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Physiological Control of Water Flux in Conifers

A Computer Simulation Model

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Summary. A water flux model with daily resolution is described which permits one to assess how changes in the rooting volume, amount of sapwood, leaf area and conductance properties interact to affect water uptake, internal storage, and transpiration.

A root zone water compartment is defined for a particular tree on the basis of root depth, lateral extension and moisture holding characteristics of the soil. Water is taken up from different subcompartments of the root zone as a function of vertical position, soil water content, and water deficit within the sapwood. Excess water entering the root zone is channeled into runoff or seepage.

The sapwood compartment of the model is restricted to the main stem of the tree and does not include sapwood in the branches or roots. The model assumes whatever water deficit is built up in the sapwood during the day will be replenished at night if the root zone water supply/capacity ratio exceeds 20%. A complex exponential equation describes the amount of water extractable from 20% to 0 capacity when no uptake is possible. The maximum change in volume of water in the sapwood of a large Douglas-fir is estimated to represent more than a 10 day supply for transpiration.

Water loss through transpiration is predicted as a function of the mean daily absolute humidity deficit, leaf area, leaf conductance and daylength. Leaf conductance is controlled by predawn plant moisture stress which in turn is a function of the rooting zone water supply.

The model incorporates two special constraints upon water uptake and transpiration. The first accounts for the effect of cold soil temperatures reducing the possible uptake by Douglas-fir to half at 2° C and to 0 at −2° C. The second represents a critical absolute humidity deficit sufficient to cause stomatal closure which results in leaf conductance being reduced to a minimum.

The model is employed to compare trees of different sizes and those with different stomatal behavior. From this experience, it is suggested that future studies include, at a minimum, simultaneous measurements of: absolute humidity deficit, leaf area, sapwood volume and change in water content, predawn stress and leaf conductance.

Introduction

To understand the factors controlling water movement through vegetation, one must view as a whole exchanges across the soil-plant-atmosphere continuum (Philip, 1966; Slatyer, 1967). It is our objective in this paper to summarize available knowledge about conifers concerning the way they take up water from the soil, store it temporarily in their sapwood, and transpire it through their leaves. A simulation model is presented for an individual tree to help evaluate various assumptions, to contrast differences related to stomatal behavior and tree isze, and to identify critical variables and relationships for future study.

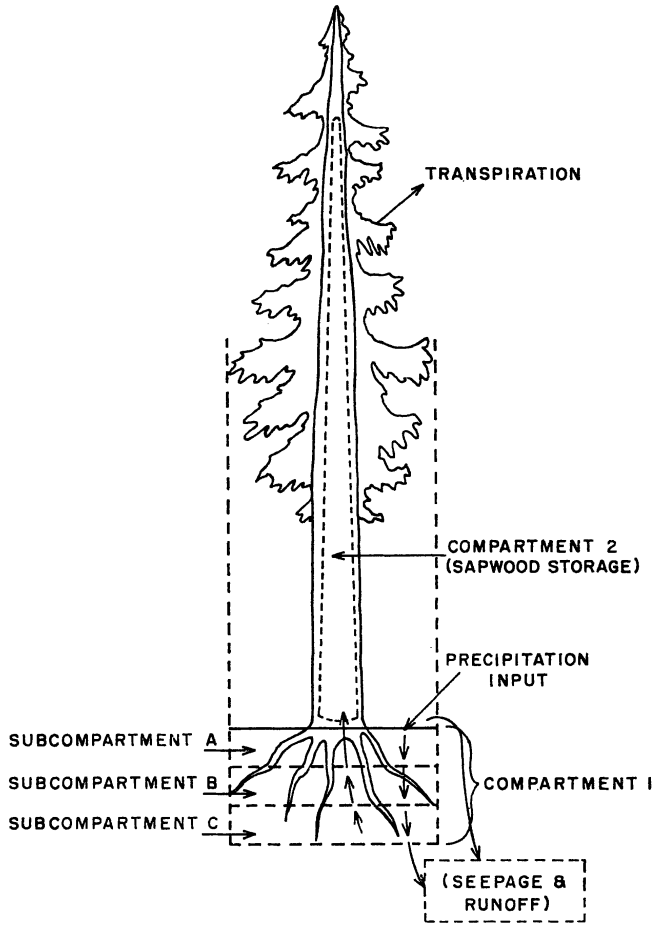

Fig. 1. Components of water flux model

In developing a water balance model for a tree, we subdivide the rooting zone into a number of subcompartments reflecting differences in rooting depth or soil development (Fig. 1). We limit the sapwood compartment to only the bole of the tree, although branches and roots could also be included. The capacities of the root zone and sapwood compartments are defined by the volume of water which can be withdrawn from them for use by the plant and not by their total water content. The amount of water transpired from the leaves to the atmosphere is calculated, but the atmosphere is considered a sink and not a compartment.

