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### R. H. WARING and S. W. RUNNING

## I. Introduction

As part of an ecosystem study, addressed are the questions of water utilization by coniferous forests and the influence water has on growth and mineral cycling. Individual trees are an integrated system by themselves. Their water flux can be envisioned as representing an integration of four components: (1) uptake, (2) internal storage, (3) the controls upon the rate of movement of water from one part of the system to another and (4) the atmospheric demand.

The objective of this chapter is to present a conceptual framework for the movement of water through individual trees from the soil to the atmosphere. Conifers are of special interest because they illustrate the importance of internal storage and exhibit year-around physiological controls upon water movement.

The demand for water, as Gates has presented in Part 3:A of this volume is a function of the atmospheric environment and leaf geometry. The movement of water in the soil to the roots and its uptake from different zones has been treated in Part 2 of this volume. The same general principles are assumed to operate on conifers but the relationships are simplified to apply them to the variable environment associated with tall trees with widely distributed roots.

In a previous paper a computer simulation model was constructed to account for daily uptake, storage, and transpiration by conifers (Running et al., 1975). The same basic design applies here but to account for significant changes in diurnal behavior the model's structure has been refined and the resolution changed to hourly. The exact equations for this hourly model await derivation and depend upon experiments requiring simultaneous measurements of important variables.

# **II.** Description of the Model

In Fig. 1, a flow diagram of a water transport system for a tree is presented which includes water flux: (1) from the soil, (2) from internal storage within the plant, and (3) by transpiration to the atmosphere. Table 1 summarizes the data requirements, internal functions, and predicted output of the model.



Water Uptake, Stora

In the soil root zone, entering or leaving is acc  $(S_x, S_y, S_z)$  is calculated but rapidly depletable s representing mature sap water in the root zone

The last Section (III) i ment  $(T_a, \Delta_c, R)$  affect le  $(A_1)$  and atmospheric of Plant water potential ( $\Psi$ when all tissue reserves content of the two stora procedure in which wa is repeated.

Effective precipitatio basic input acquired fror This model considers en and litter.

If the entire root zor the upper to lower zones from neutron probe mo *Pseudotsuga menziesii* (M zones until soil water te supply/capacity ratio of the majority of water to th decreasing amount (Run For simplicity it is assur it recharges any depleted

Water uptake then, is position, water supply, must be evaluated becar tree's rooting volume. Wit tal projection of the oute

Fig. 1. Flow diagram for si a decision matrix with yes through or accumulation of deficits in the tree and prov to extensible storage. Air ar uptake. In Section III leaf co low radiation, and internal for the period (1 h) and the sc for the new

In the soil root zone, Section I (see Fig. 1), the amount of precipitation (Ppt) entering or leaving is accounted for. Uptake  $(U_a, U_b)$  from the various soil zones  $(S_x, S_y, S_z)$  is calculated in the second Section (II) where it is routed to a small, but rapidly depletable storage  $(S_a)$  or to a larger, more slowly extractable one representing mature sapwood  $(S_b)$ . Temperature  $(T_a \text{ or } T_s)$  and the supply of water in the root zone  $(S_x, S_y, S_z)$  control the rate of uptake that is possible.

The last Section (III) is concerned with how internal water deficits and environment  $(T_a, \Delta_c, R)$  affect leaf conductance (1/r) which, together with foliage area  $(A_1)$  and atmospheric demand  $(\Delta_c)$ , determine the rate of transpiration (T). Plant water potential  $(\Psi)$  is predicted from knowledge of the transpiration alone when all tissue reserves are full. Otherwise it is a function of the relative water content of the two storage reservoirs  $(S_a/C_a \text{ or } S_b/C_b)$ . Following an updating procedure in which water is withdrawn from internal storage, the sequence is repeated.

### 1. Root Zone Water

Effective precipitation, the amount of water entering the root zone, is a basic input acquired from a general hydrologic model after Sollins et al. (1974). This model considers energy and mass exchange from the canopy, snowpack, and litter.

