

# A unified nomenclature for quantification and description of water conducting properties of sapwood xylem based on Darcy's law

DOUGLAS E. B. REID,<sup>1,2</sup> ULDIS SILINS,<sup>2</sup> CARL MENDOZA<sup>3</sup> and VICTOR J. LIEFFERS<sup>2</sup>

<sup>1</sup> Corresponding author (dereid@ualberta.ca)

<sup>2</sup> Centre for Enhanced Forest Management, Department of Renewable Resources, 4-42 Earth Sciences Building, University of Alberta, Edmonton, AB T6G 2E3, Canada

<sup>3</sup> Department of Earth & Atmospheric Sciences, 1-26 Earth Sciences Building, University of Alberta, Edmonton, AB T6G 2E3, Canada

Received November 3, 2004; accepted November 20, 2004; published online June 1, 2005

**Summary** The literature dealing with the water conducting properties of sapwood xylem in trees is inconsistent in terminology, symbols and units. This has resulted from confusion in the use of either an analogy to Ohm's law or Darcy's law as the basis for nomenclature. Ohm's law describes movement of electricity through a conductor, whereas Darcy's law describes movement of a fluid (liquid or gas) through a porous medium. However, it is generally not realized that, in their full notation, these laws are mathematically equivalent. Despite this, plant physiologists have failed to agree on a convention for nomenclature. As a result, the study of water movement through sapwood xylem is confusing, especially for scientists entering the field. To improve clarity, we suggest the adoption of a single nomenclature that can be used by all plant physiologists when describing water movement in xylem. Darcy's law is an explicit hydraulic relationship and the basis for established theories that describe three-dimensional saturated and unsaturated flow in porous media. We suggest, therefore, that Darcy's law is the more appropriate theoretical framework on which to base nomenclature describing sapwood hydraulics. Our proposed nomenclature is summarized in a table that describes conventional terms, with their formulae, dimensions, units and symbols; the table also lists the many synonyms found in recent literature that describe the same concepts. Adoption of this proposal will require some changes in the use of terminology, but a common rigorous nomenclature is needed for efficient and clear communication among scientists.

**Keywords:** *conductance, hydraulic capacity, hydraulic conductivity, permeability, water potential.*

## Introduction

Recently, there has been a dramatic increase in the publication of important work regarding the hydraulic properties of xylem in stems, branches and roots of trees (see reviews by Tyree and Ewers 1991, Sperry 1995, Gartner 1995, Whitehead 1998, Comstock and Sperry 2000, Meinzer et al. 2001, Tyree and Zimmerman 2002 and Tyree 2003) as a result of the develop-

ment of innovative techniques for measuring water flow through xylem (Booker and Kinninmonth 1978, Zimmerman 1978, Sperry et al. 1988, Tyree et al. 1995, Spicer and Gartner 1998). The physical limitations on water flow through sapwood xylem have been shown to influence stomatal behavior and transpiration in trees subject to boundary layer and soil moisture constraints (Meinzer et al. 1995), stand-level productivity (Mencuccini and Grace 1996a) and the growth of large old trees (Hubbard et al. 1999). Others have shown a direct relationship between xylem hydraulic properties and stomatal behavior of trees under well-watered conditions (Hubbard et al. 2001) and the maximum height attained by trees (Ryan and Yoder 1997, Koch et al. 2004).

There are, however, inconsistencies in the theoretical framework, nomenclature and mathematical formulations used to quantify the hydraulic properties of xylem. An analogy to Ohm's law has long been used to describe water movement between plant cells (Salisbury and Ross 1969) and the resistance to CO<sub>2</sub> and water vapor transfer in photosynthesis and transpiration (Nobel 1974, Larcher 1980), and has been widely applied to describe water movement through sapwood xylem (Tyree and Ewers 1991). Darcy's law has also been used for many years to quantify the liquid and gas conducting properties of sapwood (Siau 1971, 1983). As early as 1975, Jarvis observed that a "plethora of often misleading definitions of resistance, conductance, conductivity and permeability, with various combinations of units" had made its way into the physiological literature. In the intervening quarter century, this problem has worsened.

Inconsistent nomenclature and mathematical formulations of hydraulic characteristics of xylem have hampered understanding (Aumann and Ford 2002) and made work in tree hydraulic architecture unnecessarily difficult (Fiscus and Kaufmann 1990). There is an ongoing drift in terminology. For example, our research group, as a result of changes in views or pressure from referees, has used varying terminology and formulations to quantify the hydraulic properties of sapwood (Protz et al. 1999, Reid et al. 2003, 2004, Liu et al. 2003). An array of different terms (see Table 1) has been used

in the plant physiology literature to describe what is consistently referred to as hydraulic conductivity in other hydrologic fields. We propose that a single definition of hydraulic conductivity be adopted in order to ensure that the results and inferences presented by tree physiologists are intelligible to the widest possible audience. The definition we propose is consistent with Darcy's law, which is widely used to describe the flow of water through porous media (Freeze and Cherry 1979, Hillel 1982, Smith and Wheatcraft 1983, Chow et al. 1988, Rawls et al. 1993, Zaitchick et al. 2003). Darcy's law is also the foundation of complex models that describe unsaturated three-dimensional flow (Hillel 1982, Rawls et al. 1993, Ryel et al. 2002) and the contribution of stored water to transpirational flow in sapwood xylem of large trees (Aumann and Ford 2002).

