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Understanding and parameterizing the soil–water–atmosphere transfer through vegetation

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Abstract

We present an overview of water transport in plants, exploring how the theory has formed the basis of models of water use, carbon assimilation and plant growth. We outline the cohesion theory of water transport, and explore the vulnerabilities of the transport system to cavitation. The relationships between water relations and CO₂ gain are outlined using a detailed model of the soil–plant–atmosphere continuum, coupling vapour-phase losses of water to liquid-phase supply to the leaf. Measurements of whole ecosystem exchange of latent energy and CO₂ via eddy covariance are increasingly common. These measurements are generated almost continuously, and so provide time series of land-surface process dynamics that have proved very useful for testing models. We compare model predictions of canopy water and C exchange for temperate deciduous/broadleaf and evergreen/coniferous forest, tropical rain forest, and a range of arctic tundra vegetation types. From these comparisons, we summarize the critical issues for parameterizing water fluxes through vegetation. We then go on to discuss how land-surface schemes can be coupled to atmospheric mesoscale models.

Introduction

Water transport in plants is a classical and sometimes controversial subject that has been discussed extensively for well over a century. In this paper we present an overview of the subject, and we see how the theory has been used in the last decade to form the basis of models of water use, carbon assimilation and plant growth. The subject has special significance for the prediction of the responses of ecosystems to climate change.

The transpiration stream and the cohesion theory

The tallest known trees are as high as 100 m, and it is not surprising that the rise of water over such remarkable distances has always excited scientific curiosity. The cohesion theory of water transport, proposed by Böhm (1893) and first examined critically by Dixon (1914), is consistent with virtually all experimental observations, and forms the basis for all recent attempts to model water flow in plants. In this

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theory, water is drawn through the plant and soil by the leaves, and for most of the time the stream of water is under a great tension. The theory is called the cohesion theory because it is the natural tendency of water molecules to stick to each other that gives water the necessary strength under tension. In this part of this paper we describe the theory.

The movement of water from the soil, through the plant, to the point at which it evaporates to the atmosphere is known as the transpiration stream and is essentially a hydraulic flow through porous media. The driving force for this flow is the difference in water potential between the two ends of a chain of hydraulic resistances, in a manner which is analogous to electricity flowing through electrical resistances. These resistances comprise the tortuous pathway within the soil, roots, stem and leaves. This analogue was first proposed by Van den Honert (1948) and later developed by several people, perhaps most notably by Cowan (1965). Cowan's soil-plant-atmosphere scheme is reproduced here (Figure 1).

Water potential, Ψ , is fundamentally the free energy of water, J m^{-3} . For historical reasons, the units of water potential generally used are those of pressure, Pascals, expressed on a scale where the water potential of pure water at sea level is zero.

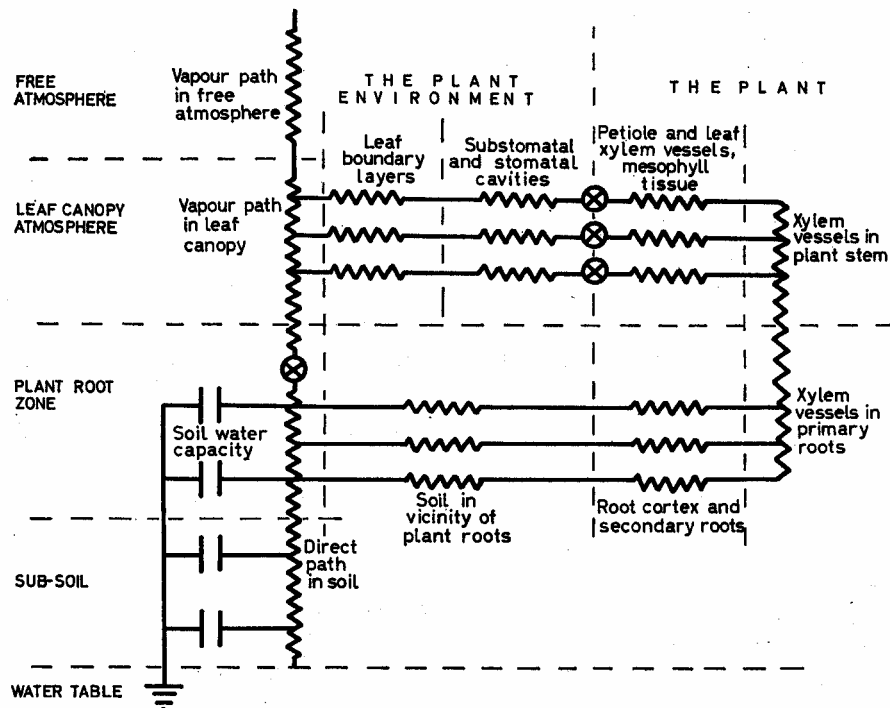


Figure 1. Cowan's representation of pathways of water transport in the soil, plant and atmosphere. Sites of phase change, liquid to vapor, are distinguished by the symbol \otimes (from Cowan 1965)

Water potential is influenced by a number of processes that influence that availability of water. For example, pure water at 10 m above sea level has a water potential of +0.1 MPa, a figure that is calculated from the work done in raising water 10 m. Water potential is reduced to well below zero when solutes are present, as a result of the attractive forces between water molecules and the solute, by the process commonly called osmosis. Water potential is also reduced by surface-tension forces, for example in the thin films of water that cling to surfaces, especially in the soil. Thus, several physical phenomena are combined to influence the availability of water. The total water potential in plant or soil is thus made up of a number of components:

$$\Psi_{\text{total}} = \Psi_s + \Psi_p + \Psi_m$$

where Ψ_s is the solute potential, Ψ_p is the pressure potential and Ψ_m is the matric potential. In practice, the water potentials of non-saline soils are dominated by matric potential whereas in the living cells of well-watered plants the matric potential is a small term compared to the considerably negative solute potentials resulting from the materials dissolved in the cell contents, and the substantially positive pressure potentials arising from the elastic properties of the cellulose cell walls.

It is useful to consider the development of the water-potential gradient by considering the loss of water by leaves. Evaporation occurs from cells inside the leaf, and water vapor diffuses through adjustable pores (stomata), through the boundary layer of the leaf to the atmosphere (Figure 1). This evaporation from leaves is termed transpiration, and its rate depends on environmental conditions, the size and number of the stomata, and the size of the leaf. Monteith (1965) made a thorough analysis of this process, in terms of the resistance-analogue model where the controlling resistance were the stomatal and aerodynamic resistance r_s and r_a respectively. This has become widely accepted and is known as the Penman-Monteith equation:

$$E = \frac{sR + \rho c_p D / R_a^{\text{heat}}}{s + \lambda(R_a^{\text{water}} + R_s) / R_a^{\text{heat}}}$$

where:

γ = the psychrometric constant (Pa °C⁻¹)

ρ = density of air (kg m⁻³)

c_p = specific heat of air at constant pressure (J kg⁻¹ °C⁻¹)

D = saturation deficit of the atmosphere (Pa)

E = evaporation rate (W m⁻²)

R = net radiation (W m⁻²)

R_a = windspeed-dependent aerodynamic resistance to H₂O or heat (s m⁻¹)

R_s = canopy stomatal resistance (s m⁻¹)

s = rate of change of saturation vapor pressure with temperature (Pa °C⁻¹).