The water flux model thus consists of two basic compartments and a series of transfer equations controlling the rate of water movement between them and the atmosphere. We shall discuss each component of the model in sequence starting with the root zone and ending with the atmospheric demand. To examine the model's behavior we will incorporate data available through the Coniferous Forest Biome, Analysis of Ecosystem program.

Description of Model Components

Root Zone Water Compartment

The amount of water stored in the root zone depends, firstly upon the soil's capacity, and secondly, upon the balance between water supplied and removed. For Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], a horizontal projection of the outer limits of the crown defines the lateral extension of the roots (Wagenkneckt, 1960). For other species such as *Pinus jeffreyi* Murr., the lateral root extension may greatly exceed the width of the crown and may be best approximated by accounting for stand density and spacing.

The depth of rooting is also variable. Douglas-fir usually has over 90% of its root biomass confined to the upper meter of soil although some roots may penetrate to a depth beyond 2 m (Santantonio, 1974). For our purposes we will assume a rooting depth of 1 m. The storage capacity can be defined as the volume of water stored in a volume of soil between the limits of 0.1 and 15 atm., tension. Each subcompartment in the root zone has its capacity determined and the sum of these represents the total capacity of the root zone.

The amount of water entering the root zone is derived from a general hydrologic model (Sollins *et al.*, 1974). This hydrology model considers energy and mass exchange from the canopy, snowpack, litter, and soil. It keeps track of excess water that enters the root zone and seeps through or runs off the surface.

If the entire root zone is at capacity, removal of water will progress from the upper to lower levels (Woods, 1965). Boersma *et al.* (1975) has shown from neutron probe moisture measurements that under a Douglas-fir forest, water is extracted mainly from the upper zones until water tensions exceed 2 atm., which corresponds to a supply/capacity ratio of 0.2, or 20% of capacity. Then the next lower compartment begins to supply the majority of water to the trees. We assume that when water enters the root zone from above, it recharges any depleted compartment back to capacity before affecting the lower subcompartments.

In the model, subcompartment A supplies water to the sapwood until the water content falls to 20% of capacity. The primary water demand is then directed to subcompartment B with subcompartment A contributing an exponentially decreasing amount.

Water uptake from the soil is treated as a daily phenomenon although this is not completely correct. In practice, uptake may be a continuous process, occurring even if the foliage is wet when there is a deficit within the tree (Lassoie, 1973). The potential uptake, as will be discussed in the next section, is any water deficit (D_s) that accumulates over the course of a day in the sapwood compartment.

The amount of uptake is calculated from each soil subcompartment based upon its vertical position, water supply, and the demand. The relationship in Fig. 2 shows that a given demand (D_s) will be met as long as the soil subcompartment has more than 20% of capacity, calibrated for our example to reflect an average tension of less than 2 atm. Thereafter only a fraction of the demand can be met from this soil subcompartment and additional water, if available, must come from another.

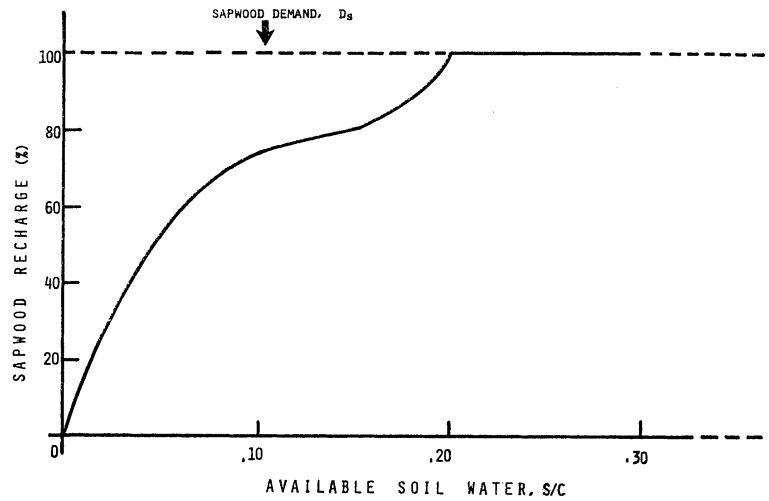

Fig. 2. The constraint of limiting water supply, $S/C \leq 20\%$ upon sapwood recharge described by Eq. (2) in text

The equations for uptake are:

$$U_a = \begin{cases} D_s \text{ if } D_s \leq R_a \\ R_a + (D_s - R_a) \cdot e\left[\frac{D_s - R_a}{S_a} \cdot \left(\frac{S_a}{C_a} - 3\right)\right] \end{cases} \tag{1}$$

where

U_a = uptake, Subcompartment A;
D_s = demand, Sapwood;
S_a = supply, Subcompartment A;
C_a = capacity, Subcompartment A;
R_a = water available without restriction $S_a - 0.2\, C_a$ Subcompartment A.