Advancement of scientific knowledge has benefited greatly from the use of conventional nomenclature to simplify the communication of complex ideas. No one convention is correct, but terms that are consistently defined provide a basis for effective communication. Our objectives are to clarify the physical meaning of hydraulic conductivity and to distinguish this term from both conductance and permeability when describing the flow of water through the porous matrix of sapwood xylem. We discuss how both Ohm's law and Darcy's law have been used to describe the hydraulic properties of sap-

wood xylem. We then suggest that a single unifying nomenclature, based on the widely understood and physically meaningful Darcy's law, be used to quantify the hydraulic properties of woody xylem (Table 1).

### Ohm's law

The simple linear model to describe the one-dimensional flow of electrical current was first suggested by Ohm (1827). Strictly speaking, Ohm's law is limited to the statement, "the current through a metal conductor is proportional to the applied voltage,  $I \propto V$ " (Giancoli 1995). Ohm's law is most frequently presented as a means to quantify the amount of electrical current ( $I$ ) flowing through a device of known resistance ( $R$ ) driven by a difference in electrical potential ( $V$ ).

$$I = \frac{V}{R} \quad (1)$$

Conductance is the inverse of resistance. If the device is a metal conductor (e.g., a wire), its physical size is not explicitly included in this common expression of Ohm's law. The size of the conducting element is implicit, however, in the calculation of  $R$ , which is directly proportional to length of the conductor ( $L$ ) and inversely proportional to its cross-sectional area ( $A$ ).

Table 1. Terms and associated dimensions, units and symbols for the quantification of hydraulic characteristics of sapwood xylem. Definitions: L = linear dimension; T = time; and M = mass.

Term	Dimensions	SI Units	Symbol	Other terms and symbols used
Volume <sup>†</sup> flow per unit time at any point	$L^3 T^{-1}$	$m^3 s^{-1}$	$Q$	$F, q, v, J$
Sapwood conducting surface area	$L^2$	$m^2$	$A_s$	
Leaf area distal to the point of hydraulic measurement	$L^2$	$m^2$	$A_L$	
Water flux	$L T^{-1}$	$m s^{-1}$	$q$	Flow, water flux density, $J$
Length of sample through which water is flowing	$L$	$m$	$L$	
Hydraulic head	$L$	$m$	$H$	
Water potential	$M L^{-1} T^{-2}$	$Pa$	$\Psi$	$P$
Dynamic fluid viscosity	$M L^{-1} T^{-1}$	$Pa s$	$\eta$	
Density of water	$M L^{-3}$	$kg m^{-3}$	$\rho_w$	
Acceleration due to gravity	$L T^{-2}$	$m s^{-2}$	$g$	
Hydraulic conductance $\left(G = \frac{Q}{\Delta\Psi}\right)$	$L^4 T M^{-1}$	$m^3 Pa^{-1} s^{-1}$	$G$	Hydraulic conductivity, $k_{AB}$ , $K$ , $k$
Hydraulic conductivity <sup>‡</sup> $\left(K_\Psi = \frac{Q}{A_s \Delta\Psi} \frac{L}{\eta}\right)$	$L^3 T M^{-1}$	$m^2 Pa^{-1} s^{-1}$	$K_\Psi$	Specific conductivity, hydraulic conductivity coefficient, conductance, permeability, $k_s$ , $\sigma$ , $K_s$ , $L$
Permeability $\left(k = \frac{Q}{A_s \Delta\Psi} \frac{L}{\eta}\right)$	$L^2$	$m^2$	$k$	Relative conductivity, specific conductivity, specific permeability, permeability constant, $k$ value, $K$ , $k_s$
Hydraulic capacity $\left(Q_h = K_\Psi A_s = \frac{k}{\eta} A_s\right)$	$L^5 T M^{-1}$	$m^4 Pa^{-1} s^{-1}$	$Q_h$	Hydraulic conductivity, conductivity, hydraulic conductance, $K$ , $k$ , $k_h$ , $K_h$ , $Q^*$ , $\hat{K}$ , COND
Leaf specific hydraulic capacity $\left(Q_L = \frac{Q_h}{A_L}\right)$	$L^3 T M^{-1}$	$m^2 Pa^{-1} s^{-1}$	$Q_L$	Leaf specific conductivity, leaf specific conductance, $K_L$ , $k_L$ LSC

<sup>†</sup> Unit volume of water can be easily converted to unit mass of water by multiplying by  $\rho_w$ .

<sup>‡</sup>  $K = K_\Psi \rho_w g$ ; generally 1 m of head is equivalent to about 9.8 kPa (Horvath 1986).

$$R = r \frac{L}{A} \quad (2)$$

Resistivity ( $r$ ) is a property of a material that describes its ability to conduct electricity (Giancoli 1995). The dependence of electrical flow on the conductor's conducting property and geometry can be shown by combining Equations 1 and 2:

$$I = A \frac{1}{r} \frac{V}{L} \quad (3)$$

Wires or other conductors are generally made of pure metals or alloys, for which resistivity and cross-sectional area are constant; therefore, resistance is the property most commonly measured. Electrical current is quantified in Amperes, which are base SI units (Nelson 1999). Thus, electrical current can be compared to mass or volume flow of water only by analogy.