For a full discussion of the Penman-Monteith equation the reader is referred to Monteith and Unsworth (1990) and Jones (1992).

Consider a well-irrigated crop, or natural vegetation shortly after rain. Applying the equation (or directly measuring rates of water use by vegetation) we find that under most daytime conditions, evaporation occurs at rates up to about 2 g H₂O m⁻² s⁻¹. Cells within the leaves, which were fully hydrated before dawn (Ψ_{total} around zero), consequently become somewhat dehydrated (Ψ_{total} less than zero). As cells contain less water, their volume reduces slightly, causing the solute concentration to increase slightly (Ψ_s , already negative, becomes more negative) and the elastic cellulose walls of the cells exert a slightly lower pressure on the cell (Ψ_p , already positive, becomes less positive). The new value of Ψ_{total} is the sum of Ψ_s and Ψ_p (the matric potential Ψ_m is negligible). Hence, the total water potential in the leaves falls below that in the well-irrigated soil, and water is drawn from high potential (soil) to low potential (leaves) through the chain of resistances (Figure 1). Essentially, the leaves 'suck'

water from the soil by this process, although the suction originates not from a vacuum, as in the normal use of the word, but from the osmotic effect of the solutes within cells being sufficiently concentrated to attract water molecules towards them. In the immediate vicinity of the cells of the leaf, there are small pipes (veins) made of xylem cells, making a hydraulic connection between the cells and the water contained in the rest of the hydraulic continuum (branches, stem, roots and soil). In the final mm or so, water travels outside these pipes, in the intercellular spaces and in the minute channels within the cellulose walls of the cells themselves.

The speed of the transpiration stream is determined by a combination of the environmental factors, as stated in the Penman-Monteith equation, and the stomatal resistance (determined by the number and diameter of the stomatal pores). The latter is under evolutionary, developmental and physiological control. Stomata tend to close when water is in short supply, effectively protecting the plant from desiccation. In fact, quite small changes in the diameter of the stomatal pores usually exert a large influence on the rate of water use. One case when this is not true, is when the aerodynamic resistance is large in relation to the stomatal resistance. Generally, it is smaller. Another case where this is not true, is when the humidity within the planetary boundary layer builds up sufficiently, as a result of transpiration at the landscape scale, to reduce the saturation deficit of the air. When the air around the leaf is water-saturated, change in stomatal resistance produces no change in transpiration.

It is beyond the scope of this article to describe the measurement of the terms discussed above: leaf water potential, transpiration rate and stomatal resistance. There are well-known texts which do this very well (Percy et al. 1989; Jones 1992).

Figure 2 shows the water-transport pathway in the soil–plant–atmosphere continuum. In fossils of the earliest land plants (in the Silurian period, 400 million years ago) the xylem is primitive, consisting of bundles of tubes, and this inferior transport system may have limited how tall they grew. In gymnosperms and angiosperms, tall trees later evolved in which the xylem is essentially all the woody parts of the plant, composed of several types of cell, with extremely strong walls made of cellulose and lignin. As well as water transport, the wood also provides the great mechanical strength required to withstand the forces of gravity and the forces of the wind. In a later section we return to consider some of these structural aspects.

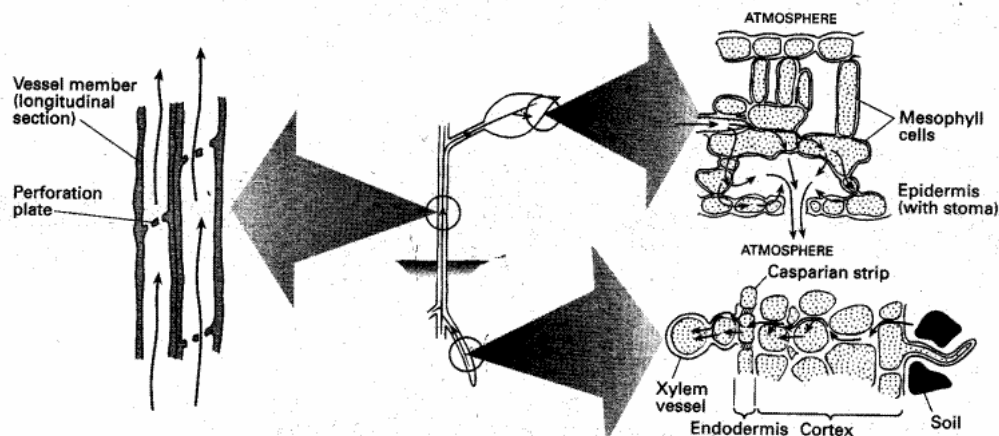


Figure 2. Pathway of water movement in plants (redrawn and adapted from Jones 1992)

Vulnerability of the pipeline

One objection to the cohesion theory is that the tensions that are expected to occur in the transpiration stream of tall trees are very large, up to -3 MPa, and close to the limit required for the breakage of water columns. It is clear that such tensions really do exist. Scholander's pressure chamber (Scholander et al. 1965), Spanner's psychrometers attached to stems (Dixon and Tyree 1984), and displacement transducers used to detect the shrinkage in diameter of the xylem tissues (Irvine and Grace 1997) all enable it to be measured, albeit indirectly. In the 1960s Milburn detected acoustic emissions from the petioles of severely water-stressed plants, which he interpreted as cavitation or 'breakage' of the water (Milburn 1966). Later, the development of ultrasonic acoustic sensors showed that cavitation in the stems of plants is a common process during normal summer conditions (Sandford and Grace 1985).

Once cavitation has occurred it is difficult to account for its reversal. Experiments on model systems show that unsaturated stems will only refill when the water potential is raised close to zero or is positive (Sobrado, Grace and Jarvis 1992). In conifer trees this does not seem to occur. In angiosperm trees and many other plants it does occur by a phenomenon known as root pressure. It is this process which, in the spring, pushes water up the stems of grapevines, for example. Root pressure is an osmotic process, not well-understood. Whereas the cohesion theory is a purely physical process, it seems that refilling is linked to the metabolism of the plant (Grace 1993).