The balance of the demand must come from U_b and U_c. If all subcompartments are at or below 20% capacity and D_s cannot be fully met, then Eq. (2) applies:

$$U_i = D_s \cdot e\left(\frac{D_s}{C_a} - 3\,\frac{D_s}{S_a}\right) \tag{2}$$

$$U = \sum_{i=a}^{c} U_i.$$

The model structure incorporates a variable, maximum root uptake rate to constrain U, if demand exceeds what the root system can supply. Unfortunately, we could not obtain an estimate for this variable and, therefore, it is not included at present.

Sapwood Compartment

From a number of indirect measurements, various authors have suggested that sapwood serves as a reservoir to meet diurnal water requirements (Kozlowski, 1972; Waggoner and Turner, 1971; Stewart, 1967; Lassoie, 1973; Doley, 1967). Seasonally, the moisture content of sapwood has been shown to change considerably in both conifers and hardwoods (Clark and Gibbs, 1957; Chalk and Bigg, 1956; Markstrom and Hann, 1972; Gibbs, 1958). Expressed as a precentage of

Table 1. Average sapwood thickness of selected conifers with inside bark diameters of 50 cm

Species[a]	Sapwood thickness (cm)
Abies magnifica	14.2[b]
Pinus ponderosa	12.7[c]
Abies procera	12.7[b]
Abies concolor	10.1[b]
Tsuga heterophylla	8.9[b]
Abies grandis	8.1[b]
Pinus contorta	6.4[c]
Abies amabilis	6.0[b]
Pseudotsuga menziesii	5.0[c]
Picea engelmanni	4.3[c]
Larix occidentalis	2.4[c]
Thuja plicata	2.2[c]

[a] Nomenclature after Peck (1961).
[b] Ruppert and Graham (1974).
[c] Lassen and Okkonen (1969).

the dry weight, the water content of the sapwood may change by a factor of 2 which is a change in relative water content of over 40% (Chalk and Bigg, 1956).

The thickness of sapwood increases asymptotically with the diameter of the tree, remaining relatively constant in the stem (Lassen and Okkonen, 1969). Considerable differences exist among species (Table 1).

We define the water storage capacity of the sapwood as:

$$C_s = A_s \cdot l \cdot \Delta_w \tag{3}$$

where
C_s = capacity of sapwood, in liters;
A_s = the average cross-sectional area of sapwood;
l = the length of the stem or section;
Δ_w = the maximum change in relative water content.

A sapwood demand, D_s, is produced whenever water supply in the sapwood drops below C_s. At any time, t, D_s is defined by:

$$D_s(t) = T_d(t) + D_s\ (t-1) - U(t-1) \tag{4}$$

where
T_d = transpiration, daily;
U = uptake.

Transpiration

For describing the flux in the gaseous phase from the leaf to the atmosphere, we employ Fick's First Law of Diffusion (Dainty, 1969; Rawlins, 1963), which assumes 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. Modified to estimate daily transpiration for a tree with a given leaf area, the equation is:

$$T_d = D_a \cdot \frac{1}{r} \cdot L_d \cdot A_l \qquad [\text{for } D_a < D_c]$$
$$T_d = 0 \qquad [D_a > D_c]$$

where

T_d = transpiration during the daylight hours in liters day^{-1};

D_a = absolute humidity deficit, defined as the daily average water vapor concentration gradient between the liquid-air interface in the leaf and the air, liters m^{-3} air;

D_c = critical absolute humidity deficit causing stomatal closure;

r = the averaged leaf resistance throughout the day, sec cm^{-1}, expressed as the reciprocal, *i.e.*, conductance;

L_d = daylength, seconds;

A_l = total leaf area of all surfaces in cm^2.

Because of their small size, conifer needles are usually within a few degrees of ambient temperature (Gates, 1968). One can therefore estimate the absolute humidity deficit by measuring the air temperature and its water vapor concentration, assuming the interior of the needles to be a saturated atmosphere at ambient temperature. The water vapor concentration of the air is evaluated from dew point temperature measurements. Both air and dew point temperatures are available from continuous records and are averaged for the daylight hours. At times the absolute humidity deficit may reach a critical value (D_c) forcing the stomata of some plants to close and transpiration to approach zero.