### Darcy's law

Darcy (1856) investigated the rate of infiltration of water through saturated sand and formulated what is commonly known as Darcy's law. Under conditions of laminar viscous flow, the volumetric flow of water is:

$$Q = AK \frac{\Delta H}{L} \quad (4)$$

where  $Q$  is flow or volumetric discharge per unit time ( $L^3 T^{-1}$ ) through a column of porous material of cross-sectional area,  $A$  ( $L^2$ ), and length,  $L$  ( $L$ ),  $\Delta H$  is hydraulic head difference across the column ( $L$ ), and  $K$  is hydraulic conductivity ( $L T^{-1}$ ) estimated from a head-based measure of the hydraulic gradient. The driving force causing water to flow is the hydraulic head per unit distance in the direction of flow, the hydraulic gradient ( $\Delta H/L$ ). Hydraulic head is potential energy per unit weight (with units of  $J N^{-1} = m$ ) (Hubbert 1940). It is the preferred measure of water potential for hydrogeologists and hydrologists because it can be equated to the elevation of the top of a water column, and thus easily measured with piezometers. Darcy's Law is typically presented in pedological and geophysical texts (Freeze and Cherry 1979, Smith and Wheatcraft 1983, Chow et al. 1988, Rawls et al. 1993) in the form:

$$q = \frac{Q}{A} = K \frac{\Delta H}{L} \quad (5)$$

where  $q$  is water flux<sup>†</sup> ( $L^3 T^{-1} L^{-2} = L T^{-1}$ ).

Total water potential ( $\Psi$ ) is the sum of hydrostatic potential (pressure or tension), osmotic potential and gravitational potential (Nobel 1999). The influence of osmosis on sap flow is

generally low because plants transport nearly pure water in xylem (Tyree 1999). Water potential is usually defined as a measure of the potential energy (i.e., capacity to do work) of a unit quantity of water (e.g., Hanks 1992). The use of various unit quantities (mass, volume or weight) to define water potential is possible because liquid water is essentially an incompressible fluid (Narasimhan 2003).

Water potential is the term most frequently used by plant physiologists to describe the potential energy per unit volume of water (Niklas 1992) and typically has units of pressure ( $Pa = J m^{-3}$ ) (Tyree 1999). Thus, Darcy's law can be expressed as:

$$Q = AK_{\Psi} \frac{\Delta \Psi}{L} \quad (6)$$

where  $K_{\Psi}$  is hydraulic conductivity ( $L^3 T M^{-1}$ ; units of  $m^2 Pa^{-1} s^{-1}$ ) determined by a pressure-based measure of the hydraulic gradient. We use the symbol  $K_{\Psi}$  to distinguish between hydraulic conductivity measured with head-based and pressure-based expressions of water potential. Both  $K$  and  $K_{\Psi}$  have identical physical meaning; only the units differ. Pressure units are the units of measurement preferred by physiologists because leaf or shoot water potential is easily measured by the pressure chamber technique (Scholander et al. 1964, Richter 1997, Cochard et al. 2001), and stem hygrometers are becoming more reliable (Stöhr and Lösch 2004).

Conductivity quantifies the ability to conduct (electricity or water) independent of conductor geometry, including cross-sectional area and length. Hydraulic conductivity as described by Darcy's law (Equation 4 or 6) is mathematically equivalent to the inverse of resistivity in Ohm's law (Equation 3). Hydraulic conductivity reflects the combined effects of the properties of the porous medium and the properties of the liquid (Hillel 1982) on the instantaneous bulk flow of the liquid through the saturated medium.

When dynamic fluid viscosity ( $\eta$ ;  $M L^{-1} T^{-1}$ ) (Whitehead et al. 1984a, Whitehead 1998) is accounted for, the property of the porous medium is permeability ( $k$ ;  $L^2$ ). When water potential is expressed in head units, permeability can be calculated from:

$$k = \frac{Q}{A} \frac{L}{\Delta H} \frac{\eta}{\rho_w g} \quad (7)$$

where  $\rho_w$  is density of water ( $M L^{-3}$ ) and  $g$  is acceleration due to gravity ( $L T^{-2}$ ). When water potential is expressed using pressure units ( $Pa$ ),  $k$  is defined as:

$$k = \frac{Q}{A} \frac{L}{\Delta \Psi} \eta \quad (8)$$

<sup>†</sup> The term *flux* is consistently applied to the movement of a substance relative to an area perpendicular to the direction of flow. Here, *flux* is defined as "amount per time per area," consistent with the convention employed by those who use Darcy's law. Those who use Ohm's law often define *flux* as "amount per time" (and prefer *flux density* for "amount per time per area"). Either definition is acceptable. We suggest that scientists indicate which definition they are using.

Expressions 7 and 8 are equivalent because the product of head, density and acceleration due to gravity has dimensions of pressure ( $\text{M L}^{-1} \text{T}^{-2}$ ).

### Hydraulic properties of trees

#### *Early works*

Farmer (1918) may have been the first to measure the “water-conductivity” of a variety of species of woody plants to explore the “limitation [that] the structure of wood” imposes on the flow of water. Measurement of the amount of water that transpires from leaves and the water potential difference between soil and leaves (analogous to electrical potential in Equations 1 and 3) was possible before reliable techniques existed to measure flow through stems. Under such circumstances, the total resistance to water flow through the plant can be quantified by an Ohm’s law analogy without explicitly quantifying the physical dimensions of stems and branches. An analogy to Ohm’s law was used by early physiologists to quantify passive conductance to the movement of water in plants (Huber 1928 (cited in Van den Honert 1948)). Huber (1956) reported the “specific conductivity,” defined by Kramer and Kozlowski (1960) as the “volume of water moved per unit of time under a given pressure through a segment of given length and cross section.” Heine (1971) presented a survey of published values, encouraged the use of “relative conductivity” as opposed to “specific conductivity,” and attempted to resolve the confusion between different expressions of conductivity. Siau (1971) expanded this discussion to introduce Darcy’s law and the terms “permeability” and “specific permeability.” Richter (1973) provided a theoretical examination of the Ohm’s law analogy with particular attention to the choice of dimensions for fluxes and resistances.