When cavitation occurs some of the capacity of the stems to transport water is lost, and hence one might expect the hydraulic resistance to increase causing the leaf water potential to decline even more, and to trigger yet more cavitation by positive feedback. This scenario is described as 'catastrophic cavitation'. However, when plants are subjected to drought it is clear that they protect themselves from catastrophic cavitation by partial closure of the stomata (Jones and Sutherland 1991; Irvine et al. 1998). This implies a signalling mechanism, whereby the stomata detect 'trouble ahead' and begin to close. Many authors have provided support for the hypothesis that roots sense the lack of water in the soil and produce a chemical signal which travels to the leaves in the transpiration stream (Davies, Tardieu and Trejo 1994). However, we have argued that this is unlikely in trees, as the time taken for a chemical to rise in the transpiration stream is too great (about 10 days in a 15-m conifer tree, and about 1 day in an angiosperm tree). It seems more likely that the plant has a mechanism to detect water tension.

Some structural aspects

The colonization by plants of the land required the evolution of efficient root systems, xylem, and an epidermis with a cuticle and stomata. True xylem and stomata are relatively recent but even some mosses have analogous structures. In this section we provide more information on the structure of the soil-plant-atmosphere system (Figure 2).

Soil is an aggregate structure, in which minerals, organic matter, water and air exist in a complex matrix with a wide range of pore diameters. The clay minerals are hydrated aluminosilicates with extraordinarily complexity, being very finely divided and highly charged and therefore very effectively attracting water and ions around

them. The extent to which soil attracts water and thus lowers the water potential depends on the extent of the clay content, and more generally on the soil texture. Water-release curves relating the water potential to the water content may be determined experimentally with a pressure-plate apparatus in which one measures the amount of water which can be squeezed out of the soil at a particular applied pressure. Some examples are shown in Slatyer (1967). Similarly, the hydraulic resistance of soil depends on the soil texture and falls sharply with the clay content. The theory of water movement in soils was developed in the 1950s by J.R. Phillip, and is discussed elsewhere in this volume.

Roots are multicellular branching structures for absorbing water and nutrients, and also for providing anchorage. Contact with the soil is enhanced by extensions of the root epidermis, known as roots hairs, which make intimate contact with the soil particles. Actually, most plants do not rely on root hairs except when they are seedlings. Beyond the seedling stage they develop a symbiotic relationship with fungi, and it is the fungal hyphae which ramify the soil pores and hugely increase the area for absorption. In the tips of the fine roots there is no xylem. The root tips are actively extending, highly lubricated with mucilage, and appear to be probing, actively seeking nutrients and water. Further back from the tip, axial cells thicken and die, forming characteristic xylem cells. By definition, xylem cells are non-living by the time they become functional as transport conduits. In roots, radial transport is mostly through the intercellular spaces and cell walls before entering the axial xylem conduits. However, all roots appear to have some cells with suberized walls (the Casparian band), so that the line of least resistance at one point in the radial path is through the protoplasm of the cells.

Stems and branches contain much xylem tissue, connecting directly with the xylem of the roots and leaves, following geometric and fractal rules in much the same way as all transport systems (rivers, roads, lungs). In trees the water is transported in the outer regions of the wood. The inner regions become dysfunctional as far as water transport is concerned, and are often filled with gums and resins forming dark-color heartwood in contrast to the transport-active sapwood. Of course, the heartwood is still important to the plant in a mechanical sense. Stems and branches are surrounded by soft tissues that are living and which serve other functions (protection, transport of sugars, with some capacity for photosynthesis). As far as water relations are concerned these tissues swell and shrink substantially as the water potential fluctuates, and they constitute short-term capacitors (Figure 1). To some extent, the xylem itself also shrinks and swells but the cell walls are have such a high elastic modulus that the dimensional changes are small (Irvine and Grace 1997). Nevertheless, this dimensional change represents a change in the water stored in the woody tissues and so is also a capacitance. Dixon, Grace and Tyree (1984) showed that bursts of ultrasound, denoting cavitation, are associated with a subsequent increase in leaf water potential as water becomes available to the leaves.

There are several types of non-living cell in the xylem (Figure 3). Tracheids are the most primitive. Water flows from one to another through adjacent holes, called bordered pits. These pits are miniature valves, preventing embolisms caused by cavitation from spreading. Angiosperms have obviously pipe-like cells, with larger diameter and almost-open ends. Water travels much more easily through such conduits, but there may be greater vulnerability to cavitation. Generally, plants in dry habitats have tracheids instead. There are also millions of cells called fibers that may function primarily to give mechanical strength. Probably they are partially water-

filled and their water content fluctuates with water potential. Thus, they may be a component of the stem capacitance.

Leaves

There is a huge range in the stomatal resistance of leaves, related to their productivity as well as water use (Schulze et al. 1994). Fast-growing plants tend to be those from moist fertile habitats, and they have large and numerous stomata. Stomata occur in various morphologies, related to the habitat to which the plant is found (Figure 4). For example, many conifers have stomata which are sunken in the leaf, thus increasing the stomatal resistance. The antechamber may be filled with waxy deposits, further increasing the stomatal resistance. There are exceptions such as one group of desert plants, known as ‘water-spenders’, which have a very large number of stomata. An example is the desert melon, *Citrullus colocynthis*, which uses its very fast transpiration rate to keep its leaves below the lethal temperature (about 50 °C). To sustain this high rate of transpiration it possesses extremely deep roots which ‘mine’ water from depths of tens of meters (Althawadi and Grace 1986).

In most cases, almost all of the water transpired is via the stomata because the rest of the leaf is coated with a cuticle which is impermeable to water vapor. However, the cuticle may be damaged by physical agencies such as wind (Van Gardingen and Grace 1991).

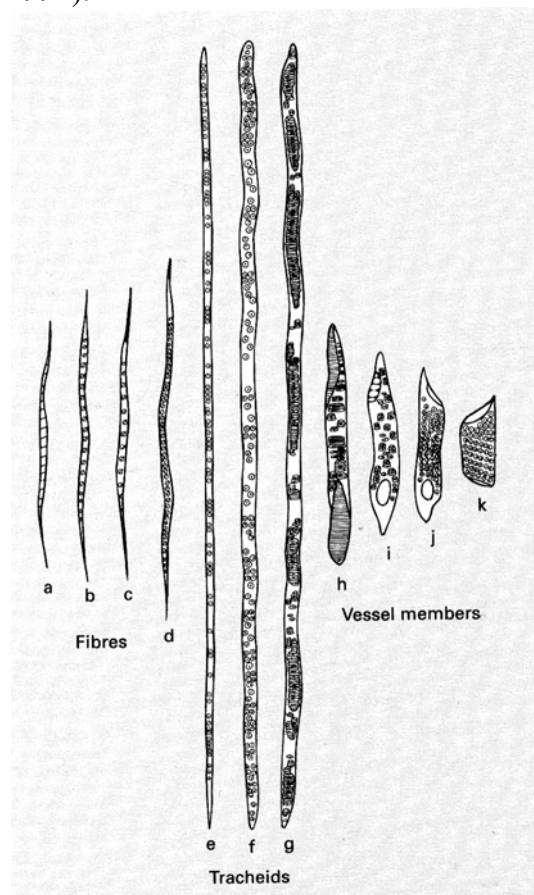


Figure 3. Types of non-living cells found in the woody stems of plants as components of the xylem. a-d are *fibres*, e-g are *tracheids*, h-k shows the postulated evolutionary sequence towards short broad *vessels* found in angiospermous plants (from Esau 1965). Scale: tracheids are several mm long