The resistance, r, includes resistance to diffusion across the boundary layer, through the stomata and cuticle and across the mesophyll cell walls. We can assume the boundary layer resistance is negligible in relation to the other resistances in conifers, again because of the small size of the leaves (Gates, 1968; Jarvis, 1971). The resistance term is of critical importance; for everytime it doubles, the transpiration will be reduced by half. We prefer to use the reciprocal of resistance, or conductance, because transpiration is more directly proportional to this expression.

Estimating Leaf Conductance

The daily mean conductance or resistance of the foliage to water transfer is a function of the predawn plant moisture stress (P). As the tree extracts water from the soil, a level is reached at which there is an increase in the plant moisture stress. This reduces the daily mean conductance as shown in Fig. 3, until the stomata are completely closed and the conductance is that for diffusion through the cuticle of the leaves (Running, 1973). The relationship described in Fig. 3 varies for different species and also differs as the proportion of foliage in different age classes changes.

Air temperatures below freezing may cause the stomata to close (Reed, 1968; Drew *et al.*, 1972), but this is not included in the model at present. Similarly, extreme absolute humidity deficits (D_c) may reduce leaf conductance to the minimum level (Running, 1973). Watts and Neilson (1975) have found that a 12 mb leaf-air vapor pressure difference closes stomata in Sitka spruce [*Picea sitchensis* (Bong.) Carr.]. Hence, we have incorporated in the transpiration equation a critical deficit, D_c, which when exceeded reduces T_d to zero. On daily basis, D_a rarely exceeds D_c. The expression, mean daily conductance, does, however, reflect diurnal fluctuations in conductance.

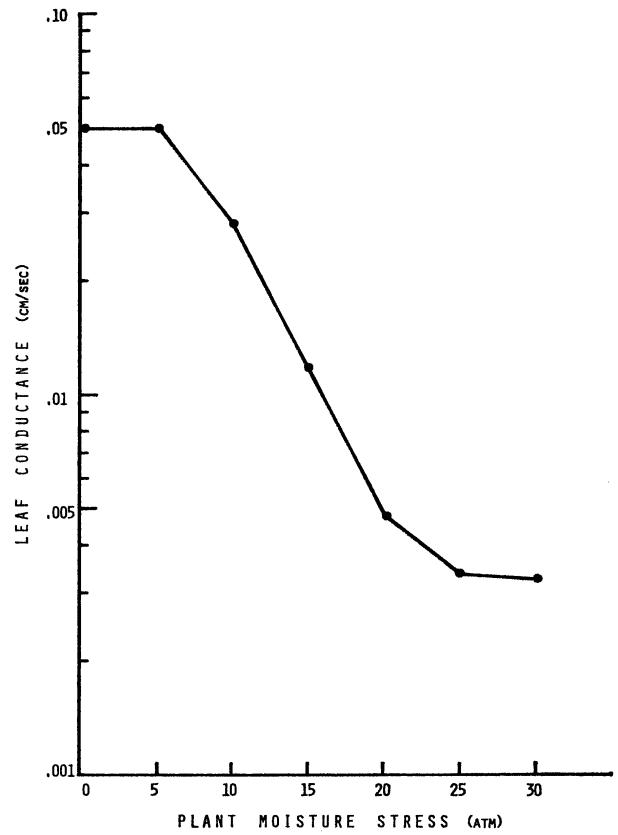

Fig. 3. Mean daily leaf conductance, $1/r$, is reduced proportionally as predawn plant moisture stress, P, increases from 5 to 25 atm, conductance measured with aspirated diffusion porometer (Turner and Parlange, 1970)

Estimating Predawn Plant Moisture Stress

As noted in the above section, predawn moisture stress must be known to estimate leaf conductance. Benecke (1972) demonstrated with *Pinus mugo* Turra., seedlings that more than half of the available water supply could be withdrawn from the root zone before significant increases in predawn plant water stress occurred. We have confirmed Benecke's experience with 1–2 m trees by observing very small increases in P over an extended period, followed by an exponential rise (Waring, 1970; Reed and Waring, 1974).

