

Extrapolating plant water flow resistances and capacitances to regional scales

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ABSTRACT

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The principal objective for models of water flow through the soil–plant–atmosphere system is the accurate prediction of leaf water potential (ψ^{leaf}) and water uptake by roots, for a given soil water potential (ψ^{soil}) and transpiration rate. Steady-state models of water flow through plants, which include only resistances, are sufficient to predict total daily water uptake by roots. Non-steady-state models, which use both water flow resistances and capacitances, are necessary for the prediction of ψ^{leaf} and instantaneous rate of water uptake for diurnal variations of transpiration rate. Potential difference resistances and capacitances are defined for water flow (volume/time) and are best used for individual plant models; resistivities and capacitivities are based on volume flux density ((volume/land surface area)/time) and should be used for plant stands. Prediction of ψ^{leaf} may not be necessary for general circulation models and global climate models (GCM) because stomatal conductance (necessary for the prediction of transpiration rate) is probably controlled by the vapor pressure difference at the leaf surface and ψ^{soil} and not by ψ^{leaf} . If liquid water flow models through plants are necessary for GCM in order to account for diurnal variations of land–surface energy partitioning, then perhaps an ecosystem time constant for water flow through vegetation of each biome type should be used.

INTRODUCTION

With modern techniques and powerful computers, there is a renewed interest in models of water flow from the soil, through the plant and into the atmosphere. These models have various spatial and temporal scales, ranging from individual plant models to general circulation models and global climate models (GCM). Significant errors can arise when formulations appropriate for one model scale are used for another scale (Allen and Starr, 1982; O'Neill et al., 1986).

Beginning with the seminal study by Van den Honert (1948), water flow through each component of the soil–plant–atmosphere system has been linked to transpiration rate with the important assumption that the plant system is under steady-state conditions. In this case, steady state does not mean the transpiration rate is constant, but rather that liquid water flows through each part of the system will not change with time for a given transpiration rate. Water flow through each plant organ is equal and is calculated from the difference in water potential divided by the resistance to water flow. This is analogous to the flow of electrons across a voltage difference through a series of resistors using Ohm's Law (Gradmann, 1928; Van den Honert, 1948; Cowan, 1965). The equations governing water flow through cells, tissues and whole plants have been reviewed many times (Slatyer, 1967; Jarvis, 1975; Molz and Ferrier, 1982; Tyree and Jarvis, 1982; Nobel, 1983; Boyer, 1985; Landsberg, 1986).

Under non-steady-state conditions, water flows through each part of the soil–plant–atmosphere system are not equal and will change with time for a given transpiration rate (Kramer, 1937, 1938). Thus, the differences of water flow out of or into a plant organ must come from or go into internal plant water storage. The adaptive significance of plant water storage for transpiration has been recognized in one of the original works that established plant ecology as a scientific discipline (Warming, 1895; from the English translation of 1909). Water storage in a plant organ is called plant capacitance and, using the electric circuit analogy, is often modeled as a grounded capacitor (Lang et al., 1969; Cowan, 1972; Sheriff, 1973; Landsberg et al., 1976; Powell and Thorpe, 1977; Molz et al., 1979; Landsberg, 1986). Water flow models that incorporate only plant resistances are henceforth termed steady-state models, and water flow models that incorporate both resistances and capacitances are termed non-steady-state models.

It is our contention that steady-state models of water flow are appropriate for the prediction of total daily transpiration and water uptake, but non-steady-state models must be used for the prediction of diurnal variations of water uptake and leaf water potential. We will first review the published literature on plant resistances and capacitances, paying particular attention to definitions and units. Then, we will analyze steady-state and non-steady-state models at various temporal and spatial scales, and suggest a possible method of parameterizing large-spatial-scale models using an ecosystem time constant for plant water flow. Finally, we will discuss the ramifications of including detailed models of plant water flow into GCM because it may not be necessary to estimate average leaf water potential for an entire GCM grid cell in order to estimate transpiration.

REVIEW OF PLANT WATER FLOW MODELS

Analogy between electron and water flow

Molz and Ferrier (1982) summarized the analogy between electron flow through a circuit and water flow through the soil–plant–atmosphere system (Table 1). The analogous quantity to electron charge is the volume of water. Both electron flow and water flow are manifestations of the energy conservation law, so there is a physical basis for using the electric circuit analogy to model water flow. There is nothing special about using the water volume instead of the water mass, but by using the volume, the quantities and units in Table 1 are consistent with both the electric circuit analogy and prior usage in plant water relations.

Water potential (ψ) represents the work involved in moving water (at constant temperature and atmospheric pressure) to a pool of pure liquid water (divided by its partial molar volume), so water potential is analogous to the electric potential difference from the ground state (Table 1). Typically, plant water potential is expressed in units of pressure because the components of the chemical potential of water in living plant cells can be expressed mechanically in terms of hydrostatic pressure (P , MPa; also called turgor pressure) and osmotic pressure (π , MPa). Neglecting the gravitational component, ψ is determined as

$$\psi = P - \pi = \psi_P + \psi_\pi \quad (1)$$

where ψ_P is the pressure potential ($=P$) and ψ_π is the osmotic potential ($=-\pi$). Xylem and soil matric potentials are the negative hydrostatic pres-

TABLE 1

Analogous quantities for flow through electric circuit and plant systems (after Molz and Ferrier, 1982). Electrical unit symbols are in parentheses to differentiate them from plant symbols

Plant water			Electric circuit		
Quantity	Units	Symbol	Quantity	Units	Symbol
Volume	m ³	V	Charge	Coulomb	(C)
Potential ^a	Pa (= J m ⁻³)	ψ	Potential	Volt	(V=J C ⁻¹)
Flow	m ³ s ⁻¹	q	Flow	Ampere	(A=C s ⁻¹)
Resistance	MPa s m ⁻³	R	Resistance	Ohm	(Ω =V s C ⁻¹)
Capacitance	m ³ MPa ⁻¹	C	Capacitance	Farad	(F=C V ⁻¹)

^aThe SI unit for pressure, the pascal (Pa), is too small for plant water flow studies; the MPa (and formerly the bar, 1×10^5 or $1E5$ Pa) is typically used as the unit for ψ . For clarity we have chosen to use MPa as the base unit for ψ and have chosen to make the units for R and C consistent with this choice.

tures exerted by surface tension effects, and should be included in the hydrostatic pressure term (Nobel, 1983).

From the base quantities of volume and ψ , the quantities of water flow, resistance and capacitance are derived in a similar manner as the same quantities for electron flow (Table 1). However, there are limits to how far the electric circuit analogy can be extended; for example, there may not be an analogous plant inductance because the water molecule has no net charge. Hydraulic head is an alternative to water potential frequently used by agricultural meteorologists, hydrologists and soil scientists; the water quantities in Table 1 can be defined using head instead of potential.