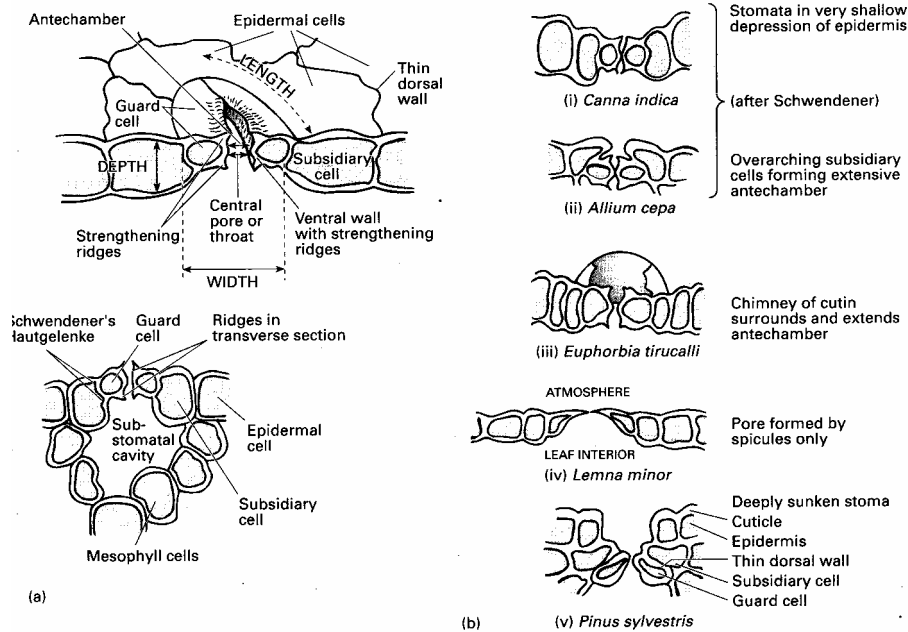


Figure 4. (a) Oblique and transverse views of the stomatal apparatus and (b) some variations between species (from Meidner and Mansfield 1968). Scale: stomatal pores are typically $40\text{--}60\ \mu\text{m}$ in their long diameter and there are up to $400\ \text{per}\ \text{mm}^2$

The relation between water loss and CO₂ gain

As well as stomata being the ports for transpiration they are also the ports for entry of CO₂ in photosynthesis. In the presence of sunlight, plants fix CO₂ to make glucose, which is then used in the biosynthesis of all the structural materials of plants. Photosynthesis is controlled fundamentally by light, temperature and the availability of plant nutrients but it is restricted when the stomata begin to close for the conservation of water. In general, plants which grow fast thus use a lot of water. This link between transpiration and photosynthesis is the reason for the link between water use and productivity (see Schulze et al. 1994).

It was soon realized that models of photosynthesis (see the survey of these by Von Caemmerer 2000) could be fruitfully linked to a soil–plant–atmosphere transport scheme (SVATS), and thus was spawned a family of numerical models capable of predicting gas exchange of vegetation (Sellers et al. 1996; Williams et al. 1996). In the following sections we describe one of them in more detail.

Simulating water control feedback loops

Numerous models have been constructed to analyse and synthesize the complex behavior of stomatal opening as a basis for understanding and predicting CO₂ capture. The models range in complexity from the empirical (Jarvis 1976; Ball, Woodrow and Berry 1987; Leuning 1990) to the more mechanistic (Dewar 1995). Here we focus on a modeling approach based on the strong observed co-ordination between the stomatal and hydraulic properties of plants (Meinzer 2002). This link is intuitive if stomata operate to maximize carbon assimilation, while maintaining leaf water balance at a level that ensures maintenance of metabolism. More detailed models of water transfer from soil to atmosphere via vegetation (Williams et al. 1996; Whitehead and Dye

1998) incorporate this philosophy by explicitly simulating the water status of leaves, as a function of gas-phase losses and liquid-phase recharge, and relating water status to stomatal opening.

To link stomatal conductance (g_s) to leaf water status, g_s must be directly linked to fluxes of water through the plant (\mathbf{J}_p). Liquid fluxes are a function of differences in water potential between soil (Ψ_s) and leaf (Ψ_l), and of the resistances of the hydraulic pathway in soil (R_s) and plant (R_p). In tall trees, the gravitational potential on water transport is also significant (h = tree height; g = gravitational acceleration; ρ_w = density of water), and thus;

$$\mathbf{J}_p = \frac{\Psi_s - \Psi_l - \rho_w g h}{R_s + R_p} \quad (1)$$

However, the relationship between \mathbf{J}_p and the water-potential drop is not unique; initially water is drawn from stores within plant tissues, so that liquid flow lags behind the evaporative demand (Schulze et al. 1985). This hysteresis can be modeled by incorporating capacitors into the electrical circuit analogue for water flow (Jones 1992). The capacitance (C) of any part of the system is defined as the ratio of the change in tissue water content (W) to the change in water potential:

$$C = \frac{dW}{d\Psi} \quad (2)$$

The rate of change of foliar water content (dW/dt) is given by the difference between the flow of water into the leaf and that lost by evaporation:

$$dW/dt = \mathbf{J}_p - E$$

Thus,

$$dW/dt = (\Psi_s - \Psi_l - \rho_w g h)/(R_s + R_p) - E \quad (3)$$

Assuming constant capacitance, the first-order differential equation describing leaf water-potential dynamics is thus:

$$\frac{d\Psi_l}{dt} = \frac{\Psi_s - \rho_w g h - E(R_s + R_p) - \Psi_l}{C(R_s + R_p)} \quad (4)$$

Williams et al. (1996) incorporated this equation into a numerical algorithm that varied stomatal conductance so that E (determined by the Penman-Montieth equation) was maintained at the level that kept Ψ_l from falling below a critical threshold value (Ψ_{lmin}). The critical value is a point below which potentially dangerous cavitation of the hydraulic system may occur (Jones and Sutherland 1991). Thus, once $\Psi_l = \Psi_{lmin}$, g_s is adjusted to set E so that $d\Psi_l/dt = 0$. This approach balances atmospheric demand for water with rates of water uptake and supply from soils, and prevents cavitation from occurring. In conditions where atmospheric demand exceeds supply (e.g. early morning) stomata open in response to declining intercellular CO_2 concentrations (Mott 1988), but opening is limited to maintain a minimum water use efficiency.