Recently, Sucoff (1972) and Hinckley and Ritchie (1973) demonstrated on a variety of coniferous trees that no increase in P occurred until almost 80% of the root zone water capacity was depleted (Fig. 4). This permits us to compute plant moisture stress from a knowledge of the root zone water supply. When the supply is greater than 80% of capacity, P remains at 2 atm., with correction of 0.1 atm/m for the tree's height. Below 20% of capacity, P is calculated from the equation:

$$P = 30 - 140 \cdot S/C + \frac{H}{10} \tag{6}$$

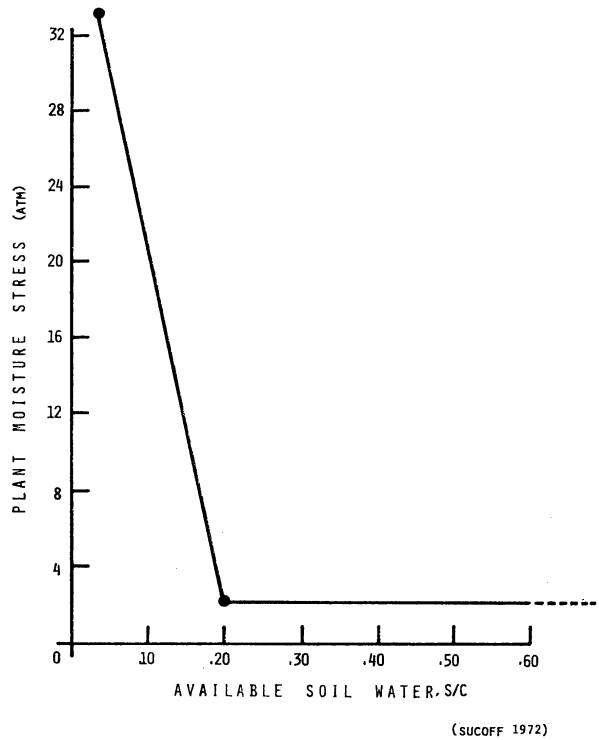

Fig. 4. Soil water supply, expressed as a fraction of capacity, S/C, has no influence upon predawn plant moisture stress, P, until reduced to less than 20%

where

P = predawn moisture stress, atm.;

S/C = the fraction of water available in the total root zone compartment varying from 0.2 down to 0;

H = mid-crown height, m.

In addition to limiting water supply, cold soil temperatures can increase plant moisture stress (Cleary, 1970). This in turn affects leaf conductance and thus transpiration. On seedlings of Douglas-fir, Reed (1972) showed new foliage wilts when root temperatures are reduced below 2°C. Havranek (1972) reported that European larch and spruce seedlings reduced their transpiration by 50% at soil temperatures of 2°C as compared to 15°C. Babalola *et al.* (1968) reported similar observations with *Pinus radiata* D. Don., seedlings, although a soil temperature of 10°C was sufficient to reduce transpiration by $^1/_2$ of that observed at 15°C. The latter authors also showed that the effect of cold soils was mainly significant when water was not limiting. We will assume, however, that between 5°C and −2°C soil temperatures, there is a linear influence upon plant moisture stress, regardless of the water supply. The simplified relationship is:

$$P = -3.85\ T_s + 22.3 \tag{7}$$

where

T_s = soil temperature at 20 cm depth, °C.

This means that when temperatures are at $-2°C$, P will equal 30 atm., and leaf conductance will be minimum (Fig. 3). At 2°C the plant moisture stress will be 15 atm., and the conductance will be half that when $T_s \geq 5°C$.

Estimating Daylength

Seasonal variations in daylength, L_d, from sunrise to sunset, are computed by a modified sine wave for 45°N latitude:

$$L_d = [3.5 (\sin (X + 79.01721)) + 12.0] \times 3600 \tag{8}$$

where X = yearday (Julian).

Estimating Leaf Area

The total leaf area, A_l, is estimated on a given mass of foliage by determining the increase in weight of a monolayer of glass beads (Thompson and Leyton, 1971). Foliage mass of the entire tree is estimated from linear relationships with the cross-sectional area of sapwood (Grier and Waring, 1974). For Douglas-fir, the equation is:

$$M_l = 0.074 (A_s) - 1.44 \tag{9}$$

M_l = leaf mass, kg

A_s = cross-sectional area of sapwood at 1.5 m, cm^2.

Mass is converted to surface area by an appropriate coefficient which for Douglas-fir is $1.3 - 1.7 \times 10^5$ cm^2 kg^{-1}, depending upon the age of foliage.

Flow Diagram and Data Requirements for Model

In order to use the model a number of variables and parameters must be known. These are summarized in Table 2. To calculate the water flux from the root zone to the sapwood and from the leaves to the atmosphere, the sequence of steps listed in the flow chart in Fig. 5 are followed.

The first part of the sequence is concerned with the routing of effective precipitation into the root zone subcompartments. The root zone water supply is calculated directly if no water has reached the soil. Where water has been added, it either infiltrates into the soil subcompartments and fills them, the excess amount seeps below the root zone, or it runs off when the intensity exceeds the infiltration capacity. The subcompartments are reevaluated each day and the total supply of water in the root zone estimated. The ratio of supply/capacity, S/C, is then calculated.

