WATER TRANSPORT AND STORAGE IN DOUGLAS-FIR:

A MATHEMATICAL MODEL

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INTRODUCTION

Diurnal variation in tree stem circumference has been known for at
least a century. These more or less regular changes have been measured with
band dendrometers ever since the invention and development of these devices
by various Austrian forest botanists (to our knowledge, the earliest descriptions
of band dendrometers are those of Böhmerle [1883] and Friedrich [1890,
1897]). An excellent historical survey of dendrometry and its use in monitoring
dimensional changes in tree stems has been given by Breitsprecher and Hughes
(1975). More recent studies reported by Dobbs and Scott (1971), Lassoie
(1973, 1975), and Parlange et al. (1975) are representative of modern work
in the field.

Tree stem fluctuations are generally small, being of the order of 0.1
percent in Douglas-fir trees of 100 cm circumference and 20 m in height
(Dobbs and Scott 1971; Lassoie 1973). Stem circumference decreases steadily
throughout most of the daylight hours but slowly recovers during the night.
Rate of shrinkage seems directly related to rate of transpiration since
shrinkage rate is appreciably reduced by rain or fog, but is increased by
strong winds. Dobbs (1966) presents experimental evidence that dimensional
change occurs chiefly in the cambial zone and adjacent inner bark, and he
concludes that such dimensional changes are caused by movements of water to
or from the sapwood in response to tension gradients. If this interpretation
is correct, understanding of the mechanisms underlying these fluc, iations
may shed light on many aspects of water movements in trees.

Jarvis (1975) describes various water transport mechanisms in consider-
able detail in a recent review of transport processes in plants. In addition,
mathematical models of diurnal dimensional change in stems have been put

forward by several workers, including Molz and Klepper (1972, 1973) and
Parlange et al. (1975). Molz and Klepper postulate that diffusion of water
from inner bark and xylem occurs in response to changes in xylem water
tension. The Molz and Klepper model is concerned primarily with lateral
movement of water in phloem tissue, which is assumed to be characterized by
a constant coefficient of diffusivity. Coupling between lateral movement of
water in the phloem and vertical transport in the stem is not rigorously
examined. Parlange et al. (1975) further develop the concepts introduced by
Molz and Klepper, pointing out that sufficiently large change in water
content across the phloem will lead to a variable coefficient of diffusivity.
Hence, according to Parlange et al., the movement of water in the phloem is
essentially a nonlinear diffusion process. Using experimental observations
of circumferential changes in cotton stems and red pine, they obtain values
of an "integrated diffusivity." They relate these values to the time lag
between changes in foliage and stem water potentials and obtain good correspondence
with observed shrinking and swelling data.

Quite a different approach to the problem is taken by Waring and
Running (1976) and Running, Waring, and Rydell (1975), who develop computer
simulation models which represent water fluxes in Douglas-fir. Their
models include possible stem storage effects, and water transport in the
tree is coupled with that in the soil. The chief objective of their modelling
effort is to parameterize the effects of changes in system parameters such
as rooting volume, sapwood storage volume, and leaf area on quantities of
water stored in or transported through an entire tree or a stand of trees,
generally over periods of time ranging from one day to an entire growing
season. Waring and Running (1976, 1978) also review much recent literature
on seasonal changes in water storage in the inner sapwood. In addition,
they develop estimates of its magnitude in old-growth Douglas-fir, including
rates of withdrawal and recharge.

In the model presented here, we are concerned with descriptions of
phenomena with time scales of the order of a day; specifically, we consider
diurnal variations in sap flow velocity and phase lags associated with
diurnal fluctuations in stem circumference. Central to the model is the
concept that vertical flow in the xylem is concentrated in a narrow band of
young outer sapwood cells adjacent to the cambium and that tissues on both
sides of this flow band act as temporary storage sites for appreciable
amounts of water. The adjacent tissues are the inner bark (which we define

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as those tissues, including the cambium and inner phloem, located between
the sapwood and the corky outer bark), and the inner sapwood. In living
trees, water in the inner bark and inner sapwood is always subject to
tensions of varying magnitude that are transmitted from the zone of vertical
flow in the xylem. These negative pressures in the xylem sap are ultimately
related to evaporative losses from the crown of the tree. Because leaf
water tensions are considerably greater than those in the roots and soil,
pressure potential gradients are set up in the water-conducting tissues of
the tree. Mass flow of water from the roots toward the leaves takes place
in response to these gradients, but lateral movement of water between outer
sapwood and adjacent tissues also occurs when potential gradients are
sufficiently large.

MATHEMATICAL MODEL

In this section, we derive partial differential equations which govern
variations in the xylem water potential and also soil water potential;
temporal fluctuations in stem dimension as a function of height above the
ground are obtained from the solutions of the boundary value problem.

Water in trees is transported from roots to leaves along tension
gradients in the conducting system caused by transpirational losses from the
leaves. As the water content of leaf mesophyll tissue decreases, negative
pressures develop in the leaf xylem. These negative pressures are transmitted
throughout the entire vascular system of the tree by cohesive forces between
the water molecules (Slatyer 1967; Zimmerman and Brown 1971). Although
sizeable tensions develop in these water columns, cavitation is prevented by
the cohesion of adjacent water molecules and by their adhesion to the cell
walls of the conducting system. Moreover, the magnitude of the water
potential in living tissues adjacent to the xylem parallels the tension in
the xylem water column.

According to the cohesion theory, the principal forces at any point
along the stem (Fig. 1) are: the tension T (Newtons) in the water column,
which acts in the direction of the crown and is related to evaporation
originating in the leaves; frictional forces F acting in the direction
opposite to the flow (i.e., downward); and the force G due to gravity. To
simplify the analysis we assume that these forces act across annular regions
of approximately uniform area A_t (m^2) throughout the stem. We define $\psi^*(z,t) =$

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Fig. 1. Schematic representation of
geometrical relationships and principal
forces implicit in the Cohesion
Theory, as they apply to the stem of
a tree. At the tree-soil interface
level, the height z = 0 (m); at the
base of the crown z = H (m). When
the tension T (N) in the water
column, which is related to evaporative
forces in the crown, exceeds the sum
of frictional F (N) and gravitational
G (N) forces, mass flow of water
occurs in the positive z-direction
(upwards).
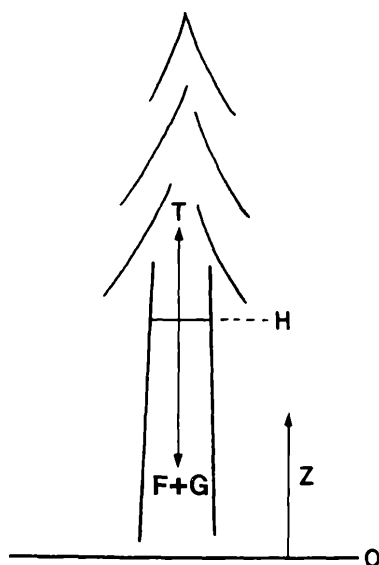
$-T/A_t$, the pressure (N m^{-2}) at height z (m) above the mean soil-root interface
at time t (sec, measured from midnight, say). The force due to gravity on a
differential section of thickness δz may be expressed as $\rho g A_t \delta z$, where ρ is
the fluid density (kg m^{-3}) and g is the acceleration due to gravity (m sec^{-2}).
The net water potential is $\psi_t^*(z,t) + \rho g z$ (N m^{-2}), and is usually denoted
by $\psi_t(z,t)$ (bar) (Slatyer 1967) (1 bar = 10^5 N m^{-2}).