The strength of this approach is that the model integrates the effects on stomatal opening of both atmospheric demand for water and rates of water supply from soil via

the plant hydraulic system. Thus, the model overcomes the problem associated with the simpler approaches that treat water supply as a single tuning factor. Also, the model can simulate stomatal closure as a result of either rate limitation on water supply (the hydraulic pathway has reached its maximum capacity) or an absolute limitation on supply (the soil matrix around the roots has a declining water potential). The difficulty with this approach to simulation is that the complexity of the model raises the parameter requirements. Hydraulic-resistance data are becoming more common (Tyree and Ewers 1996; Wullschleger et al. 1998; Becker, Meinzer and Wullschleger 2000), but there is considerable uncertainty about the relative importance and the dynamics of the different components in the hydraulic path from soil through roots to stems and leaves (Williams et al. 1998). And assumptions that leaf water potential is maintained above a critical level may not always be valid (Sperry et al. 1998; Williams, Bond and Ryan 2001).

Multilayer versus single-layer canopy models

Soil–vegetation–atmosphere models are generally of two types – ‘big-leaf’ or multilayer. ‘Big-leaf’ models are simpler, ascribing to the entire canopy a single physiological and aerodynamic resistance to water/CO₂ transfer. Multilayer models seek to incorporate at least the vertical variation in canopy structure and microclimate, and simulate the activity of the entire canopy as the summation of activity in multiple canopy layers with individual stomatal and leaf boundary-layer conductances.

There has been considerable discussion on the benefits and costs of big-leaf versus multilayer approaches (Raupach and Finnigan 1988; Williams et al. 1996; De Pury and Farquhar 1997; Williams et al. 1997; Baldocchi and Meyers 1998). The big-leaf approach is computationally simpler, but has difficulties incorporating the non-linear behavior of leaf-level photosynthesis; for example, coping with the patchy light climate within a canopy. Also, big-leaf model parameters tend to be aggregated and thus more brittle. For example, canopy conductance can be estimated from whole-ecosystem measurements, but a model to simulate its dynamics would have to take account of the potentially different response behavior of stomata in the upper and low canopies. Multilayer models have parameters that can be measured and directly related to processes (stomatal conductance can be recorded by leaf-level gas-exchange techniques, for example). But parameter requirements tend to be numerous; if parameters have to be estimated with poorly defined errors, then the resulting model is underdetermined and prone to uncertainty.

Corroboration against flux data

Measurements of whole ecosystem exchange of latent energy and CO₂ via eddy covariance are increasingly common (Valentini et al. 2000). These measurements are generated almost continuously, and so provide time series of land-surface process dynamics that have proved very useful for testing models. The soil–plant–atmosphere (SPA) model (Williams et al. 1996) was designed such that the scales of parameterization (leaf level) and prediction (canopy level) allow the model to be directly corroborated against eddy flux data. The SPA model has been corroborated against data from both temperate deciduous/broadleaf and evergreen/coniferous forest, tropical rain forest, and a range of arctic tundra vegetation types. We discuss

each of these comparisons in turn, and the lessons they have provided about parameterizing water fluxes through vegetation.

Temperate deciduous/broadleaf forest

The flux tower at Harvard Forest, Massachusetts (42°54' N, 72°18' W) is located in a 55-75-year-old mixed deciduous *Quercus/Acer* stand (Goulden et al. 1996), and data have been collected there since the early 1990s. Average annual precipitation is 1091 mm, while the June-September average is 379 mm. Mean annual temperature is 7.1 °C.

Measurements of evapotranspiration from an eddy covariance system show a strong seasonality of fluxes, but also significant day-to-day variability in rates (Figure 5). Simulations with the SPA model are able to adequately replicate the data (Figure 5), and indicate that the rates of water transfer to the atmosphere are governed on short

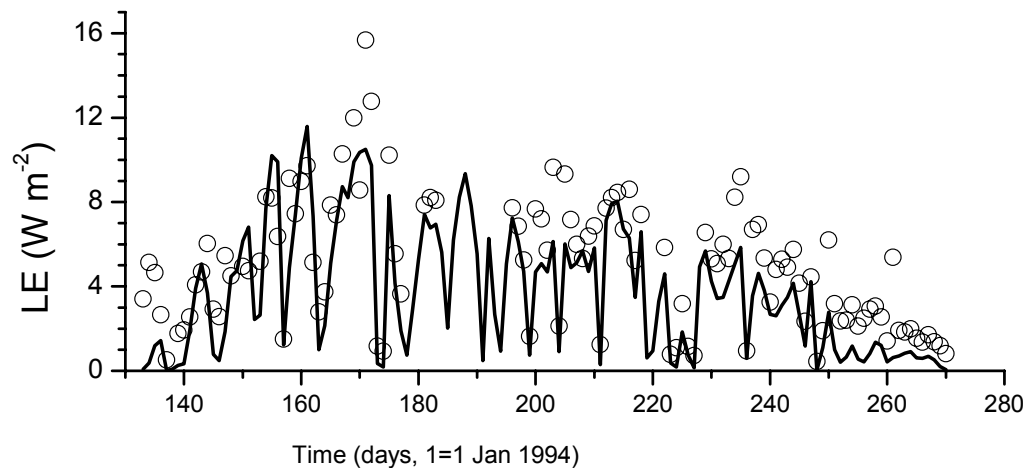


Figure 5. Measured and modeled latent energy flux during the 1994 growing season at Harvard Forest, Massachusetts. Data by permission of S.C. Wofsy, Harvard University

time scales by available energy, and over the year by seasonal variations in leaf-area index (LAI). LAI increases rapidly in the spring when frosts cease (Goulden et al. 1996), holds steady over summer and then declines as frosts return (Figure 6). Model underestimates tend to occur on or after rain days, suggesting either measurement problems or a bias in the model predictions of canopy interception and evaporation. At the end of the season there is a consistent underestimate of latent energy flux, suggesting that the parameterized reduction in leaf area at the end of the season is too low. Incorporating correct phenology is critical in simulations of deciduous forests.

In this model application no soil-moisture constraints were parameterized, i.e. soil-moisture dynamics were not simulated and so the supply of water to the canopy was considered constant throughout the year. Thus, evapotranspiration was governed completely by atmospheric demand for water and by the energy absorbed by the canopy. Model application to several other years in the 1990s suggests that a lack of soil-moisture constraint on water fluxes is the common state of affairs for this forest ecosystem, even in what are considered to be dry years. This lack of soil-moisture constraint may also be determined by a shallow water table at the site. Topographic variations in water-table depth may result in differential susceptibility to moisture stress at the broader landscape scale.