If the entire root zone is at capacity, removal of water will progress from the upper to lower zones (Woods and O'Neal, 1965). Krygier (1971) has shown from neutron probe moisture measurements that under a coniferous forest of *Pseudotsuga menziesii* (Mirb.) Franco, water is extracted mainly from the upper zones until soil water tensions drop below -2 bars, which corresponds to a supply/capacity ratio of about 0.2. Then the next lower zone begins to supply the majority of water to the trees with the upper zone contributing an exponentially decreasing amount (Running et al., 1975; see Benecke, this volume Part 2:C). For simplicity it is assumed that when water enters the root zone from above, it recharges any depleted zones back to capacity before affecting the next lower.

Water uptake then, is calculated from each soil zone based upon its vertical position, water supply, and the water deficit within the tree. Water uptake must be evaluated because the volume of water available is a function of a tree's rooting volume. With some conifers such as *Pseudotsuga menziesii*, a horizontal projection of the outer limits of the crown may adequately define the lateral

◄ Fig. 1. Flow diagram for single tree water flux model. The flow is downward through a decision matrix with yes (Y) or no (N) alternatives. Section I accounts for the flow through or accumulation of water in the rooting zone. Section II treats internal storage deficits in the tree and provides for uptake from the soil or transfer from the sapwood to extensible storage. Air and soil temperature as well as soil water content affect root uptake. In Section III leaf conductance is evaluated as it is affected by low temperatures, low radiation, and internal water deficits. Finally, transpiration by the tree is calculated for the period (1 h) and the soil and internal storages updated before repeating the sequence for the next time step. For symbology refer to Table 1 Table 1. Data requirements and output of a water flux model for a tree

Environmental variables		(I Inita)
Dew point (for cale humidity aradient		(Onits)
Air temperature	T ()	°C
Soil temperature	$T_a$ T	°C
Precipitation (effective)	$P_{s}$	$cm^{3}h^{-1}$
Time	r pt	b
Radiation, short wave	R	ly
Required parameters		
Soil root zone		
Infiltration rate	I	$cm^{3} h^{-1}$
Soil storage capacity	$C_x, C_y, C_z$	cm <sup>3</sup>
Internal storage	, , , <u>,</u>	
Extensible storage capacity	C	om <sup>3</sup>
Maximum uptake rate from soil		$cm^3 h^{-1}$
Wood storage capacity	C a max	cm <sup>3</sup>
Maximum uptake rate from soil	$U_b$	$cm^3 h^{-1}$
Maximum uptake rate from wood to	0 b max	chi ii
extensible storage	$U_{s_1}$	$cm^{3} h^{-1}$
Transpiration	- 30 max	
Leaf area (all surfaces)	4	2
Radiation critical level	$A_1$	cm <sup>2</sup>
	K <sub>c</sub>	ly
Required functions		
Uptake as a function of soil temperature		$U_{\rm a}, U_{\rm b} = f(T_{\rm c})$
Uptake as a function of root zone water		$U_{z} = f(\sum_{i=1}^{z} S / \sum_{i=1}^{z} C S)$
		$\mathcal{L}_{\mathbf{x}} = \mathcal{L}_{\mathbf{x}} \mathcal{L}_{\mathbf{x}} \mathcal{L}_{\mathbf{x}} \mathcal{L}_{\mathbf{x}} \mathcal{L}_{\mathbf{b}}$
Extensible storage empty: $S_a = 0$		$U_{b} = I(\sum_{x} S / \sum_{x} C)$
Leaf conductance as a function of sapwo	od water	$1/r - f(S_{1}/C_{1})$
Water potential as function of sapwood	water and	1/7 = 1(3b/Cb)
transpiration	indicit diffe	$\Psi = f(S, C, T)$
		I = I(5b/Cb, I)
Extensible storage full: $S_a/C_a = 1.00$		
water potential as function of transpiration	on	$\Psi = f(T)$
Extensible storage intermediate: $0 > S_a/C_a <$	1	
Water potential as function of extensible	storage	$\Psi = f(S_n/C_n)$
Leaf conductance as function of extensible storage		$1/r = f(S_{a}/C_{a})$
Leaf conductance as function of light when $R = R_c$		1/r = f(R)
Predicted by model		
Soil root rong		
Pupoff		3 1 - 1
Seenage		$cm^{3}h^{-1}$
H <sub>2</sub> O Supply	C C C	cm <sup>2</sup> h
1120 Supply	$\mathfrak{d}_x,\mathfrak{d}_y,\mathfrak{d}_z$	cm <sup>2</sup>
Internal storage		
$H_2O$ Supply	$S_a, S_b$	cm <sup>3</sup>
Uptake	${U}_{\mathrm{a}}, {U}_{\mathrm{b}}, {U}_{\mathrm{S}_{\mathrm{b}}}$	$cm^3 h^{-1}$
Transpiration		
Leaf conductance	1/r	$cm sec^{-1}$
Transpiration	T	$cm^{3} H_{2}O h^{-1}$
Water potential	$\Psi$	bars
	*	Uurs .