Water flow in the vascular system of coniferous trees occurs in the
sapwood, a tissue of elongated nonliving cells called tracheids, which
communicate with each other through a number of pores equipped with porous
membranes. Resistance to flow occurs in the cell lumen, in the tortuous
passageway through the pores, and at the pit membrane, a meshwork of many
fine fibrils. Since the dimensions of the pathway are small, the viscous
forces are very large compared to inertial forces. In such a case, the
pressure gradient is balanced by viscous forces, so that the equation
governing the motion of the fluid in the vertical direction may be written

$$- \frac{\partial \psi_t}{\partial z} + \mu \frac{\partial^2 w}{\partial z^2} = 0, \qquad (1)$$

where μ is the viscosity of the fluid (N sec m^{-2}) and w is the rate of flow
in the vertical direction (m sec^{-1}).

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Now, if the xylem could be idealized as a system of thin tubes, the volume rate of flow Q (m^3 sec^{-1}) normal to an area of A_t would be given by a version of the Poiseuille law. However, in media of more complex geometry, the Poiseuille law is usually replaced by Darcy's law:

$$Q = - \frac{k}{\mu} A_t \frac{\partial \psi_t}{\partial z} , \qquad\qquad (2)$$

where the value of the constant k (m^2), the so-called permeability of the medium, must be determined by experiment. Application of Darcy's law to water flow in saturated soils is justified by numerous observations, in which rate of flow has been found to be proportional to the pressure gradient. In the sapwood of coniferous trees, Darcy's law has been shown to be valid by a number of other workers, such as Comstock (1965) and Erickson and Crawford (1959). Since wood is not an isotropic medium, for flow in the vertical direction, it is appropriate to introduce a longitudinal permeability k_t (m^2), the value of which has been determined by experiment for a number of coniferous trees. Since the flow velocity w(z,t) is equal to $Q(z,t)/A_t$, Darcy's law can be written in the convenient form

$$A_t \ w(z,t) = - \frac{k_t}{\mu} \ \frac{\partial \psi_t}{\partial z} \qquad\qquad (3)$$

The model developed here is based on the working assumption that water moves radially between the inner bark and the xylem in response to gradients in pressure potentials between the two tissues. We assume a constant, essentially saturated water content in the inner bark. It follows that the diffusivity is approximately constant throughout the inner bark. This assumption differs from that of Parlange et al. (1975) who, as already noted, use a diffusivity depending on variable phloem water content. Our theoretical development could be extended to include such nonlinear diffusion processes in plants if appropriate. However, by way of justification of our assumption, we suggest the following mechanism of dimensional change. The outer bark, a tissue which includes the zone of mostly nonliving fiber and cork cells outside the phloem parenchyma, acts as impermeable elastic sleeve. Increasing tension in the xylem water is transmitted by cohesive forces between water molecules in the xylem to the water bathing the cells of the inner bark. As the water potential of intercellular water decreases to a level below that of the cell vacuoles, water moves out of the cells and joins the general flow toward the xylem. The chief pathway of this flow is

along and inside the cell walls of the inner bark, although some water may
move from cell to cell by osmosis across the membranes (Weatherley 1970).
Increased tension in the intercellular water of the inner bark and decreased
turgor of its living cells imply a reduction of the forces resisting the
inward movement of the outer bark. This tissue possesses some elasticity in
the tangential direction and also is pushed inward by atmospheric pressure.
Accordingly, as the inner bark loses water, it is compressed and its tissue
volume decreases, but the water content of its cell walls and protoplasts
does not change appreciably. (Anticipating the model results, the total
volume change of nonfibrous inner bark cells is less than six percent in
Douglas-fir.)

Loss of water by the inner bark cells continues until their water
potential is approximately equal to that of the intercellular water.
Jarvis (1975) has reviewed a considerable body of evidence which suggests
that the water content of the inner bark responds rather quickly to changes
in sapwood tension.

It is postulated that changes in inner bark volume are the result of
radial movement of water caused by changes in xylem water tension; consequently,
it may be assumed that

$$\delta\psi = E_* \frac{\delta V}{V_o} \tag{4}$$

is valid in the inner bark. Here, E_* ($N\ m^{-2}$) is a volume modulus of elasticity
and δV (m^3) is the volume of an element of inner bark whose mean volume is
V_o. In the absence of evidence to the contrary, it is assumed that dimensional
changes in the vertical can be neglected, so that we may develop a quantitative
description of fluid flow in a disk of constant thickness δz (m) in the stem
at height z (m). Let R_x (m) denote the outer radius of the xylem (Fig. 2),
let r_o (m) the mean thickness of the inner bark, and let $R_o + r(z,t)$ denote
the true radius at height z and time t. Thus, $r(z,t)$ measures excursions of
the inner bark radius about its mean, R_o, and can be positive or negative.
The volume of inner bark in an annular ring of thickness δz is $\pi(R_o + r)^2\delta z -
\pi R_x{}^2\delta z$. When r is neglected compared with R_o, the ratio $\delta V/V_o$ is

$$\frac{\delta V}{V_o} = \frac{2\pi(R_o + r)\ \delta r\delta z}{\pi(R_o{}^2 - R_x{}^2)\delta z} \doteq \frac{2\pi(R_o + r_o)\delta r}{A_o}$$

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where
$$A_o = \pi(R_o^2 \quad R_x^2)$$

Fig. 2. Schematic representation of
the cross section of the stem of a
tree. R_x (m) is the radial distance,
measured from the center of the tree
to the border between the inner and
outer sapwoods. $R_x + r_o$ (m) is the
mean distance, measured along a
radius, from the center of the tree
to the border between inner and
outer bark zones. Variations in
this distance about the mean $R_x + r_o$
are measured by r(z,t). Vertical
flow is concentrated in narrow zone
of outer sapwood in the annular
section whose inner and outer radii
are R_x and $R_x + r_o$, respectively.
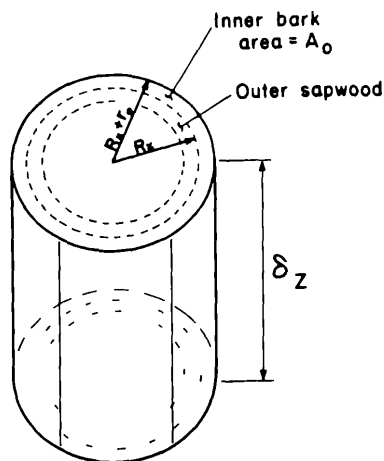
it follows that

$$\delta\psi_t = E \frac{\delta r}{r_o} \tag{5}$$

where $E = \dfrac{2\pi r_o(R_x + r_o)}{A_o}$ E_* is a linear modulus of elasticity (N m^{-2})

measured in the radial direction. Equation 5 is essentially a form of
Hooke's law, which states that change in dimension is proportional to
change in applied force per unit area (equivalently, to the change in water
potential).

Jarvis (1975) also has reviewed evidence for change in water content of
the sapwood. He concluded that at the time of his writing, the extent to
which the water stored in the sapwood interacts with that in the transpiration
stream was not determined. Subsequently, as remarked earlier, Waring and
Running (1978) estimated seasonal rates of withdrawal and recharge of water
stored in the inner sapwood of old-growth Douglas-fir. Their work supports
our assumption that water is exchanged between inner and outer sapwood along
potential gradients. Mass flow toward the inner sapwood occurs when its
matric potential falls below the pressure potential of the transpiration
stream. In sapwood cells which are not saturated with water, water movement
probably occurs along and within cell walls. Gases, including water vapor,

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in the lumens of these cells may then eventually dissolve. (Professor H.
Richter pointed out to us that Bode (1923) presents a very detailed descrip-
tion of the disappearance of gas bubbles in the xylem cells of certain
herbaceous plants, under rather similar circumstances.) We also make the
assumption that radial flow is reversible, so that at night there can be
appreciable net flow inwards and, during the day, outwards; i.e., from the
inner sapwood storage zones to the transpiration stream.