To investigate the importance of topography to plant water use, a separate study coupled the SPA model to a TOPMODEL simulation of catchment hydrology (Engel et al. 2002). The coupled model was parameterized for and corroborated against Bowen-ratio measurements and stream discharge data from a *Quercus*-dominated catchment in New York State (Black Rock Forest, 41°21' N, 74°01' E), where elevations range from 115 to 450 m above sea level. Soil thickness ranges from 0.1 m in upland areas to 1.0 m in the valley bottom. The coupled model was parameterized with independent data on upland and lowland canopy morphologies, tree heights, and root distributions. The upland stands had on average 24% lower LAI and were half the height of lowland stands. In well-watered conditions, the patterns of water use were such that both stands had similar hydraulic conductance per unit leaf area (i.e., the lower LAI in the upland stands was counter-balanced by a higher conductance due to shorter stems). During late summer drought, however, the simulations showed that moisture stress was longer and more severe in the upland systems due to thin soils and a deep water table.

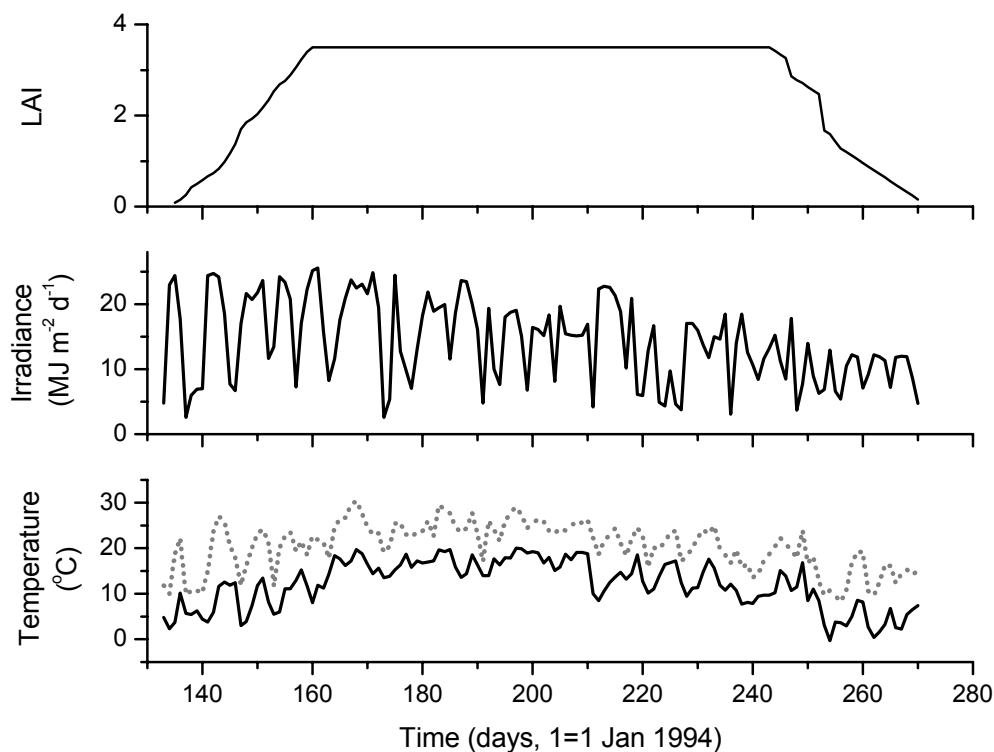


Figure 6. Variation in key drivers of vegetation water use during the 1994 growing season at Harvard Forest, Massachusetts. The upper panel shows the phenology of leaf-area index (LAI) as determined from a simple degree-day model (Goulden et al. 1996), and maximum leaf-area data from litter traps (Aber et al. 1993). The middle and lower panels show total daily short-wave irradiance and daily maximum (dots) and minimum (solid) temperatures respectively. Data by permission of S.C. Wofsy, Harvard University

Tropical rain forest

The ZF2 tower was located in a stand of virgin *terra firme* rain forest, in the Reserva Biologica do Cuieiras (a forest reserve belonging to Instituto Nacional de Pesquisas da Amazônia, used by the ABRACOS-Jacarex project). The stand is 60 km north of Manaus, in the state of Amazonas, Brazil (2°35' S, 60°07' W). The data reported here were collected over a 12-month period from 1 September 1995 to 31 August 1996.

The climate of the site is warm with frequent precipitation, with a short dry season running from July to October. Over the twelve-month study period the estimated precipitation was 2088 mm. There were 211 rain days, and the longest rain-free interval was 30 days, running from 13 July 1996 to 11 August. Annual mean temperature was 25.7 °C. The forest canopy was approximately 30 m tall, with occasional emergents to 45 m. Leaf-area index (LAI; m^2 one-sided *leaf area* m^{-2} *ground area*) values for nearby sites range from 5.7 to 6.6 (Williams et al. 1998).

The eddy flux data showed a clear seasonality in CO₂ exchange (Malhi et al. 1998), and a correlation with surface soil-moisture values suggested that drought might be responsible. However, at the time of the study there were no published data indicating that drought stress occurred in Amazonian rain forests. Studies undertaken at a nearby site at the end of the 1992 dry season indicated that pre-dawn leaf water potential in dominant canopy trees was never much below -0.5 MPa, even during the dry season (McWilliam et al. 1996), indicating that some portion of the fine roots remained in contact with freely available soil moisture throughout the year. This evidence argues against the likelihood of a soil-moisture limitation on stomatal opening, although the presence of roots at depths of 8 m (Nepstad et al. 1994) was suggestive of the importance of soil-moisture supply.

A diagnosis with the SPA model showed that the observations of latent energy fluxes during the dry season were not consistent with an assumption of freely available soil moisture. Conversely, observed fluxes during the wet season were consistent with this assumption. A decline in soil water potential was discarded as a possible explanation, given the lack of support in the data. So, the SPA model was used to determine what changes to the hydraulic resistance of the soil-plant system would be required to explain the observed reduction in dry-season latent energy fluxes (Williams et al. 1998). The modeling revealed that a tripling in resistance would be enough to constrain dry-season evapotranspiration to observed levels. With these resistances in place, hourly simulations of carbon exchange during the dry season closely matched the strongly asymmetrical observations. Further, the changes required to the parameterized resistance were closely synchronized with patterns of precipitation. It is most likely that it is the soil hydraulic resistance that rises with declining soil moisture. However, further experiments are required to determine that it is the soil, rather than the root or stem of the plant, that is most closely coupled to soil drying.

This modeling analysis indicated that the hydraulic coupling between vegetation and soil is of critical importance to simulating the seasonal variation in evapotranspiration in tropical rain forests. Lacking the long period of winter recharge in temperate climates, tropical rain forests are vulnerable to drought stress after just a few weeks without rainfall. Deep rooting does ensure that contact is maintained with a soil-moisture supply. But, the increased resistance to withdrawing water from deeper in the soil profile ensures that latent energy fluxes are reduced, with significant impacts on photosynthetic rates. Whether these findings hold across the entire

Amazon basin remains uncertain, as variation in soil types may be important. Williams et al. (2002) undertook a survey of trees in the Tapajos National Forest, Para, at the end of the dry season in November 1999. They found that, within stands on sandy soils, predawn leaf water-potential data showed that some trees were clearly water-stressed while others nearby were not. Williams et al. (2002) concluded that these differences might relate to significant variations in rooting depths. On nearby clay soils, no trees exhibited water stress. Thus, correct parameterization of vegetation water fluxes in rain forests may be a complex process related to variations in soil type and the differential rooting depth of species. In such biodiverse ecosystems as rain forests, species parameterizations are a profound challenge.

