL, Noble IR. 2000. A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. *Functional Ecology* **14**: 423–437.

Roderick ML, Berry SL, Noble IR, Farquhar GD. 1999. A theoretical approach to linking the composition and morphology with the function of leaves. *Functional Ecology* **13**: 683–695.

Rogers HH, Bingham GE, Cure JD, Smith JM, Surano KA. 1983. Responses of selected plant species to elevated carbon dioxide in the field. *Journal of Environmental Quality* **12**: 569–574.

Schlesinger WH. 1997. *Biogeochemistry: an analysis of global change, 2nd edn.* San Diego, CA, USA: Academic Press.

Schniewind AP. 1962. Horizontal specific gravity variation in tree stems in relation to their support function. *Forest Science* **8**: 111–118.

Shinozaki KK, Yoda K, Hozumi K, Kira T. 1964. A quantitative analysis of plant form: the pipe theory model I. Basic analysis. *Japan Journal of Ecology* **14**: 97–105.

Siau JF. 1984. *Transport processes in wood.* Berlin, Germany: Springer Verlag.

Skaar C. 1988. *Wood–water relations.* Berlin, Germany: Springer Verlag.

Slatyer RO. 1967. *Plant–water relationships.* London, UK: Academic Press.

Stiller V, Sperry JS. 1999. Canny's compensating pressure theory fails a test. *American Journal of Botany* **86**: 1082–1086.

Swiss KA, Firestone RA. 1999. Acceleration of bimolecular reactions by solvent viscosity. *Journal of Physical Chemistry* **103**: 5369–5372.

Telewski FW, Strain BR. 1987. Densiometric and ring width analysis of 3-year-old *Pinus taeda* L. & *Liquidambar styraciflua* L. grown under three concentrations of CO_2 and two water regimes. In: Jacoby GC Jr, Hornbeck JW, eds. *Proceedings of the international symposium on ecological aspects of tree ring analysis.* National Technical Information Service, 726–732.

Telewski FW, Strain BR. 1994. The response of trees to global change. *Journal of Korean Forestry Energy* **14**: 35–54.

Telewski FW, Swanson RT, Strain BR, Burns JM. 1999. Wood properties and ring width responses to long-term atmospheric CO_2 enrichment in field-grown loblolly pine (*Pinus taeda* L.). *Plant, Cell & Environment* **22**: 213–219.

Thomas SC. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American Journal of Botany* **83**: 556–566.

Thompson DW. 1942. *On growth and form, new (1942) edn.* London, UK: Cambridge University Press.

Thornley JHM, Johnson IR. 1990. *Plant and crop modelling.* Oxford, UK: Clarendon Press.

Tyree MT. 1997. The cohesion–tension theory of sap ascent: current controversies. *Journal of Experimental Botany* **48**: 1753–1765.

Tyree MT, Ewers FW. 1991. The hydraulic architecture of trees and other woody plants. *New Phytologist* **119**: 345–360.

Tyree MT, Sperry JS. 1989. The vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Plant Biology* **40**: 19–38.

West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. *Science* **276**: 122–126.

West GB, Brown JH, Enquist BJ. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* **400**: 664–667.

Whitehead D, Edwards WRN, Jarvis PG. 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta. Canadian Journal of Forestry Research* **14**: 940–947.

Widden M. 1996. *Fluid mechanics.* London, UK: Macmillan Press.

Wiemann MC, Williamson GB. 1989. Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Science* **35**: 197–210.

Yamamoto R. 1995. Dependence of water conductivity on pressure and temperature in plant stems. *Biorheology* **32**: 421–430.

Zimmerman MH. 1983. *Xylem structure and the ascent of sap.* Berlin, Germany: Springer Verlag.

Zimmerman MH, Brown CL. 1971. *Trees: structure and function.* New York, USA: Springer Verlag.

Zobel BJ, van Buijenen JP. 1989. *Wood variation: its causes and control.* Berlin, Germany: Springer Verlag.

Appendix A Glossary of symbols

Table A1 Main symbols used in this paper

Symbol	Units	Description
$[D]$	kg m^{-3}	Mass concentration of dry matter in a stem. In Eqns 15 and 17, units of $[D]$ are g cm^{-3}
V	m^3	Volume of stem segment
q	m^3 s^{-1}	Flow rate through a pipe (q_p is flow rate through a stem)
a	m	Pipe radius
Δp_f	N m^{-2}	Pressure drop due to frictional losses in a pipe
T	K	Temperature (T_w is water temperature)
l	m	Length of pipe & length of stem segment
η	N s m^{-2}	Viscosity
η_{rel}	–	Relative viscosity
A	m^2	Cross-sectional area of stem
A_p	m^2	Cross-sectional area of pipe within the stem
F_p	–	Volume fraction of available space in a stem occupied by pipes
N_p	Number	Number of pipes in a stem segment
ε	–	Coefficient of variation of the cross-sectional area of individual pipes within a stem