By way of recapitulation, we assume that water is transported radially
between the outer sapwood of the xylem (the principal pathway of vertical
movement of water) and both the inner sapwood and the inner bark. We now
inquire as to the importance of these radial movements in the total water
budget of the tree. To obtain a quantitative estimate, we begin by calcu-
lating the change during time δt in the amount of water contained in the
outer sapwood and inner bark of an annulus δz (m) thick at height z (m)
above the ground.

By assumption, the inner bark tissue is essentially saturated with
water at all times, so that the inner bark must gain an amount of water δV
equal to its total change of volume in unit time. An increase of water held
in the inner bark leads to an increase in tissue volume, producing a net
outward movement of the outer bark and a corresponding increase in tree stem
radius. Suppose now that the inner sapwood gains an amount of water δS and
that the rate of change of sapwood storage is proportional to that of inner
bark storage:

$$\frac{\delta S}{\delta t} = \alpha \frac{\delta V}{\delta t} = \alpha \frac{\delta A}{\delta t} \; \delta z \qquad\qquad (6)$$

This assumption is essentially an hypothesis that sapwood permeability in
the radial direction is α times as large as the permeability to flow from
sapwood to inner bark. From the foregoing arguments we now observe that the
product of $(1 + \alpha)$ and the time rate of change of the inner bark volume V
must equal the negative gradient of the flow Q in the vertical direction:

$$2\pi(1 + \alpha)(R_x + r_o) \frac{\partial r}{\partial t} = - \frac{\partial Q}{\partial z}$$

or, since $Q = A_t w$, and A_t is assumed to be roughly constant,

$$A_t \frac{\partial w}{\partial z} + 2\pi(1 + \alpha)(R_x + r_o)\frac{\partial r}{\partial t} = 0. \qquad\qquad (7)$$

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Equations 3, 5, and 7 can be combined to obtain a partial differential equation for ψ_t:

$$\frac{\partial \psi_t}{\partial t} = \frac{k_t A_t E}{2\pi\mu(R_x + r_o)(1 + \alpha)r_o} \frac{\partial^2 \psi_t}{\partial z^2} \tag{8}$$

Equation 8 has the form of a "diffusion" equation with diffusivity

$$D_t = \frac{k_t A_t E}{2\pi\mu(R_x + r_o)(1 + \alpha)r_o} \ m^2 \ sec^{-1} \tag{9}$$

Moreover, because of the linearity of the relation between ψ_t and r, we may also write:

$$\frac{\partial r}{\partial t} = D_t \frac{\partial^2 r}{\partial z^2} \ . \tag{10}$$

To find solutions for Equation 8 (or 10), it is necessary to formulate boundary conditions derived from a consideration of the physical nature of the system. Field studies on Douglas-fir (Fritschen and Doraiswamy 1973) have shown that variation in rate of water loss from a tree-soil system is approximately periodic. Maximum rate of water loss generally occurs shortly after noon, and the minimum rate somewhat before dawn. As a "first approximation," the rate of flow of water out the top of the system is represented by a trigonometric function. (Although this is only a rough approximation to the true nature of the variation, the analysis could easily be extended by the use of Fourier series to provide greater accuracy.) Restricting attention to a single mode of circular frequency $\omega = 2\pi/t_o$, we write

$$Q(H,t) = Q_o(1-\cos \frac{2\pi}{t_o} t) \tag{11}$$

where H (m) is the height of the stem immediately below the first branch of the crown, Q_o (m^3 day^{-1}) is the average volume of water used by the tree in one day, and $t_o = 8.64 \times 10^4$ seconds (one day) is the fundamental period of the process. With the use of (2), Equation (11) is written in the form

$$\frac{\partial \psi_t}{\partial z} = - \frac{\mu Q_o}{k_t A_t} \ (1-\cos \frac{2\pi}{t_o} t), \ \text{at} \ z = H. \tag{12}$$

Soil-plant interactions at the lower end of the system lead to a number of complications. A detailed treatment of the problem would require models of transport of water through the soil to the root and across the root cortex and endodermis to the root xylem and thence to the main transpiration stream. Although movement of water from the soil to an individual rootlet is reasonably well understood (Gardner 1960; Farnum and Carey 1975), mass movement into a root system is not so simply described. Each rootlet acts as a local sink, tending to deplete the soil in its neighborhood and, in this way, reducing transport to neighboring rootlets. Accordingly, a realistic model would require a description of the geometry of the entire root system. It is obvious that such geometry will vary greatly with soil type, availability of moisture and nutrients, and spatial distribution and abundance of other organisms.

These complications are avoided by idealizing the root system of a Douglas-fir tree as a large membrane or "suction plate" (Fig. 3). Thus, suppose that soil water moves vertically upward toward the tree through an unsaturated soil from a region of constant potential (such as one near a water table). For simplicity, we assume constant soil conductivity and diffusivity, a condition that is approximated in reality if soil moisture content in the region of flow varies only slightly over the period of observation. Again, for simplicity, neglect change in water content by

Fig. 3. Schematic representation of vertical flow in two connected cylinders. The upper narrow cylinder represents the stem of a tree in which flow is concentrated in the outer sapwood, modeled as a thin-walled annular cylinder. The lower, thick cylinder represents the soil. All water moving vertically in the lower cylinder is assumed to pass without loss into the upper cylinder across an interface of permeability h (m sec^{-1}), which represents the root system.
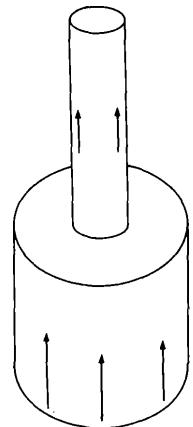
infiltration or evaporation from the soil surface or by lateral movement to
or from adjacent soil columns. Finally, we assume that the permeability of
the "suction plate" is approximately that of a root membrane. Under these
conditions, the following relations hold (c.f., Rose 1966; Eagleson 1970):

$$\frac{\partial \Theta}{\partial t} = D_s \frac{\partial^2 \Theta}{\partial z^2} ,$$

where $\Theta(z,t)$ is the soil moisture content (m^3 water/m^3 soil) and D_s (m^2 sec^{-1}) is the soil diffusivity. If variations in soil water content are small,
the soil moisture potential $\psi_s(z,t)$ (bars) is approximately proportional to
soil moisture content:

$$\frac{\partial \psi_s}{\partial t} = D_s \frac{\partial^2 \psi_s}{\partial z^2} \tag{13}$$

Suppose that some depth $z = -L$ (m), the soil moisture potential attains
an approximately constant value denoted by B_o (bars). To complete the
mathematical statement of the problem, it remains only to formulate boundary
conditions at the soil-plant interface ($z = 0$). If there is no water
accumulation at the interface, then

$$w_s A_s = w_t A_t \quad \text{at } z = 0, \tag{14}$$

where w_s and w_t (m sec^{-1}) are flow velocities in soil and tree, respectively,
and A_s and A_t are the corresponding flow areas. Assuming that both soil and
tree flow rates are described by Darcy's law, we can write

$$w_s = - \frac{k_s}{\mu} \frac{\partial \psi_s}{\partial z}$$

$$w_t = - \frac{k_t}{\mu} \frac{\partial \psi_t}{\partial z}$$

Here we have written the "hydraulic conductivity of the soil" K (m sec^{-1})
(see, e.g., Philip 1957) as k_s/μ to conform with our formulation of Darcy's
Law for the tree (Equation 2). The soil permeability k_s is, of course,
measured in m^2.