Temperate evergreen/coniferous forest

The *Metolius ponderosa* pine site is located in a Research Natural Area (44°30'N, 121°37'W, elevation 940 m) in the eastern Cascades, near Sisters, Oregon (Anthoni, Law and Unsworth 1999). The stand consists of old (~250 years), young (~45 years) and mixed old and young patches of ponderosa pine. The canopy reaches a maximum height of about 43 m, and is relatively open. The understory vegetation is sparse with patches of bitterbrush (*Purshia tridentata*) and bracken fern (*Pteridium aquilinum*), and a groundcover of strawberry (*Fragaria vesca*).

The site experiences warm, dry summers and wet, cool winters. Total precipitation in 1996 was 869 mm, a wetter than normal year, and 488 mm in 1997. Mean annual temperature was 8.4 °C in 1996 and 8.5 °C in 1997. Total irradiance was 5390 MJ m⁻² yr⁻¹ in 1996 and 5355 MJ m⁻² yr⁻¹ in 1997. Soil texture analysis indicates the soil is 73% sand, 21% silt, and 6% clay. The sandy loam soils are low in nutrients.

Eddy flux data revealed an annual cycle of evapotranspiration strongly linked to available radiation (Williams et al. 2001). The evergreen canopy and rarely frozen soils ensured that transpiration occurred throughout most of the year, in clear contrast to the deciduous site in Massachusetts. However, an analysis of the latent energy-flux data and soil-moisture data, using SPA with locally calibrated soil-water retention curves, revealed the importance of deep rooting. In the summer of 1996, precipitation rates were low enough that simulations predicted that all plant-available water was abstracted from the top 0.6 m of the soil profile. Soil-moisture data from the top 0.3 m of soil confirmed the model predictions. For the simulations to match the eddy flux data, >90% of transpired water must have been abstracted from below 1 m during the latter part of the summer (Williams et al. 2001). Thus, young trees must develop a rooting system that reaches ~1 m deep if severe drought stress is to be avoided. The presence of just two age cohorts in this stand, which is largely protected from fire, suggests that stand regeneration occurs infrequently. The modeling suggests that this is because regeneration is dependent on a series of sequential wet summers that allow young plants to establish a deep rooting system.

There is considerable debate as to whether the abstraction of water by plants is dependent on plant age and/or size (Dunn and Connor 1993; Yoder et al. 1994). In an analysis of sap-flow data obtained from small/young ponderosa pine and also large/older individuals, the SPA model indicated an increase in plant resistance with increasing plant height. Such a parameterization could explain the observations of relatively less water use by large trees, and, for small trees, the relatively larger peak sap flow and the stronger decline in water use in late season. In effect, smaller trees used more water in early summer, and so induced a stronger soil drought for

themselves in late summer. The hydrological implications of stand age are thus of considerable interest.

Arctic tundra

The Arctic Flux Study (AFS) undertook intensive field measurements during 1994-6 along a North-South gradient within, or near to, the 9200 km² Kuparuk river watershed that lies between latitudes 68° and 70° N in Northern Alaska (Weller et al. 1995). The AFS employed two mobile systems to sample fluxes over 9-14 days at each of 25 sites in a 200-km latitudinal band between the Brooks range and the coast (Eugster, McFadden and Chapin III 1997; McFadden, Chapin III and Hollinger 1998). The sampled sites were chosen to reflect the range of soil moisture, climate and major vegetation types present in the study region, based on a satellite-derived vegetation classification (Muller et al. 1998). The main vegetation categories are tussock tundra, wetland tundra, shrub tundra and heath (Walker and Walker 1996). Within these categories, there are subdivisions into acidic (pH < 5.0) and non-acidic (pH > 5.0) types, based on soil classification (Walker et al. 1998).

A particular challenge in understanding evapotranspiration in arctic ecosystems is accounting for the presence of mosses which carpet the understorey (Williams and Rastetter 1999). The approach used by the SPA model for simulating transpiration is invalid for mosses, which lack stomata. However, one of the AFS sites was located in shrub tundra on a river island, and frequent flooding had stripped away any mosses from the pebbly substrate. In this location, the SPA simulations of evapotranspiration closely matched the eddy flux measurements (Figure 7). However, at other sites SPA predictions of LE fluxes were consistently underestimates compared to observations, because evaporation from mosses was a significant fraction of total water transfer (McFadden, Eugster and Chapin III 2003). Thus, in boreal and arctic sites, submodels of moss energy balance and evaporation are critical requirements for predicting water transfer to the atmosphere.

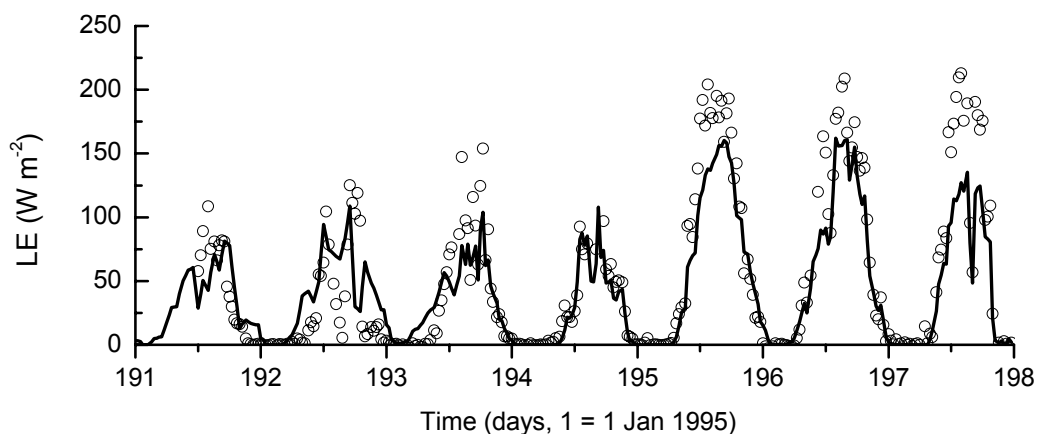


Figure 7. Simulated and observed latent energy fluxes at a shrub tundra site on the North Slope of Alaska during the summer of 1995. Data by permission of F.S. Chapin III, University of Alaska, Fairbanks

Coupling to mesoscale models and global circulation models (GCM)

Land-surface schemes in early atmospheric models (pre 1980s) were very simple, often static, representations with little or no recognition of the importance of vegetation (Sellers et al. 1989). Since that time, increasingly complex schemes have been introduced, so that the current state-of-the-art global circulation model of the UK Met Office, for instance, resolves the terrestrial biosphere into five plant functional types in its TRIFFID submodel. Each functional type (broadleaf tree, needle-leaf tree, shrub, C3 and C4 grasses) can grow and spread based on the competition between the types and on the carbon balance of each. Each vegetation type is assigned a rooting depth (Essery, Best and Cox 2001): 3 m for broadleaf trees, 1 m for evergreen trees and 0.5 m for grasses and shrubs. Canopy conductance is also parameterized specifically for each vegetation type and phenology is controlled by temperature (Cox 2001). For each plant functional type (PFT) there is also a parameter in the power law relating LAI and total stem biomass, and further parameters for the maximum LAI and for leaf mortality rates, which help determine the phenology.