#### *Application of Ohm’s law analogies*

Richter’s (1973) account of the dimensions of water flow, based on an Ohm’s law analogy, provided the basis for many advances in our understanding of the hydraulic architecture of trees. Tyree and Sperry (1988) demonstrated that “hydraulic conductance” ( $k_h$ ) (i.e., the mass flow rate of water ( $\text{kg s}^{-1}$ ) per unit pressure gradient ( $dP/dl$ )) is positively related to stem diameter. In a related paper, Tyree (1988) used an electrical analogue to develop a dynamic model for water flow in a single tree. The models of Tyree and Sperry (1988) and Tyree (1988) were the first to link the functional aspects of the hydraulic system to its branched structure (Fruh and Kurth 1999).

Tyree and Ewers (1991), in a heuristic examination of the hydraulic architecture of trees, presented an Ohm’s law analogy and provided units for water flux ( $\text{kg s}^{-1}$ ) and hydraulic conductance ( $\text{kg s}^{-1} \text{MPa}^{-1}$ ) in the context of water movement driven by a difference in water potential across a given struc-

ture. Their formulation is consistent with the quantification of electrical flux, conductance and potential. Hydraulic conductivity was defined as:

$$k_h = \frac{F}{dP/dx} \quad (9)$$

where  $F$  is amount of water flowing per unit time ( $\text{kg s}^{-1}$ ), and ( $dP/dx$ ) is the pressure gradient causing the flow ( $\text{MPa m}^{-1}$ ). However, this formulation of conductivity is not analogous to the inverse of resistivity ( $1/r$  in Equation 3), nor is it equivalent to  $K$  of Darcy’s law (Equation 4). The effect of cross-sectional area on flow is unaccounted for in Equation 9. Increases in conducting cross-sectional area with increasing stem diameter will result in greater flow, which does not necessarily reflect a change in the conducting property of the sapwood xylem.

#### *Applications of Darcy’s law*

Darcy’s law is used to quantify the conducting properties of porous media to liquids or gases and is the foundation for more complicated three-dimensional models of saturated and unsaturated flow through porous media (Hillel 1982, Aumann and Ford 2003). Zimmerman (1978), in his investigation of the hydraulic architecture of trees, defined hydraulic conductivity consistent with Siau’s (1971, 1983) definition of permeability and Jarvis’s (1975) conductivity, but did not cite either author. Jarvis (1975) also defined hydraulic conductance ( $G$ ;  $\text{m}^3 \text{s}^{-1} \text{Pa}^{-1}$ ) as:

$$G = \frac{Q}{\Delta\Psi} \quad (10)$$

where  $Q$  is volumetric flow rate, and  $\Delta\Psi$  is the water potential difference driving flow. This formulation of  $G$  is mathematically equivalent to the inverse of Ohm’s  $R$  (see Equation 1). Darcy’s law has been invoked more than 30 times<sup>†</sup> in publications where sapwood hydraulic properties are quantified (e.g., Reid et al. 2004), or when modeling the relationship between bulk flow of water through saturated woody xylem and the water potential gradient driving flow (e.g., Whitehead 1998). Some authors who cite Darcy have used the term permeability, as presented in Equation 7 (e.g., Pothier et al. 1989a, 1989b), but this definition has been referred to by a variety of other names (see Table 1). Despite these numerous references, terminology, units and symbols are not always consistent.

### A proposal for a unified nomenclature

We suggest that Darcy’s law is the more appropriate basis for a single nomenclature, even though Ohm’s law and Darcy’s law are mathematically equivalent. Darcy’s law is an explicit hydraulic theory that accounts for fluid viscosity, and offers

<sup>†</sup> Including Booker (1977), Whitehead and Jarvis (1981), Edwards and Jarvis (1982), Whitehead et al. (1984a, 1984b), Davies (1986), Edwards et al. (1986), Whitehead and Hinkley (1991), Mencuccini and Grace (1995), Mencuccini et al. (1997), Ewers et al. (2000), Mencuccini and Bonosi (2001), McDowell et al. (2002) and Mencuccini (2002), and others referenced directly in the text.



greater potential to address issues of water storage and transient flow in unsaturated sapwood xylem. The Ohm's law analogy may be more familiar, but is not a more complete theory for describing the hydraulic properties of porous media, nor easier to understand than Darcy's law. We propose, therefore, that tree physiologists adopt the units and nomenclature of Darcy's law to quantify water conducting properties of sapwood xylem (Table 1). An advantage is that Darcy's law uses terminology understood by scientists from other hydrologic disciplines.

Our key proposal is that hydraulic conductivity ( $K_\Psi$ ; Equation 6) be defined as the constant of proportionality between volume flow rate of water ( $Q$ ) per unit surface area of conducting sapwood tissue ( $A_s$ ) perpendicular to the direction of flow and the hydraulic gradient ( $\Delta\Psi/L$ ). The hydraulic gradient is the difference in water potential per unit of length across which the difference exists. We suggest the adoption of the terms and dimensions defined in Table 1 to quantify hydraulic properties of sapwood xylem. We have also suggested a set of associated symbols. These are consistent with terms and symbols used by most other disciplines that quantify the hydraulic properties of porous media. Water potential of living trees and woody plants can be measured with a variety of instruments that measure pressure or potential energy per unit volume (Cochard et al. 2001). Tree physiologists are thus likely to be more comfortable using  $K_\Psi$  ( $\text{m}^2 \text{s}^{-1} \text{Pa}^{-1}$ ) to quantify hydraulic conductivity, although  $K$  ( $\text{m s}^{-1}$ ) is also correct (see Table 1 for dimensions and unit conversion).