Substitution in (14) gives

$$\frac{\partial \psi_s}{\partial z} = \frac{A_t}{A_s} \frac{k_t}{k_s} \frac{\partial \psi_t}{\partial z} \text{, at } z = 0 \tag{15}$$

Finally, since the rate of movement of water across a membrane is proportional to the difference in water potential on the two sides of the membrane, we have the relation

$$w_s = h_s (\psi_s - \psi_t) \tag{16}$$

where h_s (m sec^{-1} bar^{-1}) is the membrane permeability, and accordingly is a measure of flow velocity at the soil-root interface per unit difference in water potential between soil and tree. A corresponding measure for flow in the tree is denoted by h_t. Since $w_s A_s = w_t A_t$, we have $h_s = h_t A_t/A_s$.

In summary, we seek the periodic solution of the following equations:

$$\frac{\partial \psi_t}{\partial t} = D_t \frac{\partial^2 \psi_t}{\partial z^2} \text{ in } 0 \leq z \leq H,$$

and

$$\frac{\partial \psi_s}{\partial t} = D_s \frac{\partial^2 \psi_s}{\partial z^2} \text{ in } -L \leq z \leq 0;$$

subject to

$$\frac{\partial \psi_t}{\partial z} \quad \frac{Q_o}{k_t} (1-\cos\frac{2}{t_o} t) \text{ at } z = H, \tag{17}$$

$$\psi_s = B_o \text{ at } z = -L,$$

$$\frac{\partial \psi_s}{\partial z} = \frac{A_t}{A_s} \frac{k_t}{k_s} \frac{\partial \psi_t}{\partial z} \text{ at } z = 0,$$

and

$$\frac{\partial \psi_s}{\partial z} = - \frac{h\mu}{k_s} (\psi_s \quad \psi_t) \text{ at } z = 0.$$

Closed-form solutions for ψ_t and ψ_s can be derived in a straightforward way and, from these expressions, it is easy to obtain formulas for flow velocities in tree and soil and for changes in stem circumference and amounts of water stored at any time in the bark. To compare the solutions with field observations, numerical estimates are required of D_t, Q_o, and other constants in the system (17).

Many of our parameter estimates and observational data come from

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studies on forest-grown Douglas-fir trees carried out by Lassoie (1973, 1975), Fritschen et al. (1973, 1977), Salo (1974), and Doraiswamy (1976) as contributions to the Coniferous Forest Biome, International Biological Program. As a part of that Program, measurements were made on 50-year-old trees, most about 30 meters tall, located within 1 km of the Allen E. Thompson Research Center, near Ravensburg, Washington (approximately 55 km southeast of Seattle). Physical characteristics of the Thompson site have been described by Cole and Gessel (1968) and Fritschen et al. (1973). Other estimates are obtained from Douglas-fir trees grown elsewhere in the western United States.

Where possible, data for parameter estimates are taken from a lysimeter system containing a living 28-m Douglas-fir tree, as described by Fritschen, Cox, and Kinerson (1973) and Fritschen, Hsia, and Doraiswamy (1977). These include clear trunk length H = 14.0 m; diameter at breast height = 0.40 m; soil flow area A_s = 30.98 m^2 (the crown projection area of the lysimeter tree); and total daily flow of water through the tree-soil system Q_o = 56.4 liters day^{-1}. The last value corresponds to the mean of the three summer months of July, August, and September 1973, when mean rate of evapo-transpiration from the lysimeter system was 1.82 X 10^{-3} m day^{-1} per unit area of crown projection. During those months, Lassoie (1975), Salo (1974), and Doraiswamy (1976) measured sap flow velocity, variations in stem circumference and area, branch xylem water potential, and rates of evapo-transpiration using the Bowen ratio technique on several trees at the lysimeter site, in addition to detailed work on relationships between rates of photosynthesis and meteorological variables.

The xylem radius R_x is taken to be 0.185 m, and the total bark thickness is about 1.0 X 10^{-2} m. Inner bark thickness r_o was measured by us (on another tree of comparable size) as 3.8 X 10^{-3} m. An estimate of A_t, the effective area of sapwood through which water flows at a radially averaged rate of w(z,t) m hr^{-1}, was obtained from measurements of radial distributions of flow velocities made by Lassoie (1975) in Douglas-fir, and Swanson (1966) and Mark and Crews (1973) in other conifers. Water flow is detected by the heat-pulse velocity technique (Swanson 1972) up to a depth of 0.08 m measured inward beyond the cambium, but important contributions to flow apparently are concentrated in a band about 0.01 m wide centered at a depth of about 0.015 m from the cambium. Since the xylem radius R_x is taken to be 0.185 m and A_t = $\pi(0.175^2 - 0.165^2)$ = 1.068 X 10^{-2} m^2, a mean

volume flow rate of 56.4 liters day^{-1} = 2.35 liters hr^{-1} gives an average
flow velocity of 0.22 m hr^{-1}. The assumption of a sinusoidal variation in
flow velocity at the top of the system gives a maximum flow rate at that
point of 0.44 m hr^{-1}, which is about twice Lassoie's observed maximum
heat-pulse velocity, but somewhat less than 0.63 m hr^{-1}, the rate reported
by Vité (1960) in _Pinus ponderosa_. Since Vité's result was based on the
movement of an injected dye, it must be interpreted with caution. As
Zimmermann (in Zimmermann and Brown 1971:170) has emphasized, injection of
a liquid can modify normal potential gradients drastically. Indeed, at the
point of injection of the liquid, the formerly negative potential becomes + 1
bar. Since according to Darcy's law, velocity is proportional to potential
gradient, flow rates of the dye should be greater than those in an intact
tree. Moreover, because flow velocities are not uniform in the area of
flow, some of the dye would flow faster than the radially averaged velocity
even if a change in potential did not occur at the point of injection, and,
of course, in any experiment the fastest-moving dye would be detected
first.

We lack accurate values of soil conductivity k_s and diffusivity D_s in
the neighborhood of the lysimeter tree. From measurements at the Allen
Thompson Research Center, Cedar River Watershed, Machno (1975) and Hatheway
et al. (1972) calculated "bulk" or average values of k_s = 6.67 X 10^{-13} m^2
and D_s = 1.35 X 10^{-7} m^2 sec^{-1} at 26 percent moisture content in the upper
0.1 m of a gravelly-to-stony phase of the Everett sandy loam series. The
soils of the lysimeter tree site, some distance away, were appreciably more
moist and more compact. We carried out parallel calculations, in which we
used parameters values of the Yolo light clay soil reported by Philip
(1957). In this soil, k_s = 2.15 X 10^{-15} m^2 and D_s = 7.67 X 10^{-9} m^2 sec^{-1}
at 20 percent volumetric water content. Presumably values at the lysimeter
site were intermediate between those of the Yolo soil and the gravelly-to-
stony Everett site value. We estimated a value B_o = -2.51 bar for the
(constant) soil water potential at a distance L = 7 cm below the root mass.