Resistances and resistivities

Not the least confusing part of this subject are the many different ways in which resistance can be and has been expressed (Table 2; after Jarvis, 1975). Resistance is defined as a flow rate divided by the potential difference inducing the flow. Its reciprocal, conductance, is also used. 'Resistance' and 'conductance' are used when the flow is defined as volume per time; 'resistivity' and 'conductivity' are used with flux density ((volume/area)/time; Jarvis, 1975). Potential or head gradient resistances and resistivities are particularly important for water transport through the soil and xylem, whereas potential or head difference resistances and resistivities are useful for describing transport through roots and leaves. It should be pointed out that stomatal conduc-

TABLE 2

Definitions of resistance and conductance with their units

	Flow		Flux density	
	Resistance	Conductance	Resistivity	Conductivity
Potential gradient	$(d\psi/dl)/q$ (MPa s m ⁻⁴)	$q/(d\psi/dl)$ (m ⁴ s ⁻¹ MPa ⁻¹)	$(d\psi/dl)/q$ (MPa s m ⁻²)	$q/(d\psi/dl)$ (m ² s ⁻¹ MPa ⁻¹)
Potential difference	$\Delta\psi/q$ (MPa s m ⁻³)	$q/\Delta\psi$ (m ³ s ⁻¹ MPa ⁻¹)	$\Delta\psi/q$ (MPa s m ⁻¹)	$q/\Delta\psi$ (m s ⁻¹ MPa ⁻¹)
Head gradient	$(dH/dl)/q$ (s m ⁻³)	$q/(dH/dl)$ (m ³ s ⁻¹)	$(dH/dl)/q$ (s m ⁻¹)	$q/(dH/dl)$ (m s ⁻¹)
Head difference	$\Delta H/q$ (s m ⁻²)	$q/\Delta H$ (m ² s ⁻¹)	$\Delta H/q$ (s)	$q/\Delta H$ (s ⁻¹)

Water flow in volume/time is q , S is surface area, ψ is potential, H is hydraulic head¹ and l is length. The ratio q/S is the volumetric flux density (q). Potential and head gradient are used for water transport through the xylem and soil; potential and head difference are used for transport across leaves and roots. (¹Units for head are meters, which give a potential when multiplied by the density of water (ρ , 1 Mg m⁻³) and gravitational acceleration (g , 10 m s⁻²); H of 1 m is equal to ψ of 0.01 MPa.)

tance and resistance to the diffusion of water vapor are used with flux density, and perhaps should be called stomatal conductivity and resistivity in order to be consistent.

The relevant areas and lengths must be carefully stated. Within six lines of text, Landsberg and Fowkes (1978, p. 499) defined various 'resistances' with units of bar s mm^{-1} , bar s mm^{-3} and bar s mm^{-4} ! Bristow et al. (1984) used the potential difference resistivity per unit root length for flow into roots. This has the same units as potential gradient resistivity, but is not comparable because the length is at right angles to the flow path rather than along it. Standardization is certainly desirable; perhaps Table 2 can contribute to it.

When comparing resistivity in different parts of the system, it is important that the unit area be defined the same for all components (Richter, 1973). Resistivities in series are only additive if the area is constant. For whole-plant canopies, the area normally used is unit land surface area. Leaf area, stem cross-sectional area, stem sapwood area, xylem lumen area and root surface area have also been used to define resistivities. For individual plant studies, it may be better to use resistance than resistivity.

Electric circuit analog models

This section uses the model of Federer (1979, 1982) as a starting point for the following discussion, but the underlying theory is similar to many other model formulations. Developing some equations for the liquid flow pathways helps clarify some of the assumptions that are usually made in models of water flow. Figure 1 shows a non-steady-state model for a single plant; the same analog model is applied here to a plant stand for a given unit of land surface area (S^{land} , m^2), where the volume flows (q , $\text{m}^3 \text{s}^{-1}$), capacitances (C , $\text{m}^3 \text{MPa}^{-1}$) and potential difference resistances (R , MPa s m^{-3}) are changed below to the corresponding volume flux densities ($q = q/S^{\text{land}}$, m s^{-1}), capacitivities ($C = C/S^{\text{land}}$, m MPa^{-1}) and resistivities (R , MPa s m^{-1}), respectively.

The root zone of a soil can be divided into several layers, each layer (i) having its own water potential in the bulk soil, ψ_i^{soil} . Rhizosphere resistivity, R_i^{soil} , and root resistivity to radial flow in the root, R_i^{root} , are in series in each layer (Cowan, 1965; Federer, 1979). The potential where water first enters the root xylem, ψ_x^{root} , is assumed to be independent of soil layer, i.e. xylem resistivity is negligible for large roots, and hence no corresponding resistor is shown in Fig. 1. Water entering from plant stem storage at ψ_s^{stem} , through a storage resistivity R_s^{stem} , is assumed to enter halfway along the xylem path and halfway up the height of the plant. The difference between the leaf water potential, ψ^{leaf} , and ψ^{soil} drives the fluxes of water. The transpiration flux

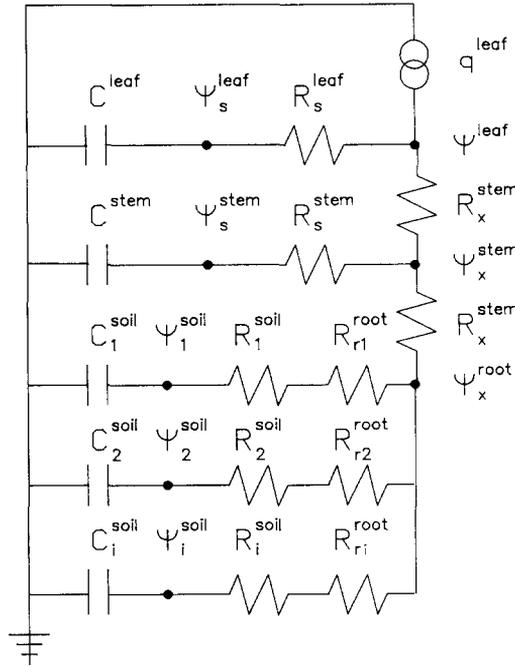


Fig. 1. Capacitances (C), potentials (ψ) and potential difference resistances (R) in the soil-plant-atmosphere pathway for liquid water flow using an electric circuit analog model. Symbols are C_i^{soil} for the soil water storage of soil layer i , ψ_i^{soil} for soil potential of soil layer i , R_i^{soil} for the soil resistance in soil layer i , R_{ri}^{root} for the root radial resistance across the root surface area for roots in soil layer i , R_x^{stem} for the resistance of the xylem from the roots to the leaves, R_s^{stem} for the resistance from stem water storage to the xylem, R_s^{leaf} from leaf water storage to the xylem, C^{stem} for the stem water storage, C^{leaf} for leaf water storage, ψ_x^{root} for the root xylem potential, ψ_x^{stem} for the stem xylem potential, ψ_s^{stem} for the stem storage potential, ψ_s^{leaf} for the leaf storage potential, ψ^{leaf} for the leaf potential and q^{leaf} for the transpirational water flow. Units for R , C , and ψ are given in Tables 1 and 3. For a steady-state water flow model, only C_i^{soil} , R_i^{soil} , R_{ri}^{root} and R_x^{stem} are used. Water from C^{stem} is added at the midpoint of R_x^{stem} . The capacitors are grounded to make the charge on the capacitor equal to the water potential. Volumetric flux density (q), capacitance (C) and resistivity (R) denote the respective quantities per land surface area.