# Water Uptake, Storag

extension of the roots (V often exhibit greater lataccounting for stand deupon soil characteristics, t trees may tap different ve volume of water availab can be withdrawn by the

There are two notabl One, represented by fin cells, shows volumetric o wood which shows little o water is replaced at least

a) Extensible Tissue F it is known that water sites of evaporation. The of supply are from lowe 1972; Jarvis, 1975; Dobbs (Doley, 1967). When con overnight (Stewart et al.,

Recently Huck et al. of their turgid diameter of 40 %, more than twice and Kozlowski, 1965; J of considerable importar soon exhausted, as dem Waggoner and Turner, required to transfer wate roots to contribute muc (Kline et al., 1976; Smith

The water in the abc by severing the stem fre stomata close. On small represents about 12 ° o c very little of this comes change in relative water band of living tissue in 1975).

b) Mature Wood Rese sible sapwood are repor Clark and Gibbs, 1957; Bigg, 1956).

In a mature Douglas is available from the sapy

extension of the roots (Wagenknecht, 1960). Other species such as the pines often exhibit greater lateral root extension which may be approximated by accounting for stand density. Although the depth of rooting depends partly upon soil characteristics, the rooting habits of conifers differ, i. e. that similar-sized trees may tap different volumes of soil (Fowells, 1965; Rutter, 1968). The actual volume of water available in the rooting volume represents only that which can be withdrawn by the roots.

#### 2. Internal Storage

There are two notably different sources of water from within the tree itself. One, represented by fine roots, leaves, phloem, cambium and young xylem cells, shows volumetric change as water enters or leaves; the other is mature wood which shows little dimensional change because it is rigid and the extracted water is replaced at least temporarily by gas (Clark and Gibbs, 1957).

a) Extensible Tissue Reserve. From dimensional measurements of tree stems it is known that water is withdrawn initially from the tissue closest to the sites of evaporation. Then, as the first reserves are depleted, the main sources of supply are from lower and lower down the stem of the plant (Schnock, 1972; Jarvis, 1975; Dobbs and Scott, 1971). Recharge follows the reverse sequence (Doley, 1967). When conditions are favorable, the extensible tissue are refilled overnight (Stewart et al., 1973; Wilson et al., 1953).

Recently Huck et al. (1970) demonstrated that roots may shrink to 60% of their turgid diameter. This represents a change in relative water content of 40%, more than twice that characteristic of diurnal changes in foliage (Clausen and Kozlowski, 1965; Jarvis, 1975). In small trees, the root storage can be of considerable importance, for the small reserves in the foliage and stem are soon exhausted, as demonstrated by shrinkage in dimensions (Lassoie, 1973; Waggoner and Turner, 1971; Jarvis, 1975). In large trees, however, the time required to transfer water from the roots to the foliage is too great to permit roots to contribute much to daily water deficits as shown by isotope studies (Kline et al., 1976; Smith, 1972; Owston et al., 1972).

The water in the above ground extensible tissue reserve may be estimated by severing the stem from the roots and observing the loss in weight until stomata close. On small 1–2 m tall Douglas-fir the reserve defined in this manner represents about 12% of the total water in the tree (Waring, unpublished); very little of this comes from the mature sapwood. Rather, it comes from a change in relative water content observed in the foliage and the 100-cell thick band of living tissue in the branches and stem (Stewart et al., 1973; Jarvis, 1975).

**b**) Mature Wood Reserve. Seasonal changes in the moisture content of inextensible sapwood are reported in both conifers and hardwoods (Stewart, 1967; Clark and Gibbs, 1957; Markstrom and Hann, 1972; Gibbs, 1958; Chalk and Bigg, 1956).