The value assigned to the root permeability h_s was 0.5 X 10^{-8} m sec^{-1}
bar^{-1}, an average for cell membrane permeability suggested by Slatyer
(1967, pp. 186, 204). As previously mentioned, a more realistic value for
this permeability would include a correction for surface area of effectively
absorbing roots in the soil under the tree.

For most calculations, the permeability of Douglas-fir sapwood was

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taken to be 9.89 X 10^{-12} m^2, the average of 10 measurements on each of four
western Washington Douglas-fir trees reported by Erickson and Crawford
(1959). Calculations were also made with a lower average permeability
value of 2.80 Darcys (2.80 X 10^{-12} m^2), reported by Markstrom and Hann
(1972), for fresh sapwood of 10 Douglas-fir trees growing near Fort Collins,
Colorado. A comparable measurement of 5.50 Darcys was obtained by Comstock
(1965) in fresh eastern hemlock sapwood. Even smaller values of conifer
permeability have been obtained by Lin et al. (1973) and Bailey and Preston
(1970), but their material was dried before measurement.

Petty and Puritch (1970) suggested that permeability might be calculated
by a modification of Poiseuille's law, making use of estimates of the
numbers and sizes of capillaries involved in the flow through conifer
tracheids. However, much of the resistance to flow is presented by the
membranes of the bordered pit-pairs. Petty and Puritch used the electron
microscope to estimate the sizes and numbers of pores in conifer pit
membranes. Subsequently, Sachs and Kinney (1974) showed that the largest
openings in conifer membranes are less than 7 X 10^{-8} m in diameter, about
30 percent of the value used by Petty and Puritch. Since permeability
increases as the third power of the diameter in the appropriate modification
of Poiseuille's law, very accurate estimates of pit membrane pore diameters
are needed, but are evidently unavailable.

Our estimate of the compressional (linear) modulus of elasticity,
E = 3.01 X 10^6 N m^{-2}, is based on two laboratory measurements we made using
an Instron TT-DL machine. Similar values have been obtained in different
tissues by other workers; e.g., Hellqvist et al. (1974). As remarked
earlier, we have no direct estimate of the radial permeability parameter
α. Hence, we made the working assumption that sapwood permeability in the
direction of the center of the tree equals that toward the bark and, con-
sequently, α = 1.0. Finally, we assumed the viscosity of xylem sap to be
0.01 poise = 10^{-3} N sec m^{-2}.

RESULTS

1.   Qualitative Predictions of the Model
Model results are depicted in Figs. 4-9 and Fig. 11. These include
variations in plant water potential, sap flow velocity, soil water flow
velocity, and profiles of plant water potential and sap flow velocity.

Variations in stems circumference are also shown in Figs. 4 and 5, since they are proportional to variations in plant water potential (see Equation 5).

From Figs. 4 and 5 it can be seen that the amplitude of time fluctuations in sap velocity and plant water potential (Figs. 7 and 8) vary with height z along the stem. Moreover, phase lag phenomena are clearly present and appear as a property of the model solutions. In the graphs, maximum plant water potential at the top of the system (i.e., at the base of the crown) occurs from 0.5 to 2.8 hr before the maximum at the soil interface, depending on soil diffusivity. In addition, sap flow velocity is out of phase with plant water potential.

The mathematical solutions are functions $\psi_t(z,t)$ and $\psi_s(z,t)$ which represent water potentials in tree and soil, respectively, at distance z above the tree-soil interface and at time t (measured in hours) from the hour at which flow velocity at the top of the system is a minimum--from
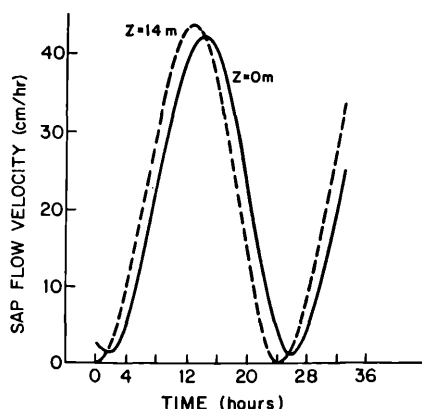

Fig. 4. Time variations in sap flow velocity in the stem of a tree at z = 0 and z = 14 (m) when Erickson stem and Everett soil parameters are used in the model ($k_t = 9.89 \times 10^{-12}$ m^2; $D_s = 1.35 \times 10^{-7}$ m^2 sec^{-1}; $k_s = 6.67 \times 10^{-13}$ m^2).
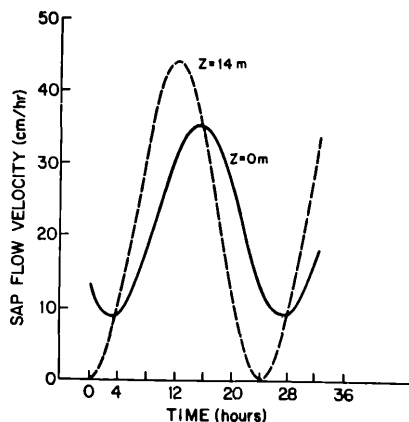
Fig. 5. Time variations in sap flow velocity in the stem of a tree at z = 0 and z = 14 m when Markstrom-Hann stem and Yolo soil parameters are used in the model ($k_t = 2.80 \times 10^{-12}$ m^2; $D_s = 7.67 \times 10^{-9}$ m^2 sec^{-1}; $k_s = 2.15 \times 10^{-15}$ m^2).

about midnight to 2 a.m. These functions are expressions of the form

$$\psi_t(z,t) = e^{\gamma z}(a_1 \cos u + b_1 \sin u) + e^{-\gamma z}(a_2 \cos v + b_2 \sin v) + cz + d \quad (18a)$$

where a_1, a_2, b_1, b_2, c, d, and γ are somewhat cumbersome functions of system parameters, including k_t, k_s, D_t, D_s, and h_s; u and v are functions of x and t:

$$u = \gamma z + 2\pi t/t_o$$

$$(18b)$$

$$v = \gamma z - 2\pi t/t_o$$

where t_o is the period of the fluctuations (one day).

Each of the four functions of the form $e^{\pm\gamma z} \cos(\gamma z \pm 2\pi t/t_o)$ represents an attenuated "traveling wave" defined over the region $0 \le z \le H$, $0 \le t \le t_o$. The endpoints of the distance interval $z = 0$ and $z = H$ correspond to the
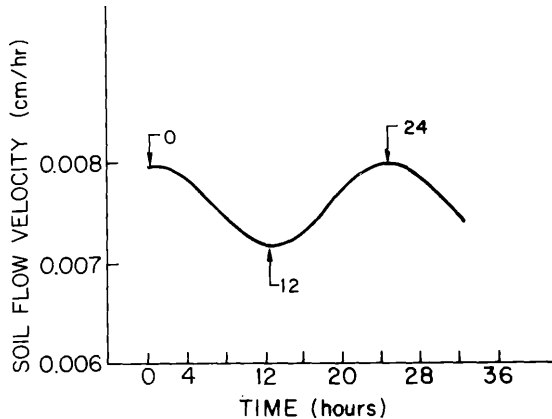
Fig. 6. Time variations in soil water flow velocity at 3.5 cm below the tree-soil interface when Erickson stem and Yolo soil parameters are used in the model ($k_t = 9.89 \times 10^{-12}$ m^2; $D_s = 7.67 \times 10^{-9} m^2 sec^{-1}$; $k_s = 2.15 \times 10^{-15} m^2$). Using this combination of parameters, the phase at the interface lags that at the base of the crown by about 12 hours. The corresponding phase lag using the Erickson-Everett parameter combination is about 9 hours; that using the Markstrom-Hann-Yolo combination is about 21 hours.

tree-soil interface and the base of the crown, respectively. At the base of the crown, the wave $a_1 e^{\gamma z} \cos(\gamma z + 2\pi t/t_o)$ has amplitude $a_1 e^{\gamma H}$; at the soil interface its amplitude is a_1.