Appendix B Segmenting woody stems

Following Fig. 2, the mass (m, kg) of a stem is:

$$m = m_q + m_d \qquad \text{Eqn B1}$$

(m_q, mass of liquid; m_d, mass of dry matter and the mass of internal air space is ignored.) The unitless ratio:

$$\alpha = \frac{m_q}{m_d} \qquad \text{Eqn B2}$$

is usually called the moisture content in the wood science literature. Eqns B1 and B2 can be combined to give:

$$m = m_d(1 + \alpha) \qquad \text{Eqn B3}$$

Our prime interest is in living trees so α would usually be greater than α_f (note that α_f is the fibre saturation point, see main text) and we restrict our derivations to that range. The mass concentration of dry matter ($[D]$, kg m^{-3}) is:

$$[D] = \frac{m_d}{V} \qquad \text{Eqn B4}$$

(V, volume (m^3).) The density (ρ, kg m^{-3}) is:

$$\rho = [D](1 + \alpha) \qquad \text{Eqn B5}$$

The mass and volume of the structure (m_s, V_s) are:

$$m_s = m_d(1 + \alpha_f) \qquad \text{Eqn B6a}$$

$$V_s = \frac{m_d}{\rho_c} + \frac{\alpha_f m_d}{\rho_w} \qquad \text{Eqn B6b}$$

(ρ_c, density of dry cell walls; ρ_w, density of liquid water and the swollen cell wall is assumed to be a linear mixture.) That latter assumption is only approximately true (Siau, 1984), but the results of the calculation are not overly sensitive to that assumption. We assume that ρ_c is 1.5 g cm^{-3}, and thereby ignore the effect of secondary compounds on the density of the dry cell walls (Siau, 1984; Skaar, 1988) which will lead to slight errors in some situations.

The mass and volume of the solution (m_u, V_u) are:

$$m_u = m_d(\alpha - \alpha_f) \qquad \text{Eqn B6c}$$

$$V_u = \frac{m_d(\alpha - \alpha_f)}{\rho_u} \qquad \text{Eqn B6d}$$

(ρ_u, density of the solution.) The volume of gas space (V_a) is given by:

$$V_a = V - V_u - V_s \qquad \text{Eqn B6e}$$

and the volumetric fraction of gas (F_a) is:

$$F_a = \frac{V_a}{V} = 1 - [D]\left(\frac{\alpha - \alpha_f}{\rho_u} + \frac{1}{\rho_c} + \frac{\alpha_f}{\rho_w}\right) \qquad \text{Eqn B6f}$$

The maximum value of F_a ($F_{a:max}$) occurs when α equals α_f, while the maximum moisture content (α_{max}) occurs when F_a is zero. Assuming that the density of the solution equals that of liquid water (ρ_w), it follows that:

$$F_{a:max} = 1 - [D]\left(\frac{1}{\rho_c} + \frac{\alpha_f}{\rho_w}\right) \qquad \text{Eqn B7a}$$

and:

$$\alpha_{max} = \frac{\rho_w}{[D]} - \frac{\rho_w}{\rho_c} \qquad \text{Eqn B7b}$$

α_f is often assumed to be constant at 0.30 (Siau, 1984; Skaar, 1988). Using that value, Eqn B7a becomes:

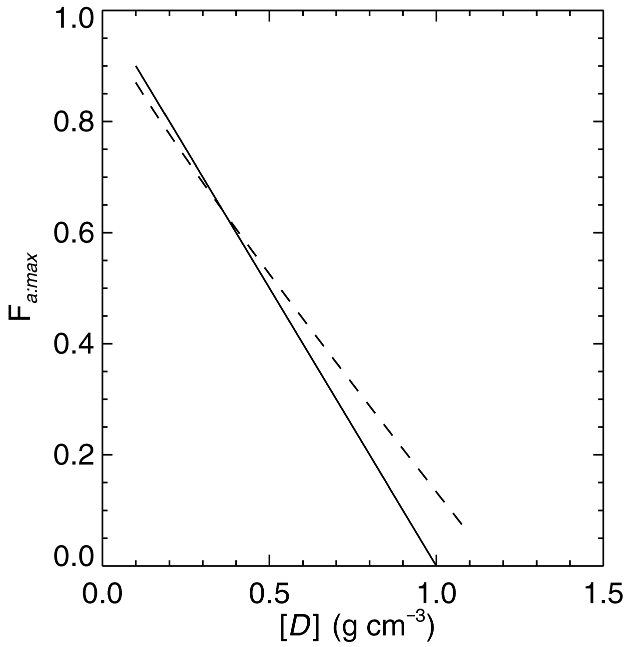

Fig. B1 Relationship between [D] and $F_{a:max}$ per Eqn B8a (full line) and per Eqns B7a and B9 (dotted line).