Next the sapwood demand, D_s, is calculated. If there is a water deficit in the sapwood then Eqs. (1) and (2) are employed to extract water from the various root zone subcompartments. The model keeps track of how much water is extracted from the soil and any remaining sapwood water deficit.

In the next sequence of steps, predawn plant moisture stress, P, is calculated, first if the soil temperature is critically low [Eq. (7)] and otherwise as a function of root zone water supply/capacity [Eq. (6)]. From the calculated P, the leaf conductance, $1/r$, is estimated from the curve described in Fig. 3. Next, the

Table 2. Data requirements for water flux model

Environmental variables		(Daily averages)
Dew point		(° C)
Air temperature	T_a	(° C)
Soil temperature	T_s	(° C)
Precipitation		(cm)
Yearday		(Julian)
Estimated parameters		
Rooting zone water capacity	$C_a+C_b+C_c$	(L)
Sapwood water capacity	C_s	(L)
Maximum soil infiltration rate		(L day^{-1})
Maximum root uptake rate		(L day^{-1})
Leaf area	A_1	(cm^2)
Mid-crown height	H	(m)
Absolute humidity deficit for minimal leaf conductance	D_c	(L m^{-3} air)

absolute humidity deficit is assessed to see if a critical demand, D_c, exists sufficient to close the stomata. If so, transpiration is estimated as 0. Otherwise, the absolute humidity deficit, D_a, is part of the transpiration equation [Eq. (5)] along with estimates of conductance, leaf area, and day length. The amount of water transpired in a day is depleted from the sapwood compartment and the whole sequence of calculations repeated for the next day with new environmental variables.

It is possible with this particular model to evaluate how changes in rooting depth, or volume, sapwood, leaf area, and leaf conductance affect water uptake and transpiration. Examples will be presented in the next section.

Simulation Results

Simulations were run to isolate the sensitive components of the model. This was done by simulating the water exchanges of trees of different species and size. Root zone capacity, sapwood capacity and the response of leaf conductance to physiological stress were found to have major effects on the transpiration rate. Three of the more interesting simulations are compared below.

Case 1

Water flux was calculated for an 83 m Douglas-fir growing at the Oregon experimental site for ecosystem analysis in the western Cascade Mountains. (Table 3). Supporting data on transpiration was available from experiments with tritium (Kline *et al.*, 1975). Climatic data were available for the growing season, a period of 170 days from May 10th to October 27 in 1972. In general the climate is mild with 2–3 months of summer drought and an average annual precipitation of 180 cm. The maximum transpiration during the period was 1 135 l per day. For the entire growing season, 66 000 l were estimated as being lost through transpiration. At least 19 000 l were added to the soil compartment