In a mature Douglas-fir forest it is estimated that more than 6 cm of water is available from the sapwood to supplement storage in the soil. This is equivalent to at least a 10-day requirement for transpiration even in midsummer. On the basis of individual trees, it is estimated that a single 80-m tall, 1.5-m thick Douglas-fir has 43001 available in just the stem wood (Running et al., 1975), assuming a change in relative water content of 40 % (Chalk and Bigg, 1956). The sapwood in the branches would have about half the storage of a comparable volume of stem wood because of its greater density. The roots, which are between 10-40% of the above ground biomass (Santantonio et al., 1976) would contribute proportionately.

The volume of sapwood to heartwood varies with the stem diameter, crown size and species. In general, the genus *Pinus* is noted for its high proportion of sapwood to heartwood. At the other extreme are the cedars and redwood (Lassen and Okkonen, 1969). The amount of sapwood in a tree increases linearly with leaf area or mass (Grier and Waring, 1974; Dixon, 1971) and asymptotically with diameter (Lassen and Okkonen, 1969). Thus an estimate of both the extensible and inextensible tissue reserves is possible without requiring destructive sampling.

Only a fraction of the water in sapwood can be extracted in a day, with the most active exchange occurring in the outer 1–2 cm band. Over a period of a few weeks, however, most of the exchangeable water can be extracted or reabsorbed (Chalk and Bigg, 1956; Gibbs, 1958; Clark and Gibbs, 1957; Fries, 1943). The gas which is introduced into the conducting elements of conifers is sealed off until redissolved by the action of valves (bordered pits) on the sides of tracheids (Gregory and Petty, 1973). The formation and removal of gas from the conducting tissue also occurs under freezing and thawing conditions (Hammel, 1967).

c) Modeling Internal Water Flux. In modeling water flux from the internal storage, it is important to determine whether the extensible reserve is full. If the supply is less than the capacity then the amount of uptake possible from the soil and mature wood must be calculated (Fig. 1). Of course, recharge cannot exceed the internal deficit. A deficit in the extensible reservoir has priority over one in the mature wood. A deficit will develop during the day whenever the rate of transpiration exceeds the rate of recharge from the soil root zone and sapwood. If transpiration ceases at night, and water available in the rooting zone exceeds 20 % of soil capacity, then complete recharge would normally occur sometime during the night (Running et al., 1975; Stewart et al., 1973). Below 20 % of capacity, uptake from the soil will be reduced exponentially to zero, when all available root zone water is exhausted.

Recharge of the extensible reserve is also affected by low air or soil temperatures. As Zimmermann (1964) has shown, stem temperatures below  $-2^{\circ}$ C stop the ascent of sap in conifers. This corresponds to the temperature when all water in the soil freezes (Nerseova and Tsytovich, 1966). In the root zone, temperatures above freezing may also inhibit uptake (Havranek, 1972; Babalola et al., 1968; Kramer, 1942; Kuiper, 1964). In modeling the relationship, Running et al. (1975) effectively reduced uptake for Douglas-fir from 100% of potential at a threshold soil temperature of 5°C to zero uptake at  $-2^{\circ}$ C. Again, because of the lag between uptake from the root system and transpiration, large trees must depend more upon their sapwood reserves, and are thus less affected by cold soils, than smaller trees. Water Uptake, Storag

The mature sapwoc from the root zone as t within the tree trunk its considerably. Due to th and extensible tissue, ho will probably have little

The maximum trans sapwood is filled with w situation has been obse the sapwood dries, the of transfer also become (1956), and those of C of the sapwood reserve of reserve is less easily ext compensates and may reported by the above of particularly following a

The maximum upta has been emptied and a time, uptake reflects of tional conducting tissu accurate water flux est methods only show good area is known and the 1960; Doley and Griev conifers is about 2 m h

The last part of the rate of water movemer is simplified by assum saturated atmosphere to the gradient in wa see Gates, this volume

To estimate transpir the foliage and the air on conifers because th air temperature (Gate the previously mentior 1974; Dixon, 1971). Fin leaf conductance are d

In modeling leaf of Hall et al., this volue (3) light. Changes in gu as responding to the

The mature sapwood has the same temperature controls on water uptake from the root zone as the extensible reserves; because of its mass and position within the tree trunk its temperature lags behind that of the air and may differ considerably. Due to the relatively low rate of water transfer between sapwood and extensible tissue, however, a small error in estimating sapwood temperature will probably have little effect over a day.