At any given height z_1, the term $e^{-\gamma z_1} \cos(\gamma z_1 - \frac{2\pi}{t_o} t)$ will have a relative maximum when $\cos(\gamma z_1 - 2\pi/t_o \cdot t) = 1$, i.e., when $t = \gamma z_1 t_o/2\pi = t_1$, say. At height z_2, a relative maximum will occur at time $t_2 = \gamma z_2 t_o/2\pi$. The difference in times at which these maxima occur is

$$t_2 - t_1 = \frac{\gamma t_o}{2\pi} (z_2 - z_1), \tag{19}$$

and there is, therefore, an apparent phase lag associated with the "traveling

wave." Clearly, it is directly proportional to the distance between the two positions on the tree and to $\gamma/2\pi = (2\pi D_t)^{-1/2}$.

Because the expression $\psi_t(z,t)$ is a combination of four waves weighted by different functions of position z, the phase lag generally will not be given by an expression quite so simple as Equation 19. However, it is possible to determine relative maxima and minima of $\psi_t(z,t)$ at several positions and for several values of γ. The resulting phase lags are plotted in Fig. 11 as functions of γ (or, equivalently, as functions of $D_t^{-1/2}$). From Fig. 11 it can be seen that the phase lags are approximately linear functions of γ over most of its range. The fact that, in the model, sap
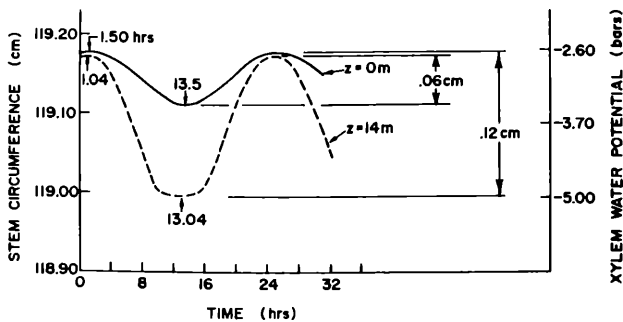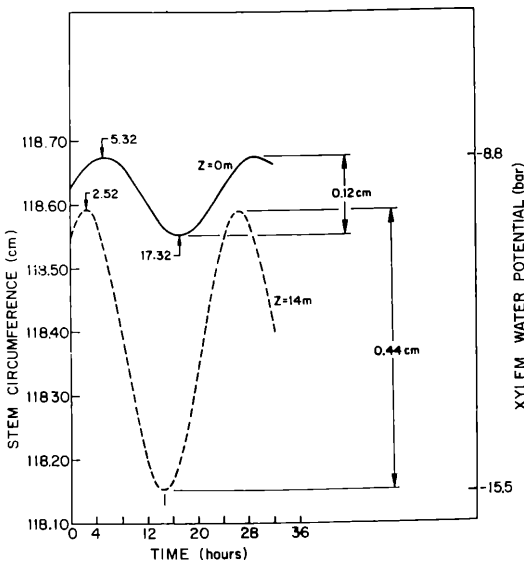

Fig. 7. Time variations in water potential and stem circumference in the trunk of a tree 40 cm in diameter at z = 0 and z = 14 m; when Erickson stem and Everett soil parameters are used in the model ($k_t = 9.89 \times 10^{-12}$ m^2; $D_s = 1.35 \times 10^{-7}$ m^2 sec^{-1}; $k_s = 6.67 \times 10^{-13}$ m^2).

Fig. 8. Time variations in water potential and stem circumference in the trunk of a tree 0.40 m in diameter at z = 0 and 14 (m) when Markstrom-Hann stem and Yolo soil parameters are used in the model ($k_t = 2.80 \times 10^{-12}$ m^2; $D_s = 7.67 \times 10^{-9}$ m^2 sec^{-1}; $k_s = 2.15 \times 10^{-15}$ m^2).

flow velocity is out of phase with plant water potential is essentially a consequence of Darcy's law, Equation (2).

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2.   Comparison with Observation

a.   Sap flow velocity

When the Erickson-Crawford estimate of k_t and the Everett soil parameters are used (see Fig. 4), sap flow velocity varies between 0 and 0.44 m hr^{-1} at the top of the system (imposed by the boundary conditions [Equations 11 or 12]) and between 0.014 and 0.426 m hr^{-1} at the tree-soil interface. Maximum flow rate at this interface lags that at the top of the system by less than two hours and lags minimum xylem water potential at the interface by only a few minutes. If we use (Fig. 5) the Markstrom-Hann estimate of k_t and the Philip (i.e., Yolo light clay) soil parameters, the sap flow velocity near the interface varies between 0.091 and 0.349 m hr^{-1}, and maximum flow rate at the interface lags that at the top of the system by about 4 hr and lags minimum water potential at the interface by about 1.5 hr.

b.   Soil water flow

Variations in rate of soil water flow can also be estimated from the model. The flow velocity at 0.035 m below the soil-tree interface varies between 0.7 X 10^{-5} and 12.4 X 10^{-5} m hr^{-1} when the Erickson-Crawford k_t value and the Everett soil parameters are used. Maximum speed in the soil lags maximum speed at the top of the stem by about nine hours. With the Markstrom-Hann and Yolo parameter values, the corresponding lag increases to about 21 hours and fluctuations in flow velocity are strongly damped (total variation is between 7.5 X 10^{-5} and 7.7 X 10^{-5} m hr^{-1}).

These results may be compared with those of Cole (1966), who studied diurnal fluctuations in flow rates 36 inches (0.91 m) below a forested Thompson site soil in early June 1966. On June 14, flow velocity varied between 1.5 X 10^{-5} and 4.8 X 10^{-5} m hr^{-1}. Maximum flow rate occurred at approximately midnight, probably 10 to 12 hr after maximum flow rate near the base of the crowns of the trees. In Fig. 6 we show the effect of combining Everett stem and Yolo soil parameters. Under these model conditions maximum flow rate of 8.0 x 10^{-5} m hr^{-1} occurs at midnight.

c.   Xylem water potential

Gradients of xylem water potential also depend on parameter estimates. The Erickson-Crawford k_t and the Everett soil parameters yield a maximum potential gradient of 0.12 bar m^{-1} which nearly coincides with maximum flow velocity at the base of the crown. The corresponding result for the Markstrom-

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Hann and Yolo parameter values is a maximum xylem potential gradient of about 0.36 bar m^{-1}, occurring two hours later (Figs. 7 and 8).

d.   Circumferential change

     We compare our model results (Figs. 7 and 8) with measurements by Dobbs and Scott (1971), who worked near LaGrande, Washington, in 1965. Their study trees were 17 to 18 m tall and 0.22 to 0.41 m d.b.h., somewhat smaller on the average than the lysimeter tree. Soil conditions were generally comparable to those at the Cedar River lysimeter site (Fritschen, personal communication). Accordingly, phase lags and total circumferential change should be roughly comparable to those at the lysimeter site.