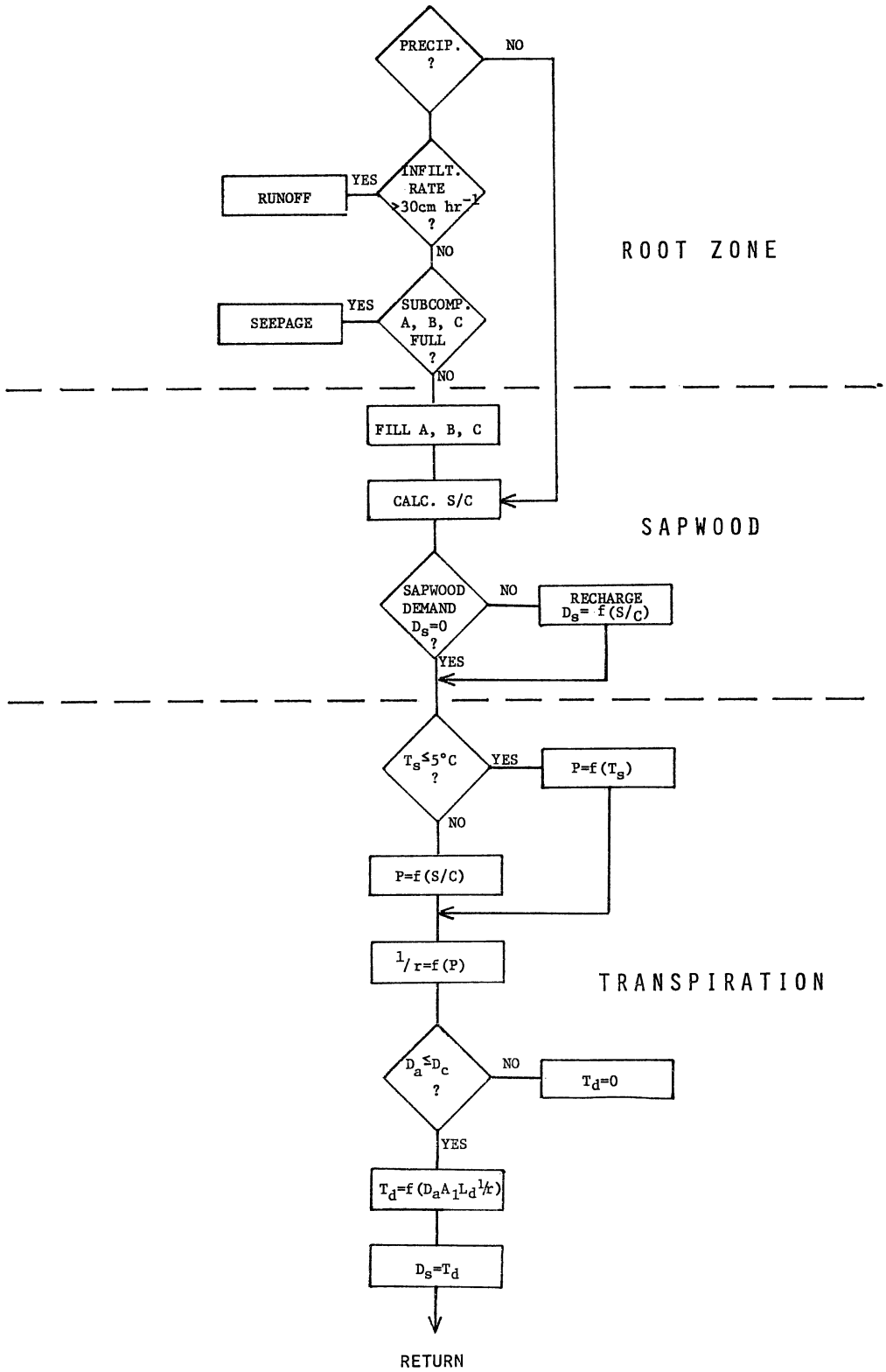

Fig. 5. Flow diagram of computer simulation model

Table 3. Case I–80 m Douglas-fir

Given	
Rooting zone capacity	47000 l
Sapwood capacity	4300 l
Leaf area	3.74×10^7 cm^2
Predicted	
Leaf conductance range	0.025–0.008 cm sec^{-1}
Plant moisture stress range	10 to 15 atm
Maximum transpiration rate	1140 l/day
Days of reduced transpiration	17 days
Total transpiration (170 days)	66000 l
Average transpiration (170 days)	390 l/day

during the period, mostly in the spring and late fall. Some seepage occurred between May 20–26.

The upper soil subcompartment A was depleted below 20% of capacity on July 5. A series of four storms refilled subcompartment A by June 9. From July 5 to July 28 a drought persisted and subcompartment B was depleted to 20% of capacity. Precipitation on August 16–18 refilled subcompartment A, but by September 4, all three subcompartments were depleted below 20% of capacity. Transpiration was thus reduced progressively as leaf conductance decreased, responding to the depleted water supply and increasing plant moisture stress.

Throughout the summer season, the sapwood level fluctuated according to the magnitude of daily transpiration and subsequent recharge. The minimum sapwood level attained was about 75% of capacity and occurred occasionally from July 4 to September 4, corresponding to the period of sustained high transpiration. From September 4 to 19, when decreased leaf conductance reduced transpiration, the sapwood was able to recharge. Before and after this period, transpiration was low enough that virtually complete recharge was predicted every night. After September 19, storms were frequent and both the upper soil subcompartments were filled by September 25. Shorter daylength and decreased atmospheric demand reduced transpiration during the remainder of the growing season.

Case 2

For comparative purposes, the model was employed for a 2 m tall Douglas-fir with the same environmental data used in Case 1 (Table 4). The root zone water capacity, sapwood capacity, leaf area and height were adjusted. By July 10, soil water supply had dropped below 20%. During the period from July 19 to September 21, transpiration was constrained by decrease in leaf conductance to less than 10% of the potential, except for an 8 day period following a storm in mid-August. After September 21, the soil compartment was again filled to capacity.