density leaving the plant is

$$q = (\psi_x^{stem} - \psi^{leaf} - 0.5\rho gh) / 0.5R_x^{stem} \tag{2}$$

where ρ is the density of water, h is the height above the ground and g is the acceleration of gravity. For simplicity, we ignore the capacitance of the leaves, which is small compared with the capacitance of the stem, and assume only one storage pool of water in the stems to obtain a single plant capacitance. The water supplied from storage, q_s^{stem} , is

$$q_s^{stem} = (\psi_s^{stem} - \psi_x^{stem}) / R_s^{stem} \tag{3}$$

The storage potential, ψ_s^{stem} , is then changed from flux into or out of storage by

$$\Delta\psi_s^{\text{stem}} = - (q_s^{\text{stem}}/C^{\text{stem}})\Delta t \quad (4)$$

where Δt is the time step in seconds. The total change over Δt must be small for eqn. (3) to be valid. Flux between ψ_x^{root} and ψ_x^{stem} is

$$q - q_s^{\text{stem}} = (\psi_x^{\text{root}} - \psi_x^{\text{stem}} - 0.5\rho gh)/0.5R_x^{\text{stem}} \quad (5)$$

This also equals the flux of water into the roots

$$q - q_s^{\text{stem}} = \sum_i (\psi_i^{\text{soil}} - \psi_x^{\text{root}}) / (R_i^{\text{soil}} + R_{ri}^{\text{root}}) \quad (6)$$

A little manipulation eliminates ψ_x^{stem} and ψ_x^{root} and gives

$$q_s^{\text{stem}} = (\psi_s^{\text{stem}} - 0.5qR_x^{\text{stem}} - \psi^{\text{leaf}} - 0.5\rho gh) / R_s^{\text{stem}} \quad (7)$$

$$q = q_s^{\text{stem}} + \sum_i (\psi_i^{\text{soil}} - qR_x^{\text{stem}} + 0.5q_s^{\text{stem}}R_x^{\text{stem}} - \psi^{\text{leaf}} - \rho gh) / (R_i^{\text{soil}} + R_{ri}^{\text{root}}) \quad (8)$$

where eqns. (7) and (8) can be solved iteratively for q . Assumptions of steady-state ($q_s^{\text{stem}} = 0$) and only one layer in the root zone lead to

$$q = (\psi^{\text{soil}} - \psi^{\text{leaf}} - \rho gh) / (R^{\text{soil}} + R_r^{\text{root}} + R_x^{\text{stem}}) \quad (9)$$

Further simplification defines the total potential difference resistivity, R^{total}

$$q = (\psi_i^{\text{soil}} - \psi^{\text{leaf}}) / R^{\text{total}} \quad (10)$$

where R^{total} is the sum of the plant organ resistivities and is also called the bulk plant resistivity.

Rhizosphere and root resistance

Work on resistance to transpiration in the 1960s focused on resistance to water movement through the soil to the root (Molz, 1981). The classic papers by Gardner (1960) and Cowan (1965) developed a theory of water flow to a single cylindrical root in which the potential difference is ψ^{soil} minus the potential at the root surface, ψ^{root} , and the conductivity depends on the soil hydraulic conductivity. The theory applies to flow per unit length of absorbing root and assumes this is measured as the length of absorbing root per unit volume of soil. The radial root resistivity, R_r^{root} , was assumed constant throughout the absorbing length and was initially thought to be small.

Newman (1969a,b) thoroughly reviewed theory and experiment comparing rhizosphere resistance with root resistance. The experiments generally were indirect and theoretical because ψ^{root} could not be measured. He concluded, as many others have since, that rhizosphere resistance is small with respect to root resistance when the soil is wet. In general, rhizosphere resistance is much smaller than root resistance until soil potential drops below -0.1 MPa

(Gardner and Ehlig, 1962; Arya et al., 1975; Landsberg and Fowkes, 1978). Molz (1981) summarizes by saying "root resistance ... seems certain to dominate in the upper 75% of the water content range under normal rooting conditions."

The Casparian strip appears to be the major resistance to radial flow into the roots (Slatyer, 1967; Newman, 1976; Zimmermann, 1983). Numerical values for root resistance are few and for a limited number of plant species. Landsberg and Fowkes (1978) gave potential difference resistivity based on root surface area of $3E6-5E8 \text{ MPa s m}^{-1}$ for several studies of wheat roots. Newman (1973) gave values on the order of $1E8 \text{ MPa s m}^{-1}$ for young herbaceous plants, and Slatyer (1967) $1E7 \text{ MPa s m}^{-1}$ for bean, oat and corn. The calculation of such resistivities is always based on assumptions that are not fully met. Root resistivities probably vary with root thickness (Hunt and Nobel, 1987a), root age and soil temperature (Tew et al., 1963; Dalton and Gardner, 1978; Running and Reid, 1980). Part of the temperature effect is the result of changing viscosity of water, but most is probably physiological change in root tissue, such as the endodermal cytoplasm (Slatyer, 1967).

Resistance to outflow of water from plant roots often appears to be higher than resistance to uptake (Molz and Peterson, 1976; Nobel and Sanderson, 1984; Dirksen and Raats, 1985). At night, in a soil that is wet at some depth and dry at another, plants can transfer water through the roots from the wetter soil to the drier one (Baker and Van Bavel, 1986; Richards and Caldwell, 1987), demonstrating that water flow can occur both in and out of roots. Many simulation models do not allow any outflow from plant roots (Molz, 1981) and, indeed, these models cannot balance water uptake with transpirational water loss except when outflow is not allowed. Continuing discussion on variable root resistance centers on metabolic (and osmotic) control (Fiscus, 1975; Dalton and Gardner, 1978; Fiscus et al., 1983; Passioura, 1984, 1988; Parker and Pallardy, 1988), or on root-soil interface resistance caused by an air gap that forms as the soil and root pull away from each other when the soil and root dry (Huck et al., 1970; Herkelrath et al., 1977; Dosskey and Ballard, 1980; Molz, 1981; Bristow et al., 1984).

Conversion of root resistivities based on unit surface area of the root (S^{root} , m^2) to resistivities based on unit land area require estimation of the length of absorbing roots per unit land area and of the diameter of the absorbing or fine roots. Roots > 1 or 2 mm in diameter may be too suberized to absorb at all, except through cracks in the suberized layer (Caldwell, 1976). Studies of fine root length are exceedingly tedious and so are seldom carried out in natural conditions. Values of the order of 0.35 mm radius and $10 \text{ m}^2 S^{\text{root}}$ per $\text{m}^2 S^{\text{land}}$ are likely for forests (Federer, 1979). Then R_r^{root} of $1E8 \text{ MPa s m}^{-1}$ based on root surface area becomes $1E7 \text{ MPa s m}^{-1}$ based on land area.

Xylem resistance

Different groups of plants have widely differing hydraulic architectures. Some understanding of this is needed to assess xylem resistance and conductance. Separation of plants into at least eight categories is necessary, but literature results for any one group are often mistakenly taken to apply to all. Also, this is probably true for root xylem resistance, but has not been studied. The groups are: (1) ferns (including tree-ferns); (2) gymnosperms (mainly coniferous trees); (3) herbaceous dicot annuals; (4) succulent dicots (including cacti); (5) woody diffuse-porous dicot trees and shrubs; (6) woody ring-porous dicot trees and shrubs; (7) grasses; (8) other monocots (including palm trees).

All groups conduct water through dead xylem cells, either vessel elements or tracheids, or both. Conifers and woody dicots have secondary cambium and produce new xylem radially in the stem each year. Tree-ferns and most monocots grow only up, not out, and must rely on the same xylem cells to function throughout the plant's life. In conifers and other primitive plants, the conducting xylem cells are tracheids, which are 20–50 μm in diameter and 1–3 mm long; these carry water with a velocity of 1–2 m h^{-1} (Zimmermann, 1983). The source of the xylem resistance is not within the tracheid lumens themselves, but in the bordered pits that connect adjacent tracheids (Jarvis, 1975; Gibson et al., 1985; Calkin et al., 1986).