The challenge in simulating the land surface globally is in coping with the vast heterogeneity in the system. The modern land-surface schemes are more closely than ever tied to the best understanding of the research community. However, the tendency of researchers to focus on a few well-instrumented study sites means that spatial data on key parameters are alarmingly scarce. Remote-sensing techniques do provide a mechanism for estimating current vegetation distributions, and thus setting the proportions of each PFT in each grid cell of the GCM with reasonable accuracy. However, PFTs are highly aggregated representations of vegetation, and there is considerable uncertainty about whether the PFT approach is really adequate. We have seen (above) how individual Amazonian tree species in close proximity can register different levels of water stress, likely to due differences in rooting depth. But the PFT approach will set a single rooting depth for all broadleaf trees in the grid cell covering the central Amazon. This homogenization of vegetation properties may have significant implications for model reliability.

Data assimilation

Understanding water transport through vegetation and soils has been greatly assisted by the generation of time series of observations of latent energy fluxes and soil moisture content. Likewise, models have proven to be useful tools for understanding the interactions between the various components of the soil–plant–atmosphere system, in that models can be used to ensure mass balance, for example. Also, data sets inevitably have gaps which need to be filled somehow, and models are a clear tool for such gap filling. However, in most studies the emphasis is either on data or models, and neither are used most efficiently to improve each other. Data assimilation (DA) sets out to extract the maximum information from both observations and models and to produce an analysis of a phenomenon that has smaller confidence intervals than either approach would provide on their own. DA was developed and has been applied in aeronautics (Maybeck 1979) and weather forecasting (Lorenz 1995), and has more recently been applied in soil science (Heuvelink and Webster 2001).

A typical DA system uses a model to forecast the dynamics of system variables. Then, when observations become available, these are compared to the forecast. The

DA system corrects the forecast according to the trust placed in model forecast and observations. The trust is explicitly specified by error estimates. The product of the DA is an analysis of the system variables, which will have a smaller confidence interval than either forecast or observations alone. A DA system is reliant on various assumptions, however, the most important of which are that the system and measurement noise are both white and gaussian.

Data-assimilation methodologies can improve the predictive capacity of models of vegetation water use. These improvements can be broken down into several key advances. Firstly, DA can assist in model improvement. By assimilating several time series into a model, such as eddy flux estimates of evapotranspiration, sap-flow estimates of tree water use, and soil-moisture sensors, the capability of the model to fully explain all these dynamical processes can be fully tested, and improvements to the model can be carefully adjudged. Secondly, DA may help to provide better estimates of some unknown or poorly quantified parameters, such as rooting depth. DA can constrain the model with all available data, while taking account of data uncertainty, and so allow these parameters to be better estimated. Thirdly, DA offers considerable utility in extrapolating knowledge to the landscape, by assimilating remotely-sensed (RS) images. At their most basic, RS data can provide information on land cover and on LAI. Assimilating these data into a regional model will improve phenological certainty, which is critical on governing LE fluxes, as noted above. More advanced remote sensing may provide information on the degree of moisture stress in foliage, and assimilating these data into a model that is simultaneously forecasting soil moisture dynamics, and coupling soil moisture to canopy processes, should increase confidence in prediction and understanding vegetation drought stress at landscape scales.

Strengths, Weaknesses, Opportunities and Challenges

What are the strengths and weaknesses of, and opportunities and challenges concerning the resistance approach to modeling soil–vegetation–atmosphere transfer of moisture?

Strengths

The strength of the resistance approach is that it is based on a physical, mechanistic representation of the soil–plant–atmosphere system. Incorporated in a model, this approach can be parameterized from tree and soil functional data (such as sap-flow data, or soil-water retention curves), and tested against independent land-surface flux data from eddy flux towers. Model-data discrepancies can then be analysed to determine weaknesses in model formulation. The design philosophy of SPA, for instance, has been to ensure that all parameters are independently measurable and verifiable, so that interpretations of model activity are relatively transparent.

Weaknesses

While parameters may be measurable in theory, some have proved challenging to quantify due to technical or logistic difficulties. Rooting depth is a challenging parameter, rarely quantified accurately, and likely to vary spatially. Details of the relative sensitivity of soil, root and plant resistance are also poorly understood, so that simulations of vegetation response to soil drying can be poorly constrained (Williams,

Bond and Ryan 2001). Detailed measurements in soils and plants can overcome this problem, but are time-consuming. Another problem is the issue of species differences. Models such as SPA are kept simple by treating the canopy (or each layer in the canopy) as an individual functional unit. Land-surface schemes in GCMs make similar assumptions, although they allow competition between functional types. However, the functional-type approach is open to criticism as a poor representation of reality, particularly of biodiversity. How ecosystems respond to global change is likely to be dependent on biodiversity, and there is a significant challenge to modeling such interactions.

Opportunities

Data assimilation provides a clear opportunity for improving and testing model representations of the soil-vegetation-atmosphere system. Data time series on soil moisture, sap flow, latent energy fluxes, leaf-area index, for example, are becoming increasingly available. Assimilating these into models such as SPA should provide a transparent and powerful test of the model assumptions, and shrink the confidence intervals on model predictions. Remote-sensing data provide another, linked opportunity. Generating landscape predictions of soil-vegetation-atmosphere transfer requires detailed information on spatial variation on controlling factors. Remote sensing provides an opportunity to estimate the required land-surface properties.

Challenges

There are some challenges associated with the data-assimilation and remote-sensing opportunities. Firstly, there is the difficulty in relating remotely-sensed reflectance to ecologically meaningful parameters, such as LAI. The remote-sensing community tends to use complex, highly detailed forward models of canopy structure to develop these relationships. Ecological models, such as SPA, tend to represent the canopy much more simply. To assimilate remotely-sensed data into soil-vegetation-atmosphere models will require the construction of some hybrid canopy representation. The second challenge concerns landscape predictions. Upscaling using models corroborated at a few field sites to generate estimates over a larger region is a common methodology, but there is concern that the approach lacks a stringent approach to error estimation. The challenge for future workers is to generate confidence intervals on estimates at study sites and also in regional extrapolations, to show how sparseness of observations translates into confidence (or lack thereof) in model predictions.

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