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The maximum transfer from sapwood to extensible tissue occurs when the sapwood is filled with water and the extensible reserves have been exhausted. This situation has been observed under clear weather conditions in the spring. As the sapwood dries, the water potential gradient may increase, but the paths of transfer also become more tortuous. From the studies of Chalk and Bigg (1956), and those of Clark and Gibbs (1957), it is estimated that about 5% of the sapwood reserve can be extracted daily. As water is extracted, the remaining reserve is less easily extracted, but an increased water potential gradient partly compensates and may explain the nearly linear decrease in moisture content reported by the above cited authors. Recharge may actually be somewhat faster, particularly following a thaw (Fries, 1943).

The maximum uptake by roots should occur when the sapwood reservoir has been emptied and the soil root zone has recently been recharged. At such a time, uptake reflects considerably more than transpiration. Because the functional conducting tissue changes as water is extracted, it is difficult to obtain accurate water flux estimates from heat-pulse or isotope measurements. These methods only show good agreement with actual water uptake when the conducting area is known and the flow rates are small (Heine and Farr, 1973; Ladefoged, 1960; Doley and Grieve, 1966). The maximum vertical movement reported in conifers is about  $2 \text{ m h}^{-1}$  (Owston et al., 1972).

#### 3. Transpiration and Its Control

The last part of the water transport system involves the controls on the rate of water movement through the leaves to the atmosphere. The calculation is simplified by assuming that the rate of water vapor transferred from the saturated atmosphere within a leaf to the outside atmosphere is proportional to the gradient in water vapor concentration (Dainty, 1969; Rawlins, 1963; see Gates, this volume Part 3:A).

To estimate transpiration, the water vapor concentration gradient,  $\Delta c$ , between the foliage and the air is estimated first. Errors in estimating  $\Delta c$  are minimized on conifers because the needles are usually within a few degrees of ambient air temperature (Gates, 1968). Next the area of foliage is estimated through the previously mentioned relationship with conducting area (Grier and Waring, 1974; Dixon, 1971). Finally, from experimental observations equations to predict leaf conductance are developed.

In modeling leaf conductance, three major controls are envisioned (cf. also Hall et al., this volume Part 3:D): (1) temperature, (2) water deficits, and (3) light. Changes in guard cell concentration of  $CO_2$ , K<sup>+</sup> and ABA are envisioned as responding to the above basic controls so are not treated in the model.

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a) Temperature. Reed (1968) and Drew et al. (1972) demonstrated that the stomata of both Douglas-fir and Ponderosa pine close if the air temperature is below  $-2^{\circ}$ C. Thus, under these conditions, the model assumes minimum leaf conductances. Low soil temperatures may indirectly affect leaf conductance by inhibiting uptake, which in turn may result in a deficit in the extensible tissue.

**b**) Water Deficits and Water Potential. As Jarvis (1975) has emphasized, a large water potential gradient between the roots and leaves does not indicate necessarily that a water deficit exists within the plant. He points out that in a completely rigid flowpath, a potential difference is necessary to drive steady-state flow against the frictional resistance when input and output flow rates are equal. This situation exists in trees when soil water is available and the evaporative demand is not extreme. Lassoie (1973), for example, has reported more than a 10-bar change in the water potential gradient during the day with almost no diameter variation in the stem of a Douglas-fir. If no water deficit develops in the extensible tissue the stomata may remain open and one may find a linear relationship between increasing transpiration and decreasing (more negative) leaf water potential (Landsberg et al., 1975; Jarvis, 1975).

A change in relative water content of the extensible tissue, on the other hand, can directly affect the stomata. Again, there is not a simple relationship with water potential because the cell turgor is greatly affected by changing solute concentration. Even conifers, which are rarely found growing on saline soils, show rather large changes in solute potential depending upon tree height, season, and degree of desiccation (Richter et al., 1972; Larcher, 1972; Hellkvist et al., 1974).