     As already noted, maximum circumferential change in the Dobbs-Scott tree "A" was about 0.11 cm at internode 13 (counted from the apex); at internode 22, the total variation was about half this value. Phase lags between maxima at these two positions were generally between two and four hours. As may be noted in Figs. 4 and 5, total calculated circumferential change near the top of the system is 0.06 to 0.12 cm, according to our choice of parameter values. Near the ground, it is 0.12 to 0.44 cm, in qualitative but not close quantitative agreement with the Dobbs-Scott results.

e.   Temporary water storage

     An estimate can be made of the amount of water moving from storage in the inner bark and sapwood into the transpiration stream in the outer sapwood, based on a calculation of total inner bark volume $V_B(t)$ (cm^3):

$$V_B(t) = \int_0^H A(z,t) \, dz \qquad\qquad (20)$$

Change in inner bark volume between times t_1 and t_2, $\delta V_B = V_B(t_2) - V_B(t_1)$, is equivalent to the change in water volume of water stored in the inner bark during that time interval. Since the time rate of change of water volume stored in the inner sapwood is proportional to that of the inner bark (Equation 6), total storage change in the tree over the time interval t_1 t_2 is

$$\delta V_t = (1 + \alpha) \delta V_B, \qquad\qquad (21)$$

where the radial permeability α is of the order of unity, by assumption, and

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where $V_t(t)$ (cm^3) is the total volume of water stored in the tree at time t. Unfortunately, no direct field measurements of change in volume of water stored are available. However, a measured total circumferential change of 10^{-3} m in a tree of stem diameter 0.40 m and height 14 m (Dobbs and Scott, 1971) corresponds to a total change in storage (in the inner bark and sapwood) of about 10.6 liters, which is at the upper range of values predicted
5 by using Equation 21 -- about 5 to 10 liters, depending on choice of parameter values (Fig. 9).

DISCUSSION

1.   Mechanistic Considerations

The present model may be compared with the one suggested by Weatherley (1970) and modified by Jarvis (1975). Weatherley conceives of a system (see Fig. 10) consisting of two porous pots L and R which represent crown and root systems. They are filled with water and connected by a tube of low resistance that represents the transpiration pathway. Weatherley connects a single manometer representing water storage tissues to the tube. As water is lost from pot L, tension in the tube increases and is transmitted to the manometer, so that water lost by L is replaced from both the tube and the manometer. The mercury in the manometer rises until it reaches some constant
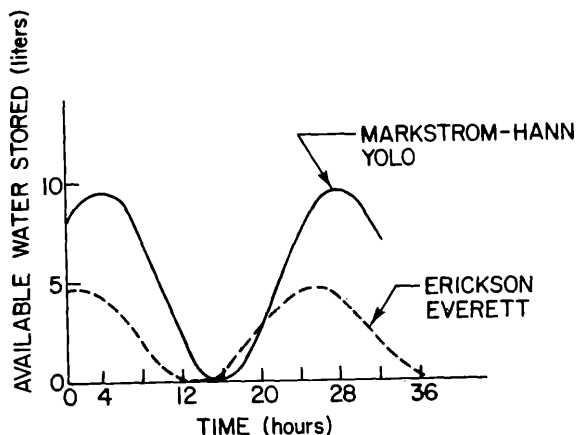
Fig. 9. Time variations in available water stored in the inner bark and the inner sapwood when contrasting sets of parameters are used. We define available stored water as the volume of water which moves out of the storage areas under conditions of the model experiments, as set out in the text. Effects of low conductivity are exhibited by the Markstrom-Hann stem and Yolo soil parameters (k_t = 2.80 x 10^{-12} m^2; D_s = 7.67 x 10^{-9} m^2 sec^{-1}; k_s = 2.15 x 10^{-15} m^2). Erickson stem and Everett soil parameters are k_t = 9.89 x 10^{-12} m^2; D_s = 1.35 x 10^{-7} m^2 sec^{-1}; k_s = 6.67 x 10^{-13} m^2.

level H corresponding to the tension of the water in the transpiration stream when a steady state has been reached. As Weatherley points out,
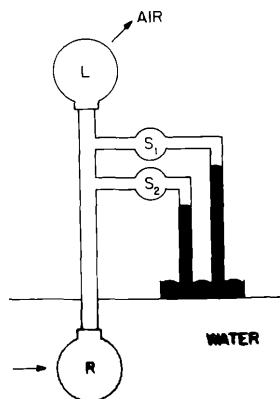
Fig. 10. Schematic representation of water movement between two porous pots, L and R, and two storage areas S_1 and S_2. Pot L (which represents the root system of a plant) takes up water from its surrounding medium, while pot R (representing the crown) gives off water to the air. Depending on differences in water potential between positions on the tube connecting the two pots and the storage areas, water moves into or out of S_1 and S_2, and mercury shaded dark, falls or rises. (Modified from Weatherly [1970] and and Jarvis [1975]).

according to this model, there can be no wave potential passing downward through the plant.

A slight modification of the Weatherley model, however, does allow for such waves. If, instead of a single manometer, several are attached at different positions along the transpiration pathway, a sequence of events envisaged by Jarvis (1975) will take place. As water is lost from L by transpiration, it is replaced by water in the main pathway and by water in the manometer nearest L. Tension in both increases to some level greater than that in the next manometer, which then begins to lose water to the transpiration pathway.

In our model, the equation of continuity (i.e., Equation 7) provides for water transfer from a continuous set of manometers (the inner bark) to the sapwood. Moreover, as water is withdrawn, bark elasticity guarantees a change in water potential in the inner bark. We assume that as water is withdrawn from the inner bark, tension in it and in the sapwood comes into equilibrium rather quickly. This is in agreement with the view of Jarvis (1975), who pointed out that since storage tissues in the plant are finite sources of water, as water is withdrawn from them, their water potential decreases (equivalently, tension increases) until it is about the same as that of the main transpiration pathway.

According to the present model, storage in the stem is appreciable: in mature Douglas-fir 5 to 10 liters of water (the exact value depending on parameter estimates) are withdrawn from stem storage during a summer day. This amounts to approximately 10 to 20 percent of total water consumption. Substantial amounts are also stored in foliage and roots. The biological significance of this storage seems clear. The tree suffers a net loss of

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water during the day but makes a net gain at night. Water which is taken up
at night is temporarily stored in the inner bark, the inner sapwood of the
stem and roots, and in the leaves, to be used during the following daylight
hours. In consequence, excessive potential gradients are not required to
supply water to the foliage, as would be the case if only water stored in
the soil could be drawn upon.

The present model can be used to calculate the consequences of the lack
of a storage mechanism by assuming $E \to \infty$ and $\alpha \to 0$. Then there is no change
in inner bark volume and inner sapwood storage, and the governing system of
equations reduces to Darcy's law and the equivalent boundary conditions:

$$\frac{\partial \psi_t}{\partial z} = - \frac{\mu Q_o}{k_t A_t} \left(1 - \cos 2\pi \frac{t}{t_o}\right)$$

throughout the tree. Integration of this expression over the clear trunk
interval $z = 0$ to $z = H$ yields

$$\psi_t(H) - \psi_t(0) = - \frac{\mu H Q_o}{k_t A_t} \left(1 - \cos 2\pi \frac{t}{t_o}\right).$$

It follows that the minimum value of the xylem water potential below the
crown is

$$\psi_t(H) = \psi_t(0) - \frac{2 H Q_o}{k_t A_t}$$

Now there is some value $\psi_{tm}(H)$ below which $\psi_t(H)$ cannot drop if the stomata
are to remain open and photosynthesis continue. Therefore,
$\psi_t(H) \geq \psi_{tm}(H)$ and

$$Q_o \leq \frac{k_t A_t}{2 \mu H} [\psi_{tm}(H) - \psi_t(0)]$$

which shows clearly that, in the absence of a storage capability, total
daily water consumption Q_o is limited strictly by a minimum allowable
potential gradient in the tree $[\psi_{tm}(H) - \psi_t(0)]/H$. A storage capability

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relaxes this restriction and thus permits several hours additional photo-
synthesis during periods of potential peak water use.