In woody dicots, water is carried primarily by vessel elements, which are large diameter cells with dissolved end walls and stacked end to end to form a long continuous vessel. Vessels in diffuse porous trees are 15–150 μm in diameter, 100 mm long and carry water at 1–6 m h^{-1} . In ring-porous trees, the vessels are 60–400 μm in diameter, ≥ 1 m long and conduct water at 6–40 m h^{-1} . Resistance to water flow through wood can be measured by forcing water under pressure through a stem segment. Such work indicates that water flow is laminar and the Hagen–Poiseuille law for flow in capillaries applies (Heine, 1971; Zimmermann, 1983; Schulte et al., 1989). Water flow through a single vessel is, therefore, proportional to the fourth power of its radius. Deviations from the Hagen–Poiseuille law can be attributed to rough vessel element walls (Jeje and Zimmermann, 1979) and small variations in diameter along the length of the vessel (Schulte et al., 1989).

Measured potential gradient resistivities range from 200 to 30 000 MPa s m^{-2} for conifers and 30 to 3000 MPa s m^{-2} for dicot trees, based on sapwood cross-sectional area of the bole (Heine, 1971; Ewers, 1985). Assuming the sapwood basal area (sapwood area per tree \times the number of trees per land area) is 20 $\text{m}^2 \text{ha}^{-1}$ and the trees (either woody dicot or conifer) are 20 m tall, then 1000 MPa s m^{-2} potential gradient resistivity based on sapwood area converts to $1\text{E}7 \text{MPa s m}^{-1}$ potential difference resistivity based on land surface area. This is equal to $1\text{E}7 \text{MPa s m}^{-1}$ estimated above for root resis-

tivity per land surface area. Xylem resistivity in a forest is at least the same order of magnitude as root resistivity and should not be neglected (eqn. (9)).

Comparisons of resistance on the basis of sapwood area with that of land surface area are complicated by estimation of the portion of the sapwood that is actually conducting. In conifers, conduction may vary across the sapwood, which is approximately the outer 10–20 annual rings. In diffuse-porous dicot trees, conduction decreases linearly inward over about 10 rings. In ring-porous trees, almost all water transport is in the outermost one or two annual rings (Waring and Schlesinger, 1985). In monocots, herbaceous dicots and ferns, vascular bundles are scattered throughout the stem. Stem resistivities in the literature must be evaluated to see if they are based on lumen area, conducting xylem area, sapwood area, stem area, one-sided leaf area, total leaf area or land surface area.

Many of the more recent studies determined xylem potential gradient conductivities per unit leaf area supplied by the xylem (called leaf-specific conductivities) in order to show how these conductivities vary throughout the stem (Zimmermann, 1978, 1983; Tyree et al., 1983; Ewers and Zimmermann, 1984a,b; Tyree, 1988). In general, boles have leaf-specific conductivities about four to five times higher than the lateral minor stems, which hold most of the leaves, suggesting that these minor stems contribute most of the resistance to water flow through the xylem. Furthermore, when the potential gradient of stems and roots for a given transpiration rate is calculated from a series of water potential measurements, the largest potential drop occurs in the minor lateral stems, suggesting that these minor stems constitute the largest single resistance in the whole soil–plant–atmosphere system (Hellkvist et al., 1974; Zimmermann, 1983; Tyree, 1988; Tyree and Sperry, 1989). The variation in hydraulic architecture of a single tree thus presents a considerable challenge in formulating a single xylem resistivity.

Total resistance

The total potential difference resistivity of a plant canopy is the leaf–soil potential difference divided by the water flux density (eqn. (10)). A great many plant canopies have ψ^{leaf} of about -1.5 MPa when ψ^{soil} is > -0.1 MPa and transpirational flux density is about 0.5 mm h⁻¹. The potential difference resistivity thus defined is about $1\text{E}7$ MPa s m⁻¹, which is the same order of magnitude as the estimated xylem and root potential difference resistivities determined above. Abdul-Jabbar et al. (1984) gave values of $3\text{E}6$ to $1.2\text{E}7$ MPa s m⁻¹ from the literature. Total plant resistivity varies a little among species (Boyer, 1971). In general, few comparisons under the same ambient conditions have been carried out, but total resistivity appears to vary less than the component resistivities. In view of the order of magnitude uncertainties

in the estimation of root and xylem resistance, the use of a whole-canopy potential difference resistivity seems more justified for GCM.

Capacitance

Many studies have measured instantaneous transpiration rate, ψ^{leaf} and ψ^{soil} , and then estimated total plant resistance using eqn. (10); these studies have generally concluded that R^{total} or R^{total} varies diurnally with flow rate. These studies also have generally ignored the effects of plant capacitance. Although plant resistances do change from osmotic effects (Fiscus et al., 1983; Passioura, 1984, 1988), plant growth (Boyer, 1985), stem water content (Edwards and Jarvis, 1982) and xylem embolism (Tyree and Dixon, 1986; Sperry et al., 1988a,b; Tyree and Sperry, 1988, 1989), These changes are more important over a season than over a day (however, see Passioura and Tanner, 1985). Over a day, plots of the variation in transpiration rate of ψ^{leaf} form a hysteresis loop (Jarvis, 1975; Hinckley et al., 1978; Schulze et al., 1985). Constant plant capacitance with constant plant resistance can fully explain the daily hysteresis between transpiration and ψ^{leaf} (Hinckley et al., 1978; Jones, 1978; Waring and Running, 1978; Running, 1980a; Wronski et al., 1985; Katerji et al., 1986; Hunt and Nobel, 1987a; Tyree, 1988).

Following the electric circuit analogy, capacitance (C) is defined as

$$C = dV/d\psi \quad (11)$$

where V is the volume of water. Capacitance may be determined from the slope of a pressure–volume curve (Powell and Thorpe, 1977; Waring and Running, 1978; Running, 1980a; Tyree and Jarvis, 1982). The slope of a pressure–volume curve is not constant throughout its range, therefore capacitance is not constant. However, the initial slope of a pressure–volume curve is approximately constant over a range of relative water content (RWC) from 0.95 to 0.80. RWC is defined as V/V_0 , where V_0 is the volume at $\psi=0$ MPa. Most measured ψ in the field are usually within this range of RWC. Moreover, soil-moisture release curves show that C^{soil} is not constant, but the change in volumetric water content over a day is small. Therefore, as a first approximation, constant plant and soil capacitances may be used for modeling diurnal water flow through the soil–plant–atmosphere system.

For plant tissues of living cells, the bulk elastic modulus (ϵ , MPa) of a tissue is defined as VdP/dV and controls the initial slope of the pressure–volume curve (Molz and Ferrier, 1982; Tyree and Jarvis, 1982). For the range covered by the initial slope

$$C = V/(\epsilon + \pi) \quad (12)$$

which shows that larger plants will have larger capacitance simply because they have a larger volume of water in living cells. Equation (12) follows from

differentiating eqn. (1) with respect to volume, eqn. (11), the definition of ϵ , and assuming no change of total osmotically active solutes so $d\pi/dV = -\pi/V$.