We discourage the use of the term "specific conductivity" to describe  $K_\Psi$  because "specific" has a variety of meanings and could be a source of confusion for readers from different backgrounds. As was pointed out by Heine (1971) and Jarvis (1975), some have suggested that the term "specific" be used only where "divided by mass" is the intended meaning (Symbols Committee of the Royal Society 1975); however, it can also mean "divided by area." Moreover, the phrase "specific conductivity" is sometimes used synonymously with temperature-compensated electrical conductivity to describe water quality (Stuart et al. 1995, Patni et al. 1996) or the chemical composition of soil amendments (Bouranis et al. 1997).

An advantage of Darcy's law and  $K_\Psi$  is that permeability,  $k$ , can be directly determined. Permeability allows researchers to disentangle the combined effects of the dynamic fluid viscosity of the liquid and the conducting property of the porous medium. Permeability can be correctly quantified using either head or pressure units for water potential (Equations 7 or 8) and by substituting  $A_s$  for the area term. Because most measurements are made under laboratory conditions where temperature effects on the viscosity of water are negligible,  $k$  and  $K_\Psi$  are likely to show strongly similar patterns of variability between samples. Determination of  $k$  in the field requires measurement of the fluid temperature (Whitehead et al. 1984b). In research reporting "specific conductivity," flow measurements are sometimes corrected to what would be expected at 20 °C (e.g., Spicer and Gartner 1998, 2001, Gartner et al. 2003, Liu et al. 2003). Correcting to a standard temperature accounts for slight differences in the viscosity of the flowing liquid. We

suggest, however, that this unnecessarily complicates the literature because permeability,  $k$ , specifically accounts for the effect of viscosity.

If  $K_\Psi$  or  $k$  is known, the capacity of a stem segment to conduct water, or the hydraulic capacity, can be defined as:

$$Q_h = K_\Psi A_s = \frac{k}{\eta} A_s \quad (11)$$

where  $Q_h$  ( $\text{m}^4 \text{MPa}^{-1} \text{s}^{-1}$ ) describes volumetric flow ( $\text{m}^3 \text{s}^{-1}$ ) per unit of hydraulic gradient ( $\text{MPa m}^{-1}$ ). This parameter is useful for describing the combined effects of hydraulic conductivity and conducting sapwood area in regulating flow through stems or in modeling flow through whole trees under a known hydraulic gradient. Although the phrase and symbol are new to the literature, the idea is not. This term is equivalent to  $k_h$  as defined by Tyree and Ewers (1991) (see Equation 9), hydraulic conductance per unit length (Nobel 1999), and the definition we have published elsewhere using the symbol  $Q^*$  (Liu et al. 2003, Reid et al. 2003, 2004). We propose the symbol  $Q_h$  because  $Q^*$  is generally used as the symbol for net radiation in describing bulk transfer of water to the atmosphere (Oke 1987). Use of " $Q$ " with a subscript 'h' indicates it is a measure of flow normalized for a unit hydraulic gradient. Adoption of  $Q_h$  as the standard symbol has the advantage of allowing continued use of this term, while clearly distinguishing it from hydraulic conductivity ( $K_\Psi$ ) and permeability ( $k$ ).

Because leaves are dependent on the xylem for the supply of water, the water conducting properties of xylem can influence photosynthetic efficiency. Zimmerman (1978) first recognized the functional biological importance of this physiological relationship by introducing the term "leaf specific conductivity." Zimmerman calculated this parameter by substituting leaf area distal to the stem segment measured in place of the area term in Equation 6. Although we recognize the utility of this measure, we believe that the term "leaf specific conductivity" is inappropriate because this formulation does not describe a property of the conducting tissue (i.e., a measure of conductivity) per unit area or mass of leaves, but describes a functional relationship between the flow capacity of a stem or branch and the distal leaf area it supports. Further, the use of a similar symbol (typically  $k_L$  or  $K_L$ ) incorrectly implies that it is a hydraulic property of xylem, analogous to  $K_\Psi$  or  $k$ . We suggest this relationship between the water conducting property of xylem and leaf area can be appropriately quantified by dividing  $Q_h$  by the leaf area distal to the stem segment measured (i.e.,  $Q_h/A_L$ ). We propose using leaf specific hydraulic capacity as the standard term to describe this important functional relationship. We suggest  $Q_L$  as the standard symbol to distinguish this term from  $K_\Psi$  and  $k$ , and the use of a capital "L" for a subscript to differentiate the term from leaf-related sap flow ( $Q_i$ ) (Edwards et al. 1996).

### Comment on conductance

Though potentially useful, conductance is not analogous to

$K_{\Psi}$ ,  $k$ ,  $Q_h$  or  $Q_L$  because surface area of conducting tissue is explicit in defining  $K_{\Psi}$  and  $k$ , and the length of the sapwood xylem is explicit in defining the hydraulic gradient for all four terms. Conductance ( $G$ ) (Equation 10) integrates the influences of length, cross-sectional area and conductivity on the instantaneous flow of water through a porous medium. We advocate the continued use of  $G$  for conductance based on precedence, and because 'G' or 'g' with various subscripts are already widely used for conductance in the context of water movement in trees and other plants (e.g., Rayment et al. 2000, Martínez-Vilalta et al. 2003). Division of  $Q_h$  by the length of a sample is mathematically analogous to  $G$ ; however, we suggest that the term conductance only be used to describe the limitation on water flow through sapwood xylem when the dimensions of the tissues through which water flows are accounted for (Mencuccini and Grace 1996b) or unknown (Tyree et al. 1995), and  $K_{\Psi}$  can reasonably be expected to remain more or less constant along the entire path length.