At this point in the discussion, it may be noted that the use of a form
of Hooke's Law in the model derivation is valid only if the change in tissue
water content of the inner bark is small. The self-consistency of the model
can be tested by using it to estimate the approximate magnitude of such
change; thus,

$$\frac{\delta V}{V_o} = \frac{2\pi (R_x + r_o)\delta r}{\pi[(R_x + r_o)^2 - r_x^2]} \doteq \frac{2(R_x + r_o)}{(2R_x + r_o)} \frac{\delta r}{r_o} \doteq \frac{\delta r}{r_o} \, ,$$

provided $R_x \gg r$. In the prototype tree considered here, $R_x = 19$ cm, $r_o =$
0.4 cm. The predicted total daily change in circumference is $2\pi \, \delta r \doteq$
0.1 cm. Therefore, $\delta V/V_o = 0.1/(2\pi)(0.4) \doteq 4$ percent. Examination of the
tissue moisture characteristic curve presented by Hellqvist et al. (1974,
Fig. 17) suggests that for changes in $\delta V/V_o$ of less than 6 percent, the
relationship between ψ and V/V_o is essentially linear, thereby lending some
validity to the use of Hooke's law.

2.   Effect of Uncertainty of Parameter Estimates

The results set forth in Figs. 4-9 are sensitive to the values of the
constants substituted in the formulas. We have already noted that the phase
lags in the tree vary appreciably with soil characteristics. Using the
value of D_t corresponding to the Erickson-Crawford estimate of k_t, when we
change from the Everett sandy loam to the Yolo light clay, time lag in
circumferential change increases from 0.65 to 1.89 hour. Since k_s and D_s
increase with increasing soil moisture content, we would expect phase lags
to decrease appreciably with increases in soil moisture.

The model results are especially sensitive to variations in D_t, as can
be seen in Fig. 11. D_t depends on wood longitudinal permeability k_t, flow
area A_t, and inner bark elasticity E, as well as on sap viscosity μ, xylem
radius R_x, inner bark thickness r_o, and the radial permeability parameter α.
In ring-porous hardwoods, k_t increases with the number of vessels per unit
cross-sectional area of conducting sapwood, and this may be different in
roots, stems, branches, and the vascular tissue of leaves. In conifers,
which lack vessels, there are often differences in annual ring thickness in

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different parts of the tree. Since permeability decreases with sapwood age, it must be inversely related to number of annual rings per centimeter. Moreover, in any given annual ring, earlywood is more permeable than latewood (Kozlowski et al. 1966). Thus, longitudinal permeability may be expected to increase with increasing growth rate.
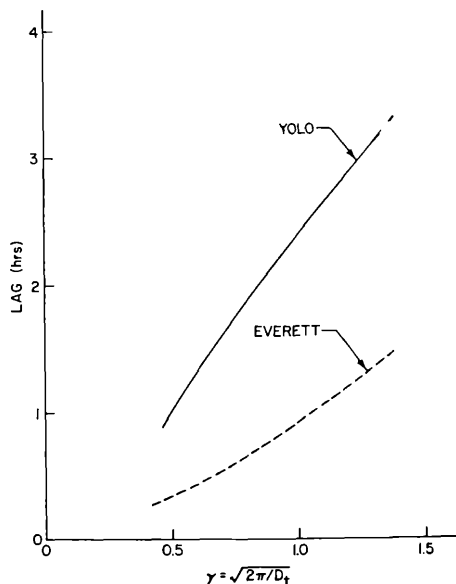

Fig. 11. Phase lag in stem water potential between heights $z = 0$ and $z = 14$ m as functions of $\gamma = (2\pi/D_t)^{1/2}$. Note that phase lag is appreciably greater in the Yolo soil ($D_s = 7.67 \times 10^{-9}$ m^2 sec^{-1}; $k_s = 2.15 \times 10^{-15}$ m^2) than in the Everett gravelly sand ($D_s = 1.35 \times 10^{-7}$ m^2 sec^{-1}; $k_s = 6.67 \times 10^{-13}$ m^2).

Changes in longitudinal permeability k_t are not readily separable from changes in the magnitude of flow area A_t, since A_t is defined as that zone with appreciable vertical flow and, hence, with appreciable permeability. On the other hand, k_t attains maximum values in the young sapwood and decreases toward the center of the tree. Accordingly, average permeability may decrease with an increase in assumed flow area. Clearly, accurate field and laboratory measurements of these quantities and various other parameters are greatly to be desired.

Since our estimate of E, the inner bark modulus of elasticity, is based on only two specimens taken from a single tree, it may not be "representative." On that tree, we observed that E varies with position, the phloem of younger parts of the main stem being stiffer (having larger values of E) than those near the ground. In addition, variations in thickness and furrowing of outer bark probably modify the response of the inner bark to changes in xylem pressure potential.

Finally, the assignment of the value 1.0 to the radial permeability parameter α amounts to little more than a conservative guess. Larger values of α reduce D_t, leading to larger phase lags. With $\alpha = 1$, the calculated phase lags in water potential vary between extremes of 0.46 and 2.80 hours, depending on the estimates of longitudinal permeability k_t and the soil parameters k_s and D_s. As already noted, the Erickson-Crawford (1959) estimate of k_t, used in calculating the results shown in Figs. 5 and 6, is 3.58 times as large as the one obtained by Markstrom and Hann (1972). (If we had used the Markstrom-Hann value, calculated phase lags would have increased from 0.46 to 1.14 hours on the sandy loam soil and from 1.37 to 2.80 hours on the light clay.) Despite the uncertainty of the several parameter values, reasonable agreement is achieved between theory and observation in the magnitude of stem phase lags. The closeness of the agreement is partly fortuitous. Nevertheless, the qualitative prediction of the existence of "stem waves" with their associated phase lags is significant.

In some respects our theory quantifies processes suggested by Weatherley (1970) and Jarvis (1975). Although correspondence between theory and observation is generally good, many improvements are possible, and the following areas are suggested for additional study of the soil-stem system: more realistic representation of the soil component, which includes dependence of soil conductivity k_s and diffusivity D_s on moisture content, more accurate evaluation of anatomical parameters, more realistic representation of movement of water from soil to plant, and inclusion of the processes which occur in the crown of the tree.

SUMMARY

Evidence has been presented that some of the water taken up from the soil by trees is shunted to temporary storage reservoirs in the roots, stems, and leaves. It has been shown that observed small changes in stem dimension and associated phase lags can be accounted for at least in part by a theory of water transport which includes movement from the main transpiration stream in the outer sapwood to storage zones in the inner bark and inner sapwood.

Xylem water potential is shown to be governed by a diffusion equation, and flow velocity in the sapwood is proportional to water potential gradient (Darcy's law). If water is transpired periodically by the foliage over time (with maximum rate of water loss occurring after midday, for example),

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changes in xylem water potential move down the stem in traveling waves of finite velocity. These longitudinal waves of water potential are externally manifested by time lags in dimensional change in the stem and by changes in vertical water transport velocity in both the stem and the soil.

Model predictions compare favorably with data obtained on Douglas-fir trees growing in western Washington State.

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