One typical non-steady-state model is shown in Fig. 1, where each plant organ is modeled as a single grounded capacitor connected to the xylem resistance catena through a storage resistor. Similar models were used by other investigators (Landsberg et al., 1976; Powell and Thorpe, 1977; Jones, 1978; Wronski et al., 1985; Edwards et al., 1986), and particularly by Nobel and collaborators, to investigate capacitance as functional adaptations to desert environments (Nobel and Jordan, 1983; Hunt and Nobel, 1987a; Schulte and Nobel, 1989).

The resistance-capacitance circuit analog in Fig. 1 is complicated enough to represent the dynamics of water flow through each plant organ, but simple enough to be solved analytically (e.g. Powell and Thorpe, 1977; Wronski et al., 1985). The parameters for such a model are determined from combining many small resistances and capacitances determined for an individual plant in parallel or in series. If the electric circuit analog is taken literally, then more complicated models can be solved using available electric circuit simulation programs (Molz et al., 1979). One such program accurately predicted diurnal variations of ψ^{leaf} using the same plant resistances and capacitances for both wet and dry soil (Hunt and Nobel, 1987a). Leaf capacitance is small, but is important for the prediction of ψ^{leaf} and subsequently the driving force for water flow through the soil-plant-atmosphere system. At the minimum, dynamics of water flow through a whole plant can be represented using a single capacitor and one or two resistors (Jones, 1978; Milne et al., 1983; Wronski et al., 1985).

There are three pools of stored water in the stems of woody plants. The first pool is in the living cells of the xylem parenchyma, cambium and phloem; this pool of stored water changes diurnally and is responsible for diurnal changes of stem diameter (Dobbs and Scott, 1970; Lassoie, 1973, 1979; Jarvis, 1975).

The second pool is in the lumens of the conducting xylem tissue and changes seasonally (Clark and Gibbs, 1957; Dobbs and Scott, 1970) owing to cavitation (breakage of the water column) and embolism (entry of air into the lumen; Tyree and Sperry, 1988). Cavitation and embolism require positive pressures of water in the xylem to be reversed, which occurs during the spring if at all. It is unlikely that reversal can occur overnight. The seasonal change of the second pool of stored water is from 2 mm (Roberts, 1976) to a maximum of 27 mm (Waring and Running, 1978). However, for most forest stands, the seasonal change of xylem lumen water is probably < 10 mm, so this pool can be neglected in soil-plant-atmosphere models simulating diurnal water flow.

The third pool is water bound in the cell walls of the xylem tissue, where

the water potential is equal to the negative hydrostatic pressure and is in equilibrium with the potential of the other two pools. In a significant study, Brough et al. (1986) showed that only 5% of the diurnal changes of stem water content can be attributed to the first pool in living cells, most of the diurnal change in stem water is from the third pool. Thus, it is the third pool of stored water that acts as the single stem capacitor in non-steady-state models of water flow.

ANALYSIS OF WATER FLOW MODELS AT VARIOUS HIERARCHICAL SCALES

Steady-state versus non-steady-state models

Water flow model parameters for various species from a grass to a small deciduous hardwood tree were compared to determine how the parameters may vary according to biome type. The data indicated that resistances and capacitances may be inversely correlated as plants become larger (Table 3). These parameters were used to simulate the effects of capacitance on daily water balance. A numerical simulation program of the circuit in Fig. 1 (but

TABLE 3

Some measured values of potential difference resistances and capacitances for various species

Quantity	Units	Grass ^a	Shrub ^a	Conifer ^b	Hardwood ^c
Genus		<i>Hilaria</i>	<i>Encelia</i>	<i>Pinus</i>	<i>Malus</i>
Species		<i>rigida</i>	<i>farinosa</i>	<i>contorta</i>	<i>pumila</i>
Height	(m)	0.4	0.3	5.3	2.5
S^{leaf}	(m ²)	0.044	0.22	5.8	6.5
g_{smax}	(mm s ⁻¹)	12	9.0	1.5	5.8
Conducting xylem		Vessels	Vessels	Tracheids	Vessels
V^{leaf}	(m ³)	2.1E-6	3.0E-6	0.2E-3	1.1E-3
V^{stem}	(m ³)	0.01E-3	0.45E-3	3.7E-3	74E-3
C^{leaf}	(m ³ MPa ⁻¹)	1.4E-6	13E-6	10E-6	19E-6
C^{stem}	(m ³ MPa ⁻¹)	1.1E-6	29E-6	170E-6	350E-6
R_s^{leaf}	(MPa s m ⁻³)	56E6	8.4E6	10E6	3.8E6
R_s^{stem}	(MPa s m ⁻³)	45E6	45E6	25E6	20E6
R_x^{stem}	(MPa s m ⁻³)	33E6	1.1E6	6.9E6	1.4E6
R_r^{root}	(MPa s m ⁻³)	790E6	220E6	11E6	7.2E6
τ	(h)	0.2	2.3	1.5	2.2

S^{leaf} is the total two-sided leaf area of the plant, g_{smax} is the maximum stomatal conductance, C is the capacitance for the specified organ, R_s is the storage resistance for the specified plant organ, R_x is the xylem resistance for the specified organ, R_r^{root} is the root radial resistance, and τ is the whole-plant time constant which was determined from the time necessary to reach within 37% of the final (steady-state) of ψ^{leaf} for a step decrease in transpiration rate. E-6 and E6 stand for $\times 10^{-6}$ and $\times 10^6$, respectively.

^aHunt and Nobel (1987a), Nobel and Jordan (1983); ^bRunning (1980a,b); ^cLandsberg et al. (1976), Powell and Thorpe (1977).

with only one soil layer) was used to estimate water potentials and water flows at a given transpiration rate and ψ^{soil} for both the steady-state (resistor circuit analog) and non-steady-state (resistor–capacitor circuit analog) models.

The differences between a steady-state model and a non-steady-state model are very significant over a day (Fig. 2). The main effects of adding capacitance are the higher ψ^{leaf} and lower maximum instantaneous rate of water uptake. Moreover, minimum ψ^{leaf} lagged behind maximum transpiration rate by 1 h for *Encelia farinosa* (Fig. 2(B)). Simulations of a plant with a small capacitance, such as a grass (*Hilaria rigida*), show little lag when capacitance

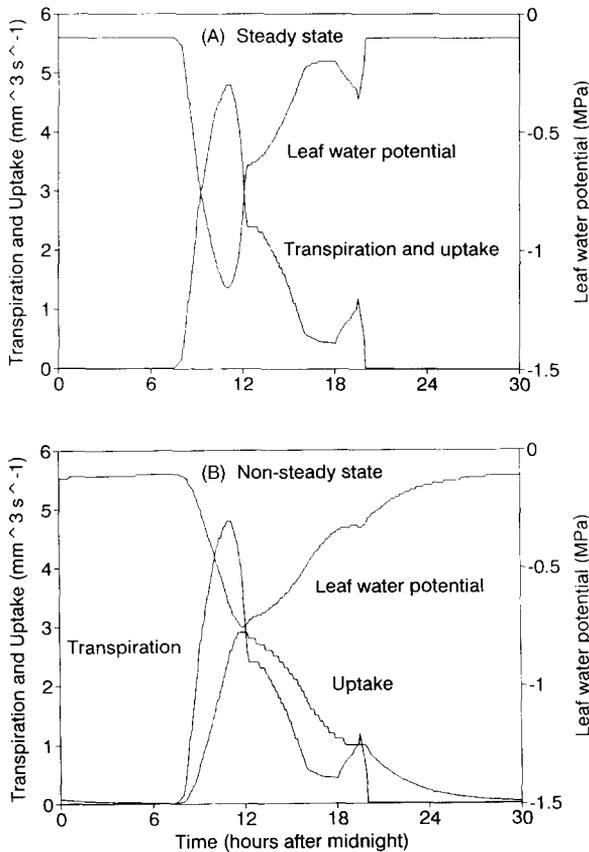


Fig. 2. Simulated transpiration rate, rate of water uptake by roots and leaf water potential for *E. farinosa* using a steady-state model (A) or non-steady-state model (B). Model parameters for *E. farinosa* are given in Table 3. The transpiration rate was calculated from the Penman–Monteith equation for a warm August day in Missoula, MT, where stomatal conductance was determined from maximum conductance, solar radiation, vapor pressure difference and $\psi^{\text{soil}} = -0.1$ MPa. For both (A) and (B), total daily water uptake by the roots equals total daily water loss by transpiration. Moreover, the daily totals and instantaneous rates of transpiration for the steady-state model are the same as those for the non-steady-state model because stomatal conductance was not controlled by ψ^{leaf} .