It is sometimes useful to calculate leaf specific hydraulic conductance (or conductance per unit leaf area) when investigating canopy water relations of trees or stands. When  $Q$ ,  $\Delta\Psi$  and  $A_L$  are quantifiable, leaf specific hydraulic conductance can be used to better understand dynamic water stress in the canopy caused by transpiration (e.g., Phillips et al. 2002). We suggest researchers examining this issue use the symbol  $G_L$  to denote leaf specific hydraulic conductance because conductance is both qualitatively and quantitatively different from hydraulic conductivity ( $K_{\Psi}$ ), permeability ( $k$ ), hydraulic capacity ( $Q_h$ ) and leaf specific hydraulic capacity ( $Q_L$ ).

## Conclusion

This proposal provides tree physiologists a consistent set of terms and units that are familiar to the broader scientific community, and are suitable for continued investigation into the movement of water through sapwood xylem. The adoption of the convention we propose does not diminish the insights in published works that have used the Ohm's law analogy. Nevertheless, we suggest that Darcy's law provides the most defensible and theoretically sound framework for the quantification of the water conducting properties of sapwood xylem. Our main purpose is to suggest standard definitions for hydraulic conductivity and permeability, and to simplify and standardize the nomenclature. We have also illustrated the mathematical equivalence of Darcy's law and Ohm's law, provided clarification on the meanings of conductance, flow and flux, and summarized the terms we propose with their associated formulae, units and dimensions (Table 1). The difficulty with our proposed scheme is that it will require researchers in this field of work to change, in some way, the language they have been using. However, if they do change, the ease with which ideas are communicated will be greatly enhanced. Furthermore, acceptance of this proposal should aid multidisciplinary efforts, such as the new field of eco-hydrology (Baird and Wilby 2001, Eagleson 2002), which integrates plant physiology, physical hydrology and hydrogeology.

## Acknowledgments

We thank our colleagues who provided useful discussion, particularly Dr. Ken Stadt who provided a careful review of an earlier version of the manuscript and Dr. Yongsheng Feng. Dr. David Whitehead provided editorial suggestions and encouragement. Dr. Peter Becker provided valuable comments on earlier versions of the manuscript. Financial support was provided by NSERC, Weldwood of Canada and Weyerhaeuser Canada.

## References

- Aumann, C.A. and E.D. Ford. 2002. Modeling tree water flow as an unsaturated flow through a porous medium. *J. Theor. Biol.* 219: 415–429.
- Baird, A.J. and R. Wilby. 2001. *Eco-hydrology: plants and water in terrestrial and aquatic environments*. Routledge, New York, 402 p.
- Booker, R.E. 1977. Problems in the measurement of longitudinal sapwood permeability and hydraulic conductivity. *N.Z. J. For. Sci.* 7: 297–304.
- Booker, R.E. and J.A. Kinninmonth. 1978. Variation in longitudinal permeability of green radiata pine wood. *N.Z. J. For. Sci.* 8: 295–308.
- Bouranis, D.L., A.G. Vlyssides, J.B. Drossopoulos, D.G. Economides, B. Mourafeti and D.G. Drissis. 1997. Physicochemical characteristics of a new organic soil conditioner from composted sludges from a pulp deinking process. *Commun. Soil Sci. Plant Anal.* 28:1549–1564.
- Chow, V.T., D.R. Maidment and L.W. Mays. 1988. *Applied hydrology*. McGraw-Hill, New York, 572 p.
- Cochard, H., S. Forestier and T. Ameglio. 2001. A new validation of the Scholander pressure chamber technique based on stem diameter variations. *J. Exp. Bot.* 52:1361–1365.
- Comstock, J.P. and J.S. Sperry. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. *New Phytol.* 148:195–218.
- Darcy, H. 1856. Détermination des lois d'écoulement de l'eau à travers le sable. *In* Les Fontaines Publiques de la Ville de Dijon. Appendix Note D. Victor Dalmont, Paris, pp 590–594. Available in English at <http://biosystems.okstate.edu/darcy/English/>.
- Davies, W.J. 1986. Transpiration and the water balance of plants. *In* Plant Physiology: A Treatise. Vol. IX. Water and Solutes in Plants. Ed. F.C. Steward. Academic Press, New York, pp 49–137.
- Eagleson, P.S. 2002. *Ecohydrology*. Cambridge University Press, Cambridge, 443 p.
- Edwards, W.R.N. and P.G. Jarvis. 1982. Relations between water content, potential and permeability in stems of conifers. *Plant Cell Environ.* 5:271–277.
- Edwards, W.R.N., P.G. Jarvis, J.J. Landsberg and H. Talbot. 1986. A dynamic model for studying flow of water in single trees. *Tree Physiol.* 1:309–324.
- Edwards, W.R.N., P. Becker and J. Čermák. 1996. A unified nomenclature for sap flow measurements. *Tree Physiol.* 17:65–67.
- Ewers, B.E., R. Oren and J.S. Sperry. 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell Environ.* 23:1055–1066.
- Farmer, J.B. 1918. On the quantitative differences in the water-conductivity of the wood in trees and shrubs. *Proc. R. Soc. Lond. B Biol. Sci.* 90:218–250.
- Fiscus, E.L. and M.R. Kaufmann. 1990. The nature and movement of water in plants. *In* Irrigation of Agricultural Crops. Vol. 30. Eds. B.A. Stewart and D.R. Nielsen. Ame. Soc. Agron., Madison, WI, pp 191–241.