$$F_{a:max} = 1 - 0.97[D] \approx 1 - [D] \qquad \text{Eqn B8a}$$

(units of [D], g cm^{-3}.) Note that $F_{a:max}$ is also equal to the combined fractional volume of air space and solution, so Eqn B8a can also be written as:

$$\frac{V_a + V_u}{V} \approx 1 - [D] \qquad \text{Eqn B8b}$$

which is Eqn 6b in the main text. Observations show that α_f may be > 0.30 when [D] < 0.5 g cm^{-3} (Skaar, 1988). To take into account the dependence of α_f on [D], the following empirical relationship can be used (see Appendix C for derivation):

$$\alpha_f \approx 0.2 / \sqrt{[D]/\rho_w} \qquad \text{Eqn B9}$$

instead of adopting a constant value. The general nature of the relationship between $F_{a:max}$ and [D] is unchanged by the use of Eqn B9 (Fig. B1), and in the analysis in the main text we used Eqn B8b.

In the normal course of events, α would fluctuate depending on leaf habit (e.g. deciduous trees) and weather conditions. The magnitude of those fluctuations can be estimated by the consequent variations in the density of the stem. Following the previous logic, the minimum density (ρ_{min}) would occur when α equals α_f, and the maximum density (ρ_{max}) would occur when α equals α_{max}. The resulting relationship between [D] and ρ (Fig. B2) shows that the day-to-day fluctuations should be larger in stems with a small [D].

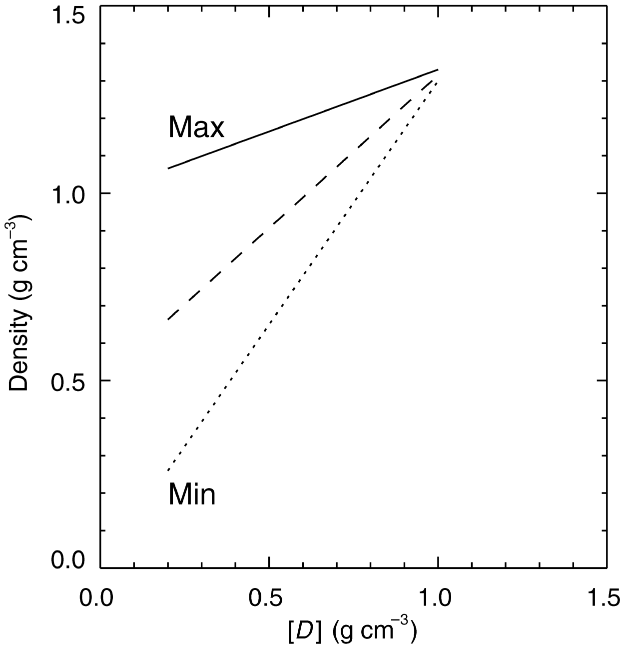

Fig. B2 Estimates of the range in density (dashed line, midpoint value) as a function of the mass concentration of dry matter ([D]) in tree stems. Calculations are based on the following equations; ρ_{min} = 1.3 [D], ρ_{max} = 0.33 [D] + 1 (where units of [D] and ρ are g cm^{-3}) which are derived from Eqns B5 and B7b assuming that α_f is 0.30. The density of the mid-point value is the average of the min. and max. equations and is; ρ_{mid} = 0.83 [D] + 0.5. Since ρ = [D] + [Q], where [Q] is the mass concentration of liquid, it follows that the value of [Q] at the mid-point is; Q_{mid} = 0.5 – 0.17[D], and is only weakly dependant on [D].

Appendix C. Derivation of relationship between [*D*] and α_f (Eqn B9)

Data from Skaar (1988) were used to derive the following empirical relationship (see Fig. C1):

$$\alpha_f = 0.22 / \sqrt{[D_0]/\rho_w} \qquad \text{Eqn C1}$$

([D_0], mass concentration of dry matter in a dry stem (i.e. at $\alpha = 0$).) However, for our purposes we require the relationship between α_f and [D], where [D] is the mass concentration of dry matter in a stem when $\alpha \geq \alpha_f$. To derive that relation one can write:

$$V = V_0 + \frac{\alpha_f m_d}{\rho_w} \qquad \text{Eqn C2}$$

(V, $\alpha \geq \alpha_f$; V_0, volume when α is zero and the last term describes the swelling of the stem (see Fig. 2 and Eqn B6b.) Now:

$$[D] = \frac{m_d}{V} = \frac{m_d}{m_d / [D_0] + \alpha_f m_d / \rho_w} \qquad \text{Eqn C3}$$