Table 4. Case II–2 m Douglas-fir

Given	
Rooting zone capacity	450 l
Sapwood capacity	3.2 l
Leaf area	3.5×10^5 cm^2
Predicted	
Leaf conductance range	0.05–0.003 cm sec^{-1}
Plant moisture stress range	2 to 30 atm
Maximum transpiration rate	16.6 l/day
Days of reduced transpiration	54 days
Total transpiration (170 days)	723 l
Average transpiration (170 days)	4.3 l/day

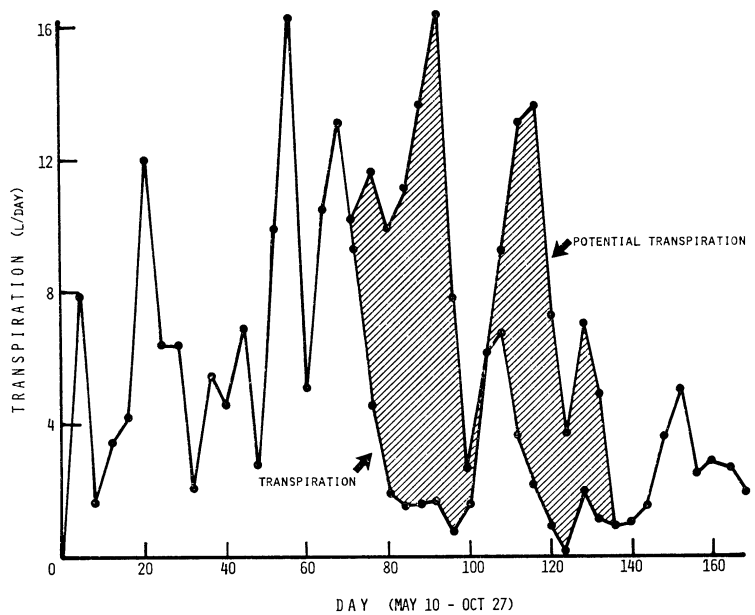

Fig. 6. Predicted transpiration, T_d, for a 2 m tall Douglas-fir growing in the Cascade Mountains of central Oregon. Climatic data from Analysis of Ecosystem Program, US/IBP. The hatched area reflects the difference between predicted and potential transpiration estimated without stomatal control

In contrast to the first case where the large tree had its transpiration constrained only 17 days, the small tree was restricted to some extent over a total of 54 days (Fig. 6). In part, this reflects the much higher maximum conductance of small trees associated with their large percentage of current foliage. Also the small tree has essentially no sapwood capacity whereas the large tree could meet water demands for at least 10 days from its sapwood reservoir.

Case 3

From a previous study, Running (1973) observed that noble fir (*Abies procera* Rehd.) exhibited little stomatal control, at least to plant moisture stress of 15 atm. Assuming a constant leaf conductance of 0.05 cm sec^{-1} for a fir of similar size to that in Case 2, we calculated that all water in the root zone compartment would be depleted by the middle of August. This would suggest, even with subsequent control of water loss at higher stress, that lethal conditions would develop under the specified environmental conditions. In fact, noble fir is not to be found anywhere in the vicinity of the climatic station, occuring only at higher elevations.

Discussion

The results obtained with this water flux model suggest a number of important avenues for future research that may shed light on the adaption of conifers to water deficits. In arid zones the advantage of greater rooting depth or lateral extension can be assessed quantitatively through the model by increasing the capacity of compartment 1, the root zone water supply. An increased root zone water supply may result in extending the period during the growing season when stomatal control does not limit optimal gas exchange by the leaves.

The importance of sapwood as a major water reservoir is indicated by the model, particularly in areas where periodic drought is common. Furthering this idea, the ratio of sapwood to leaf area may prove to be a measure of drought adaptation in conifers. In drought prone areas there would be an advantage for widely spaced trees with a high ratio of sapwood to leaf area such as in the *Pinus ponderosa* Dougl., forests of the western United States. A large sapwood volume coupled with a small leaf area may also be advantageous in the spring when air temperature and radiation are adequate for growth, but low soil temperatures limit water uptake by roots.

The critical role of stomatal conductance as the tree's major physiological control of water loss is evident by comparing results of Cases 2 and 3. Although in this model we predict conductance directly from plant moisture stress, our field research suggests humidity, temperature and radiation all play a part. Future improvements also include distinguishing differences in leaf conductance resulting from needle age and physiological conditions. At present we are studying diurnal variations in stomatal behavior and sapwood moisture content to better understand short term dynamics of the system.

In summary we find this preliminary model has led us toward a more functional evaluation of the anatomy and morphology of trees. Relationships between sapwood and leaf area appear significant and warrant special study. The linkage between soil water depletion and plant water stress is a key part of the system. The importance of stomatal control in gas exchange is again emphasized.

These interrelationships suggest future research should simultaneously measure a number of variables not commonly assessed such as total tree leaf area, sapwood volume, and rooting zone volume. These measurements should be coupled with physiological and gas exchange research.

This model will serve as a prototype for future models of two kinds. First, we intend to build a high resolution hourly model which will incorporate diurnal

variations in plant moisture stress, sapwood moisture content and leaf conductance of individual trees. Second, by generalizing this effort, we plan to assess the adaptive efficiencies of stands with different compositions and canopy densities.

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