- Freeze, R.A. and J.A. Cherry. 1979. Groundwater. Prentice Hall, Englewood Cliffs, NJ, 604 p.
- Fruh, T. and W. Kurth. 1999. The hydraulic system of trees: theoretical framework and numerical simulation. *J. Theor. Biol.* 201:251–270.
- Gartner, B.L. 1995. Patterns of xylem variation within a tree and their mechanical consequences. In *Plant Stems: Physiology and Functional Morphology*. Ed. B.L. Gartner. Academic Press, New York, pp 125–149.
- Gartner, B.L., J. Roy and R. Huc. 2003. Effects of tension wood on specific conductivity and vulnerability to embolism of *Quercus ilex* seedlings grown at two atmospheric CO<sub>2</sub> concentrations. *Tree Physiol.* 23:387–395.
- Giancoli, D.C. 1995. Physics: principles with applications. 4th Edn. Prentice Hall, Englewood Cliffs, NJ, 1020 p.
- Hanks, R.J. 1992. Applied soil physics: soil water and temperature applications. 2nd Edn. Springer-Verlag, New York, 176 p.
- Heine, R.W. 1971. Hydraulic conductivity in trees. *J. Exp. Bot.* 22: 503–511.
- Hillel, D. 1982. Introduction to soil physics. Academic Press, Orlando, FL, 364 p.
- Horvath, A.L. 1986. Conversion tables of units in science and engineering. Macmillan, London, 147 p.
- Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol.* 19:165–172.
- Hubbard, R.M., V. Stiller, M.G. Ryan and J.S. Sperry. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell Environ.* 24:113–121.
- Hubbert, M.K. 1940. The theory of ground-water motion. *J. Geol.* 48:785–944.
- Huber, B. 1928. Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen. *Jb. wiss. Bot.* 67:877–859.
- Huber, B. 1956. Die Saftströme der Pflanzen. Springer-Verlag, Berlin. (In Kramer and Kozlowski 1960.)
- Jarvis, P.G. 1975. Water transfer in plants. In *Heat and Mass Transfer in the Plant Environment*. Part 1. Eds. D.A. deVries and N.G. Afgan. Scripta Book, Washington, DC, pp 369–394.
- Koch, G.W., S.C. Sillet, G.M. Jennings and S.D. Davis. 2004. The limits to tree height. *Nature* 428:851–854.
- Kramer, P.J. and T.T. Kozlowski. 1960. Physiology of trees. McGraw-Hill, New York, 642 p.
- Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, Berlin, 303 p.
- Liu, X., U. Silins, V.J. Lieffers and R. Man. 2003. Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. *Can. J. For. Res.* 33:1295–1303.
- Martínez-Vilalta, J., M. Mangirón, R. Ogaya, M. Sauret, L. Serrano, J. Peñuelas and J. Piñol. 2003. Sap-flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. *Tree Physiol.* 23:747–758.
- McDowell, N.G., N. Phillips, C. Lunch, B.J. Bond and M.G. Ryan. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiol.* 22:763–774.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species—the influence of boundary-layer and hydraulic properties. *Oecologia* 101: 514–522.
- Meinzer, F.C., M.J. Clearwater and G. Goldstein. 2001. Water transport in trees: current perspectives, new insights and some controversies. *Environ. Exp. Bot.* 45:239–262.
- Mencuccini, M. 2002. Hydraulic constraints in the functional scaling of trees. *Tree Physiol.* 22:553–565.
- Mencuccini, M. and L. Bonosi. 2001. Leaf area/sapwood area ratios in Scots pine show acclimation across Europe. *Plant Cell Environ.* 19:939–948.
- Mencuccini, M. and J. Grace. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiol.* 15:1–10.
- Mencuccini, M. and J. Grace. 1996a. Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. *Tree Physiol.* 16: 459–468.
- Mencuccini, M. and J. Grace. 1996b. Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant Cell Environ.* 19:939–948.
- Mencuccini, M., J. Grace and M. Fioravanti. 1997. Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. *Tree Physiol.* 17:105–113.
- Narasimhan, T.N. 2003. Maxwell, electromagnetism, and fluid flow in resistive media. *EOS* 84:469, 474–475.
- Nelson, R.A. 1999. Guide for metric practice. *Phys. Today* 52:11–12.
- Niklas, K.J. 1992. Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago, 607 p.
- Nobel, P.S. 1974. Introduction to biophysical plant physiology. W.H. Freeman, San Francisco, 488 p.
- Nobel, P.S. 1999. Physiochemical and environmental plant physiology. Academic Press, San Diego, 474 p.
- Ohm, G.S. 1827. Die galvanische Kette, mathematisch bearbeitet. Berlin. 1st Edn. T.H. Reimann, Berlin, 245 p.
- Oke, T.R. 1987. Boundary layer climates. 2nd Edn. Routledge, New York, 435 p.
- Patni, N.K., L. Masse and P.Y. Jui. 1996. Tile effluent quality and chemical losses under conventional and no-tillage. 1. Flow and nitrate. *Trans. Am. Soc. Agric. Engr.* 39:1665–1672.
- Phillips, N., B.J. Bond, N.G. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiol.* 22:205–211.
- Pothier, D., H.A. Margolis and R.H. Waring. 1989a. Patterns of change in saturated sapwood permeability and conductance with stand development. *Can. J. For. Res.* 19:432–439.
- Pothier, D., H.A. Margolis, J. Poliquin and R.H. Warin. 1989b. Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can. J. For. Res.* 19:1564–1570.
- Protz, C.G., U. Silins and V.J. Lieffers. 1999. Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine. *Can. J. For. Res.* 30:1088–1095.
- Rawls, W.J., L.R. Ahuja, D.L. Brakensiek and A. Shirmohammadi. 1993. Infiltration and soil water movement. In *Handbook of Hydrology*. Ed. D.R. Maidment. McGraw-Hill, New York, pp 5.1–5.51.
- Rayment, M.B., D. Loustau and P.G. Jarvis. 2000. Measuring and modeling conductances of black spruce at three organizational scales: shoot, branch and canopy. *Tree Physiol.* 20:713–723.
- Reid, D.E.B., U. Silins and V.J. Lieffers. 2003. Stem sapwood permeability in relation to crown dominance and site quality in self-thinning fire-origin lodgepole pine stands. *Tree Physiol.* 23:833–840.
- Reid, D.E.B., V.J. Lieffers and U. Silins. 2004. Growth and crown efficiency of height repressed lodgepole pine; are suppressed trees more efficient? *Trees* 18:390–398.
- Richter, H. 1973. Frictional potential losses and total water potential in plants: a re-evaluation. *J. Exp. Bot.* 24:983–994.