Fortunately, it is possible through the pressure extraction technique developed by Scholander et al. (1965) to measure both water potential and solute potential. Such a procedure was followed by Hellkvist et al. (1974), to provide the solute and water potential curves for Sitka spruce [*Picea sitchensis* (Bong.) Carr.] in relation to relative water content (Fig. 2). In general, these curves tend to be less steep for conifers, such as Douglas-fir, pine and juniper, which are more drought adapted (Scholander et al., 1965; Jarvis and Jarvis, 1963). When the solute potential is equal to the water potential one can be assured that the stomata are completely closed and all transpiration will be cuticular.

c) Water Potential and Leaf Conductance. When equilibrium conditions are approached just before dawn, there is a predictable relationship between plant water potential and maximum possible leaf conductance when the stomata first open (Fig. 3). If no further change in the relative water content of extensible tissue occurred, this leaf conductance would exist throughout the day, despite a diurnal decrease in water potential. Under high humidity gradients leaf conductance will decrease slightly, apparently due to changes in guard cell turgor alone (Running, 1976; see Hall et al., Part 3:D of this volume). However, in the normal course of a clear warm day, even when predawn water potentials are less than -5 bars, water can be withdrawn from the extensible tissue, reducing the relative water content and the water potential. When this happens a point is reached, usually around 0.8 relative water content, where stomata begin to close abruptly. On small Douglas-fir and Ponderosa pine the closure threshold

Fig. 2. Change in solute ( relative wa

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Fig. 3. Maximum morning l Each point represents a ca over fou

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Fig. 2. Change in solute  $(\Psi_s)$  and water potential  $(\Psi)$  of Sitka spruce with decreasing relative water content of twigs. (After Hellkvist et al., 1974)



Fig. 3. Maximum morning leaf conductance as a function of predawn plant water potential. Each point represents a canopy average from at least 10 leaf conductance measurements over four age classes of needles on 2–3 m Douglas-fir

in terms of water potential is -20 and -17 bars respectively (Running, 1976; Lopushinsky, 1969).

In the present model (Fig. 1), leaf conductance as well as water potential are assumed to be proportional to relative water content. Once the relative

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water content has been reduced to a minimum (about 0.5), all of the extensible storage has been depleted and conductance will be minimum, usually around  $0.003-0.005 \,\mathrm{cm \, sec^{-1}}$ . The water potential under the latter circumstances is a function of the relative water content of the sapwood (S<sub>b</sub>/C<sub>b</sub>) and will range between -20 to -60 bars.

In the case where the rate of water uptake from the soil is sufficient to maintain full turgor of the extensible tissue, the leaf conductance can approach its maximum of around  $0.25 \text{ cm sec}^{-1}$  for new foliage of a wide variety of conifers. Water potential then is a simple linear function of transpiration (as stated previously).

d) Light. Low light levels can also affect leaf conductance. The particular level at which stomata begin to close varies. Pioneer plants generally have relatively high light thresholds while advanced successionary species have low (Woods and Turner, 1971). Red pine (*Pinus resinosa* Ait.) has been reported to have a threshold of 0.2 langleys (Waggoner and Turner, 1971) and for Douglas-fir closure begin below 0.1 langley. Thus, the stomata are normally closed when it is dark. However, if the plant rapidly recovers turgor, as illustrated by night-time water potential of around -3 bars, then the stomata of Douglas-fir and a variety of other conifers remain open. Seedlings of *Pinus contorta* var. *murrayana* (Balf.) Engelm., however, remain closed at night even with high water content (Lopushinsky, personal communication).

In the model (Fig. 1, Section III), if radiation (R) is below a critical level, the leaf conductance will be decreased below that predicted from knowledge of relative water content. When there is no internal water deficit, leaf conductance will not be reduced by low light.

The significance of the light effect is that, in a forest, many of the branches are often shaded and near or below the critical level, especially during the winter at latitudes greater than about 40°. This means that not only transpiration but photosynthesis may also be reduced. At night, if stomata remain open, some water will be transpired if the temperature is not at or below dew point. This can account for the occasional low values of water potential observed at night on well-watered soils.

e) Transpiration. Calculation of transpiration is the last major step in the water flux model. It is calculated as a function of the water vapor concentration gradient,  $\Delta c$ , the total leaf area,  $A_1$ , and the leaf conductance, 1/r. Following this, the amount of water in each of the storage reserves is recalculated, and the sequence repeated for the next time step (Fig. 1).