is introduced. Simulations of plants with large capacitances and small resistances, such as a lodgepole pine or an apple tree, have a slightly smaller lag period than *E. farinosa*. Use of a steady-state model will give reasonable predictions of ψ^{leaf} for a grassland, but predictions of ψ^{leaf} using the same steady-state model with resistances accurately parameterized for a forest will be in error because of a considerable lag period.

The simulation results (Fig. 2) show another important point; total daily transpiration is nearly equal to total daily water uptake by the roots for both the steady-state and non-steady-state water flow models; inclusion of capacitance has no practical effect on daily totals. Running (1984) showed the same point for forest stands by comparing one simulation model, H2OTRANS, which uses hourly time steps and capacitance terms, with another simulation model, DAYTRANS, which uses daily time steps and no plant capacitance terms. Over a growing season, the DAYTRANS predictions were almost identical to those of H2OTRANS for cumulative transpiration and soil water depletion (Fig. 3). Moreover, the predictions of soil water depletion by both models were similar to measured soil water depletion.

Thus, non-steady-state models with plant capacitance are necessary for predicting diurnal variations of water uptake by the roots and leaf water potential, but steady-state models without plant capacitance suffice for predicting

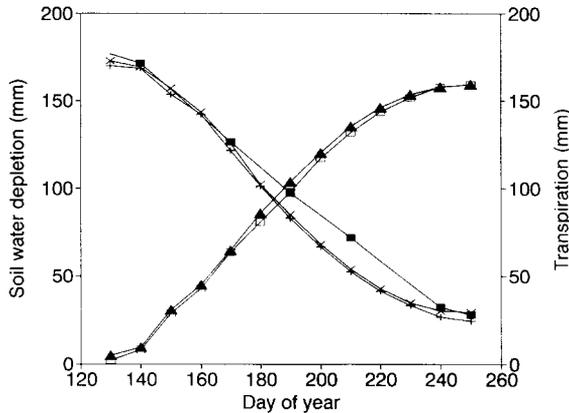


Fig. 3. Comparison of hourly time resolution water flow model with capacitance with daily time resolution model without capacitance over a growing season. Simulations compare H2OTRANS (hourly time step) and DAYTRANS (daily time step) numerical results to observe data on lodgepole pine at the Frasier Experimental Forest (CO, USA) during the summer of 1978. Symbols are: simulated cumulative transpiration by H2OTRANS (\square) and by DAYTRANS (\blacktriangle), simulated soil water depletion by H2OTRANS ($+$) and by DAYTRANS (\times), and measured soil water depletion (\blacksquare). Soil water depletion from a maximum soil water content of 250 mm was measured using a neutron probe; there were no observed data for transpiration. For seasonal and annual simulations, daily time steps appear adequate for modeling transpiration and soil water depletion (Running, 1984).

daily and seasonal totals of transpiration and water uptake. In general, for any spatial area from individual plants to large forest stands, the choice of a steady-state or non-steady-state model is dependent on the model's time resolution and purpose.

Plant water flow time constants

One method for determining the necessity of capacitance for soil-plant-atmosphere models is the comparison of a modeled time constant with the model time step (Allen and Starr, 1982; O'Neill et al., 1986). Time constants can be defined using the electric circuit analogy. For a resistor and capacitor in series, the time constant (τ , s) is equal to the product of the resistance and the capacitance. Thus, τ for water flow into and out of storage in the stem is equal to resistance to and from storage (R^{stem}) multiplied by C^{stem} (Fig. 1). Complete response to a step change in potential is usually said to have occurred after 3τ . When the model time step is about equal to τ , capacitance must be included in water flow models.

A whole-plant τ can be defined as the length of time necessary to reach 63% (\exp^{-1}) of the final steady-state value for a step change in conditions. Using the same resistances for a series of simulations (small resistances that are appropriate for a large tree), C^{stem} was varied from 1 to 1000 $\text{m}^3 \text{MPa}^{-1}$ and

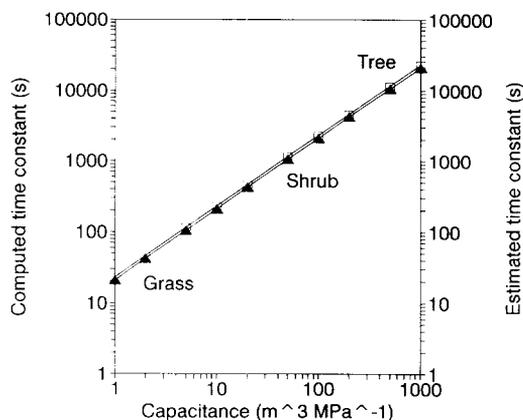


Fig. 4. Relationship of whole-plant time constant (τ) with stem capacitance for a step decrease in transpiration rate (computed τ , \square) and for the product of $(R_r^{\text{root}} + 0.5R_x^{\text{stem}} + R_s^{\text{stem}})$ and C^{stem} (estimated τ , \blacktriangle). Resistances and transpiration rate were the same for each numerical simulation: $\psi^{\text{soil}} = -0.1 \text{ MPa}$, $R_r^{\text{root}} = 10\text{E}6 \text{ MPa s m}^{-3}$, $R_x^{\text{stem}} = 2\text{E}6 \text{ MPa s m}^{-3}$, $R_s^{\text{stem}} = 10\text{E}6 \text{ MPa s m}^{-3}$, $R_s^{\text{leaf}} = 5\text{E}6 \text{ MPa s m}^{-3}$ and $C^{\text{leaf}} = 1\text{E}-6 \text{ m}^3 \text{MPa}^{-1}$. The resistances are appropriate for large plants (large C^{stem} , small R), the whole-plant τ will be greater with larger resistances, which are appropriate for smaller plants (small C^{stem}). Thus, these simulations indicate the minimum τ that would be expected for a given biome from grasslands to forests.

τ was determined by following ψ^{leaf} for a step decrease of transpiration rate (Fig. 4). The increase in τ was from about 20 s for the smallest capacitance to 6 h for the largest capacitance (Fig. 4), which is smaller than a grass and larger than a very large tree, respectively. Whole-plant τ was approximately equal to the product of $(R_r^{\text{root}} + 0.5R_x^{\text{stem}} + R_s^{\text{stem}})$ and C^{stem} (Fig. 4). For a step increase in transpiration rate, τ varied from about 10 s to 3 h over the same range of capacitance, and was about equal to the product of $(0.5R_x^{\text{stem}} + R_s^{\text{stem}})$ and C^{stem} . The step decrease in rate determines the amount of lag and hysteresis, whereas the step increase in rate determines how fast the plant will respond to sunrise.