- Richter, H. 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. *J. Exp. Bot.* 48: 1–7.
- Ryan, M.J. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. *Bioscience* 47:235–242.
- Ryel, R.J., M.M. Caldwell, C.K. Yoder, D. Or and A.J. Leffler. 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130:173–184.
- Salisbury, F.B. and C. Ross. 1969. *Plant physiology*. Wadsworth Publishing, Belmont, CA, 747 p.
- Scholander, P.F., H.T. Hammel, E.A. Hemmingsen and E.D. Bradstreet. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proc. Nat. Acad. Sci. USA* 52: 119–125.
- Siau, J.F. 1971. *Flow in wood*. Syracuse University Press, Syracuse, NY, 131 p.
- Siau, J.F. 1983. *Transport processes in wood*. Springer-Verlag, Berlin, 245 p.
- Smith, L. and S.W. Wheatcraft. 1983. Groundwater flow. *In* Handbook of Hydrology. Ed. D.R. Maidment. McGraw-Hill, New York, pp 6.1–6.58.
- Sperry, J.S. 1995. Limitations on stem water transport and their consequences. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, New York, pp 105–124.
- Sperry, J.S., J.R. Donnelly and M.T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ.* 11:35–40.
- Spicer, R. and B.L. Gartner. 1998. Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood. *Tree Physiol.* 18:777–784.
- Spicer, R. and B.L. Gartner. 2001. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. *Trees* 15:222–229.
- Stöhr, A. and R. Lösch. 2004. Xylem sap flow and drought stress of *Fraxinus excelsior* saplings. *Tree Physiol.* 24:169–180.
- Stuart, M.A., F.J. Rich and G.A. Bishop. 1995. Survey of nitrate contamination in shallow domestic drinking water wells of the inner coastal plain of Georgia. *Ground Water* 33:284–290.
- Symbols Committee of the Royal Society. 1975. Quantities, units, and symbols: a report. 2nd Edn. The Royal Society, London, 53 p.
- Tyree, M.T. 1988. A dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. *Tree Physiol.* 4:195–217.
- Tyree, M.T. 1999. Water relations of plants. *In* Eco-hydrology. Eds. A.J. Baird and R.L. Wilby. Routledge, New York, pp 11–38.
- Tyree, M.T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. *Trees* 17:95–100.
- Tyree, M.T. and F.W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119:345–360.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88:574–580.
- Tyree, M.T. and M.H. Zimmerman. 2002. *Xylem structure and the ascent of sap*. 2nd Edn. Springer-Verlag, Berlin, 283 p.
- Tyree, M.T., S. Patino, J. Bennink and J. Alexander. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flow meter in the laboratory and field. *J. Exp. Bot.* 46:83–94.
- van den Honert, T.H. 1948. Water transport in plants as a catenary process. *Discuss. Faraday Soc.* 3:146–153.
- Whitehead, D. 1998. Regulation of stomatal conductance and transpiration in forest canopies. *Tree Physiol.* 18:633–644.
- Whitehead, D. and T.M. Hinckley. 1991. Models of water flux through forest stands: critical leaf and stand parameters. *Tree Physiol.* 9:35–57.
- Whitehead, D. and P.G. Jarvis. 1981. Coniferous forests and plantations. *In* Water Deficits and Plant Growth. Vol. 6. Ed. T.T. Kozlowski. Academic Press, New York, pp 49–52.
- Whitehead, D., W.R.N. Edwards and P.G. Jarvis. 1984a. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can. J. For. Res.* 14:940–947.
- Whitehead, D., P.G. Jarvis and R.H. Waring. 1984b. Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. *Can. J. For. Res.* 14:692–700.
- Zaitchick, B.F., H.M. van Es and P.J. Sullivan. 2003. Modeling slope stability in Honduras: parameter sensitivity and scale of aggregation. *Soil Sci. Soc. Am. J.* 67:268–278.
- Zimmerman, M.H. 1978. Hydraulic architecture of some diffuse-porous trees. *Can. J. Bot.* 56:2286–2295.