# **III.** Applications

From experience with the daily resolution model (Running et al., 1975) one can expect major differences in water balance depending upon the size of a tree and the extent of its rooting system. For example, from a similar environmental data base, it was calculated that an 80 m Douglas-fir would exhibit major stomatal control as a result of soil drought for only 17 days out of a total of 170 during the growing season (Table 2). A 2 m Douglas-fir, on the other hand would control

Water Uptake, Stor

Table May 10-October 27,

Given

Rooting zone capacity Extensible storage capacity Sapwood storage capacity Leaf area Climatic data, averaged da

Predicted

Leaf conductance range Water potential range (at c Maximum transpiration ra Days of reduced transpirat Total transpiration (170 da Average transpiration (170

> Tab! May 10 – October 2

Given

Rooting zone capacity Extensible storage capacity Sapwood storage capacity Leaf area

Climatic data, averaged da

Predicted

Leaf conductance range Water potential range (at d Maximum transpiration ra Days of reduced transpirat Total transpiration (170 da Average transpiration (170

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From an understand fully explain how it is p similarly under well-hyc when evaporative dema the other, further deple control will result in dif

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Table 2. Simulation results for an 80 m Douglas-fir May 10–October 27, 1972, Cascade Mountains of Oregon (Running et al., 1975)

GivenRooting zone capacity47,000 lExtensible storage capacity50 lSapwood storage capacity4,300 lLeaf area3.74 · 107 cm²Climatic data, averaged daily1

### Predicted

the second s
0.025 - 0.008 cm sec <sup>-1</sup>
-5 to $-15$ bars
1140 l day <sup>-1</sup>
17 days
66,000 1
$390  \mathrm{l}  \mathrm{day}^{-1}$

Table 3. Simulation results for a 2 m Douglas-fir May 10 – October 27, 1972, Cascade Mountains of Oregon (Running et al., 1975)

Given	
Rooting zone capacity Extensible storage capacity Sapwood storage capacity Leaf area Climatic data, averaged daily	450 1 0.5 1 3.2 1 3.5 · 10 <sup>5</sup> cm <sup>2</sup>
Predicted	
Leaf conductance range Water potential range (at dawn) Maximum transpiration rate Days of reduced transpiration by drought Total transpiration (170 days) Average transpiration (170 days)	0.14-0.003 cm sec <sup>-1</sup> -2 to -30 bars 16.6 l day <sup>-1</sup> 54 days 723 l $4.3 l day^{-1}$

transpiration to a fraction of the potential possible for 54 days (Table 3). In these comparisons a greater internal resistance to water is assumed to exist in large conifers (Hudson and Shelton, 1969). This results in generally lower average leaf conductances throughout the day.

From an understanding of the water transport system one can now more fully explain how it is possible for two conifers of the same height to respond similarly under well-hydrated conditions and modest evaporative demand. Yet, when evaporative demand increases and the rooting depth of one is less than the other, further depletion of soil reserves and differing degrees of stomatal control will result in different water balances. Borchert (1973) suggests a further implication of such a water transfer model in his simulation of rhythmic growth in trees. He proposes that the periodicity of flushing and the foliage size is in a large part a function of internal water deficits that may occur, even under constant environment, when the amount of foliage area exceeds the root absorptive capacity necessary to meet the transpirational demand.

Further, adaptive significance becomes apparent for species with low leaf areas, and large volumes of sapwood growing where drought is frequent. It is clear that differences in leaf conductance exhibited in relation to light, temperature, and moisture stress may help explain the positions that different species fill in forest succession.

# **IV.** Conclusions

The present concept of the water transport system has been modified as research points out deficiencies in previous assumptions. A lag between transpiration and uptake commonly observed in trees requires recognition of internal storage. The fact that foliage and other living tissue lose or regain their turgor faster than exchange is possible from sapwood signifies that at least two kinds of internal storage reservoirs should be considered.

Observations that light, reduction in relative water content, and low temperatures may all affect stomata have been incorporated in a system context. From this standpoint the response of plant water potential has also been reevaluated.

Much still remains unclear or unquantified. The expressed requirements for simultaneous measurements of important variables will require more integrated research to rigorously test and modify the concepts summarized here. It is to be hoped that such research will progress to further the understanding of plant water relations.

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