The resistances of real plants vary with plant size, where S^{root} increases with S^{leaf} and causes R_r^{root} to decrease, so increases of C^{stem} with increases of plant size do not mean that τ will automatically increase. In Table 3, τ was about equal for the shrub, *E. farinosa*, the lodgepole pine and the apple tree. Whole-plant τ was still about equal to the product of $(R_r^{\text{root}} + 0.5R_x^{\text{stem}} + R_s^{\text{stem}})$ and C^{stem} for a step decrease in transpiration rate. These simulations (Fig. 4; Table 3) show the need to accurately determine non-steady-state model parameters for different-sized plants.

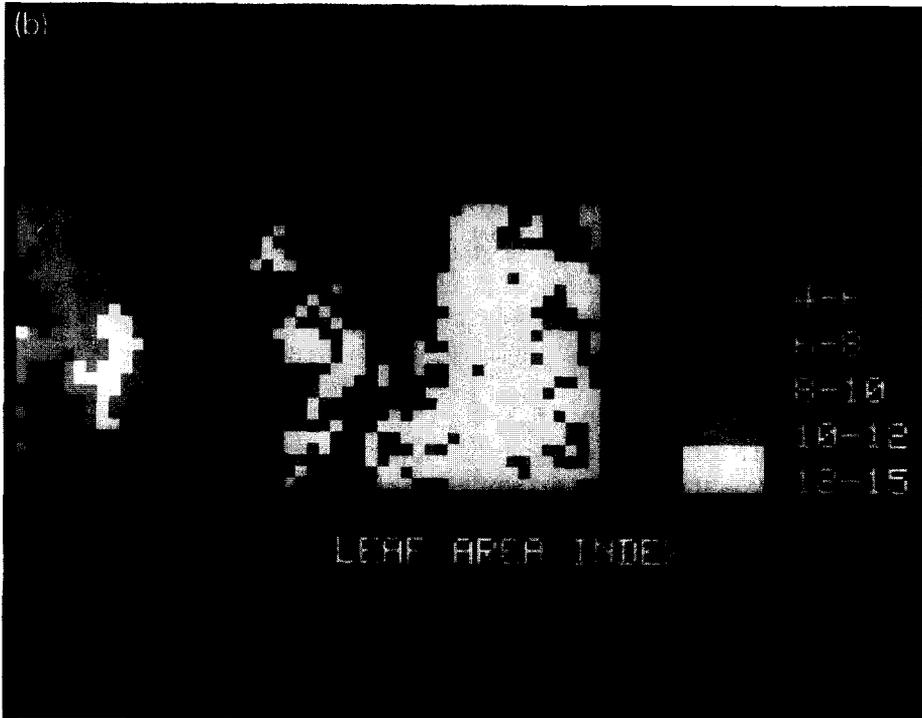
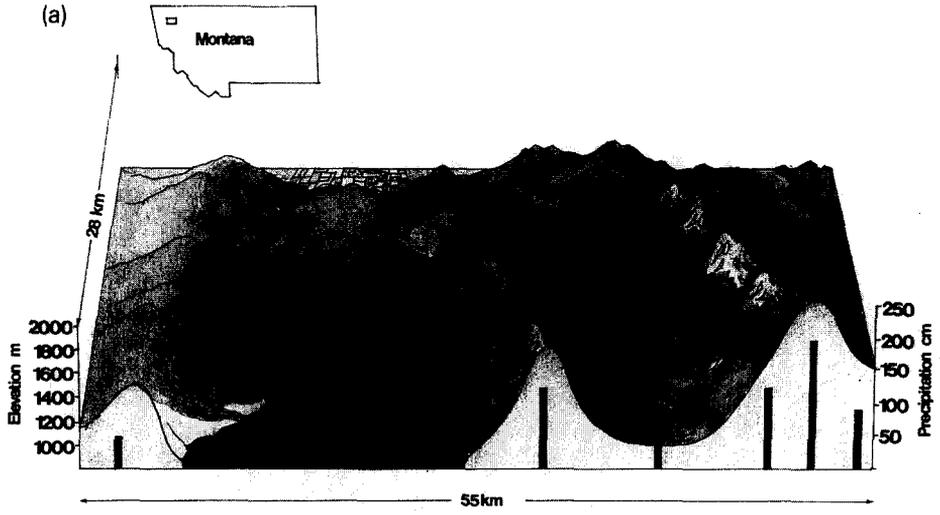
Ecosystem time constants

Capacitances in parallel are additive, whereas resistances in parallel are added by reciprocals. So, if n plants were n parallel paths in an electric circuit for an entire ecosystem, then based on whole-plant τ being about equal to $(R_r^{\text{root}} + 0.5R_x^{\text{stem}} + R_s^{\text{stem}}) \times C^{\text{leaf}}$ from above, an ecosystem time constant (τ) may be defined using an 'average plant' as

$$\tau = (n C^{\text{stem}}) / [n / (R_r^{\text{root}} + 0.5R_x^{\text{stem}} + R_s^{\text{stem}})] \quad (13)$$

which is equal to τ of the whole plant. This does not mean that C^{stem} , R_x^{stem} , R_s^{stem} and R_r^{root} for individual plants equal the respective quantities C^{stem} , R_x^{stem} , R_s^{stem} and R_r^{root} for ecosystem models; these quantities are equally scaled by the number of plants per land surface area to determine ecosystem τ .

Allometric relationships are of the form $\log y = a + b \log x$ and are generally used to estimate some size variable from another easily measured size variable (i.e. tree volume from tree diameter). The area of sapwood xylem in a stem cross-section is allometrically related to leaf area index ($\text{LAI} = S^{\text{leaf}}/S^{\text{land}}$, $\text{m}^2 \text{m}^{-2}$) for many different species (Waring, 1983; Waring and Schlesinger, 1985). Inverting allometric relationships between LAI and sapwood area may be used to estimate R_x^{stem} . However, the allometric equations relating LAI and xylem sapwood area have considerable variations among species (Waring, 1983; Waring and Schlesinger, 1985) and within a single species owing to stand age, health and density (Pothier et al., 1989).