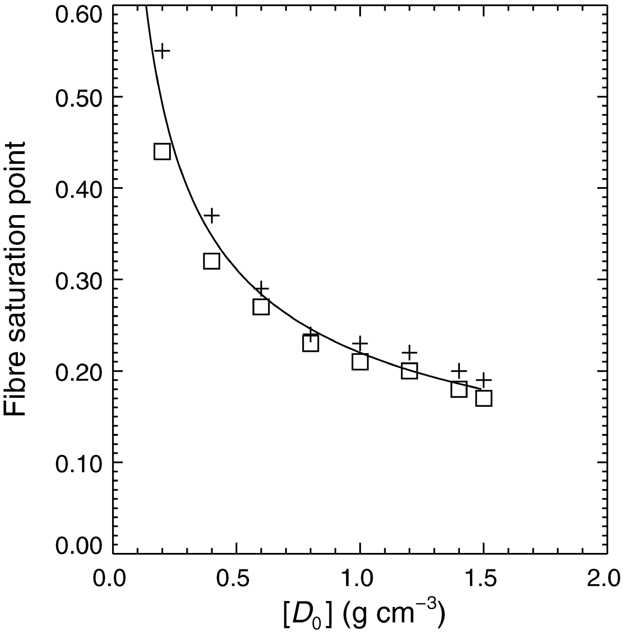

Fig. C1 Relationship between mass concentration of dry matter in a dry stem ($[D_0]$) and the fibre saturation point (α_f). Data (+, open square) are from Skaar (1988) as follows: +, from Fig. 1.32 where the data of Feist-Tarkov were ignored; (open square, calculated from the regression given in Fig. 1.33. The full line is a fitted equation ($y = 0.22/\sqrt{x}$). We do not give statistical information for the fitted equation as the original data had scatter which we have ignored.

and dividing through by m_d gives:

$$[D] = \frac{1}{1/[D_0] + \alpha_f/\rho_w} \quad \text{Eqn C4}$$

Eqn C1 can then be substituted into Eqn C4, and a relation derived between $[D]$ and α_f. However, because Eqn C1 is itself empirical, we then derived a second empirical relation of the same form relating $[D]$ and α_f as follows:

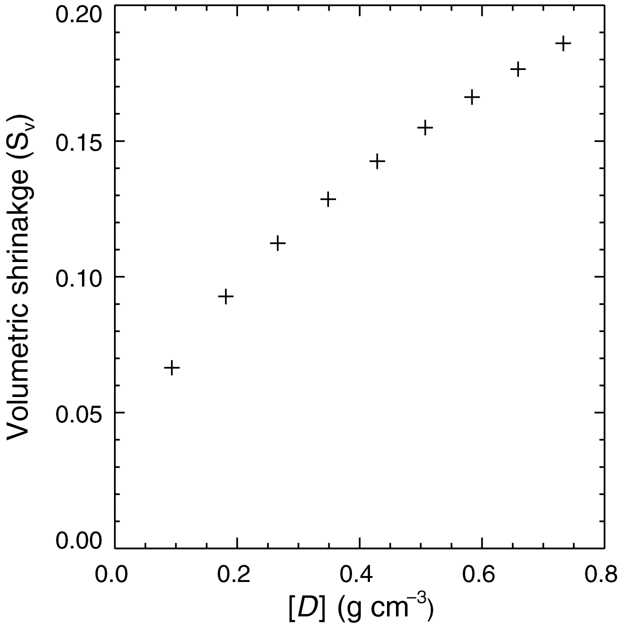

Fig. C2 Empirical relationship between mass concentration of dry matter ($[D]$) and volumetric shrinkage coefficient (S_v). S_v was computed as follows; first compute α_f as a function $[D_0]$ (Eqn C1), then compute $[D]$ from α_f (Eqn C5), and finally compute S_v (Eqn C6).

$$\alpha_f = 0.2/\sqrt{[D]/\rho_w} \quad \text{Eqn C5}$$

which is Eqn B9.

As a rough check on the above procedure, the volumetric shrinkage coefficient (S_v) can be derived as α declines from α_f to zero. S_v is defined as:

$$S_v = \frac{V - V_0}{V} = 1 - \frac{[D_0]}{[D]} \quad \text{Eqn C6}$$

The predicted relationship between S_v and $[D]$ (Fig. C2) follows the general trend observed in measurements (Skaar, 1988).