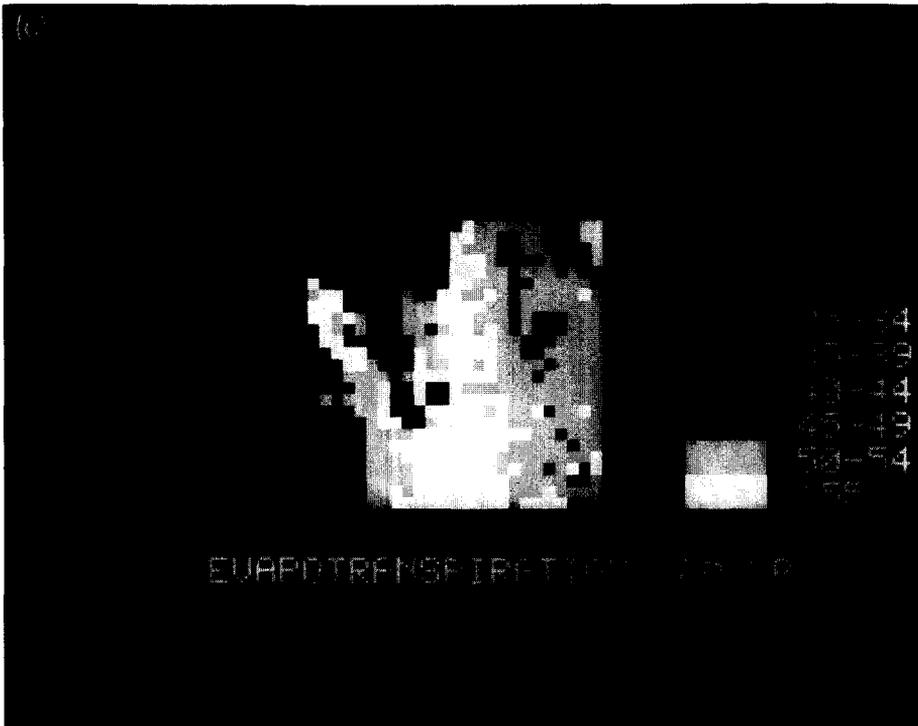


Fig. 5. Region diagram (a), total leaf area index (b) and annual evapotranspiration (c) of the Flathead and Seely-Swan valleys in northwestern Montana (USA) after Running et al. (1989). The area covered is 28×55 km; the 1.1 km grid cell was defined by the NOAA/AVHRR sensor. The region diagram (a) shows prominent physiographic features, average elevation of mountain ranges (scale left) and annual precipitation (black bars, scale right). Leaf area index was determined using NOAA/AVHRR sensor data, transpiration was estimated using the models of Running et al. (1987) and Running and Coughlan (1988).

Moreover, $S^{\text{root}}/S^{\text{land}}$ may be allometrically related to LAI and may be useful in estimating R_r^{root} . Allometric relationships between root and leaf surface area have been found for many species (Fiscus and Markhart, 1979; Fiscus, 1981; Kummerow, 1983; Hunt and Nobel, 1987b; Van Praag and Weissen, 1988); however, these allometric relationships contain variation of as much as an order of magnitude. Thus, it is unlikely that allometric relationships based on LAI can be used to accurately parameterize soil-plant-atmosphere models for single ecosystems. An easier alternative at present would be to use the whole-plant τ in Fig. 4 for a given biome type grassland, shrubland and forest as the ecosystem τ .

Implementation of plant water flow models for large spatial scales

We have illustrated the fact that soil-plant-atmosphere models of water flow through single plants are well developed. Additionally, we showed that

electrical circuit analogs provide a clear theoretical logic for scaling these models to ecosystem vegetation water flow. However, we see substantial practical problems in the scaling of these ideas to a regional plant water flow model. Figure 5 shows an attempt to describe regional plant canopy structure and evapotranspiration over an area approximately 3% of the size of a single GCM cell (Running et al., 1989).

One ecosystem variable that is routinely estimated from remotely sensed data is LAI, by using combinations of red and near-infrared radiances (Tucker, 1979; Asrar et al., 1984; Peterson et al., 1987). The estimation of LAI by satellites is probably not accurate to better than $\pm 1 \text{ m}^2 \text{ m}^{-2}$. The biome definition for ecosystem τ is fairly easy to obtain from Landsat Thematic Mapper data with a spatial resolution of 30 m. However, for the scene in Fig. 5, 30 m pixels would result in 1200 million pixels to process. Moreover, with coarse spatial resolution satellites such as the Advanced Very High Resolution Radiometer (1.1 km pixels) used for estimating LAI in Fig. 5, biome definition is not easy without substantial ancillary data. One source of ancillary data may be active microwave remote sensors such as synthetic aperture radars, because backscatter polarization indices contain information on the amount of woody biomass (Cimino et al., 1986; Westman and Paris, 1987; Wu and Sader, 1987).

Even if the biome type and LAI of a region are well characterized, quantifying the surface environmental conditions that drive plant water flow over a region at high time frequency is difficult. The basic environmental drivers of incoming solar radiation, temperature, humidity and precipitation are highly variable over regions of GCM grid-cell size, yet directly control plant water flow. Over the scene in Fig. 5, incoming solar radiation varies by 30%, surface temperature by 10°C and precipitation by 200% owing to topographic variability. Soil water-holding capacity varies from 60 to 260 mm. Techniques for handling this variability are being developed (e.g. Band et al., 1991).

A precursor to the final forest ecosystem simulation in Fig. 5 was a mountain climatological simulator to provide two-dimensional estimates of daily meteorological conditions for the landscape (Running et al., 1987). The microclimate model was prefaced by a topographic model that defined slopes, aspects and elevations of the surface elements. This simple microclimate model required 90% of the total computer time needed for the entire ecosystem simulation. Finally, the variability of soil water-holding capacity and hydrologic dynamics across a GCM cell is tremendous, and intimately coupled to the climatic atmospheric supply and vegetation demand of water that is central to soil-plant-atmosphere models.

The point we wish to emphasize here is that we do not see highly refined plant water flow models as being appropriate for regional scale research (Running and Coughlan, 1988) when other critical factors concerning plant

water flow are treated so coarsely. A basic principle of efficient systems modeling is that each component be modeled to an approximately equivalent level of complexity. Thus, an ecosystem τ may be the only practical method of including models of non-steady-state water flow through plants into GCM.

WHAT IS THE PURPOSE OF PLANT WATER FLOW MODELS IN GCM?

Global climate models need accurate predictions of diurnal variations of transpiration rate and soil water evaporation rate over vegetated land surfaces (Dickinson et al., 1986; Sellers et al., 1986; Dickinson, 1987; Sellers and Darman, 1987). So, models of water flow through the soil-plant-atmosphere system should be added to GCM only if they make predictions of stomatal conductance (g_s , mm s^{-1}), and hence diurnal variations of transpiration rate, more accurate.

Global climate models use very large spatial scales and short time steps (BATS/CCM1 models use about 5° latitude \times 5° longitude and a 1800 s time step, respectively; Dickinson et al., 1986). If GCM require predictions of ψ^{leaf} for the estimation of g_s , then non-steady-state water flow models would be needed or errors would occur over a diurnal cycle. The errors would be large when GCM that were validated using grasslands (where $\tau \ll$ time step) are applied to forests (where $\tau >$ time step; Fig. 4). Yet, the daily totals of transpiration and water uptake by the roots should agree with measured hydrologic balances for both forests and grasslands, as discussed above.

The main question is whether prediction of ψ^{leaf} is necessary for the prediction of stomatal conductance and, thus, transpiration. Recent studies on the relationship between plant water status and g_s have concluded that ψ^{soil} and vapor pressure difference (VPD), but not ψ^{leaf} , are the significant variables controlling g_s under normal conditions (Bates and Hall, 1981; Gollan et al., 1986; Schulze, 1986). The use of pre-dawn ψ^{leaf} for the control of g_s from earlier studies is consistent with this interpretation (because pre-dawn ψ^{leaf} is nearly equal to ψ^{soil}); hence, soil water variables were used indirectly to drive soil-plant-atmosphere models (Federer, 1979, 1982; Running, 1980b). When the leaf reaches $\psi_P = 0$ MPa, ψ^{leaf} may control g_s by releasing various plant hormones, but this needs more study (Schulze, 1986). If seasonal and diurnal variations of g_s can be accurately predicted from maximum g_s , VPD and ψ^{soil} , without estimating ψ^{leaf} , then we see no compelling reason for using either a steady-state model or a non-steady-state model of water flow in a GCM.

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