INTERNAL REPORT 79

MODELING WATER UPTAKE ON CONIFEROUS FOREST OREGON WATERSHED 10 SYNTHESIS

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In the Coniferous Forest Biome, many of the understory as well as dominant plants are evergreen and thus water uptake is a year around process. The flow of water from the soil through plants to the atmosphere affects the entire forest ecosystem. As water is evaporated, it absorbs heat and influences the energy budget; as it is conducted through vascular plants, it carries nutrients; and as it is removed from the soil, it reduces seepage and water available to free-living soil organisms.

It is important in an ecosystem model that the hydrologic, biologic, and meteorological processes be coupled in a realistic manner. It is the objective of this report to suggest a coupling that is both practical and theoretically sound.

GENERAL MODEL STRUCTURE

We can diagram the flow of water through the terrestrial ecosystem using the convention of Forrester (1968) as illustrated in figure 1. This model will serve as a focus for our discussion and has been developed into a computer simulation. In the model, precipitation is a driving force, monitored in the forest, both above and below the canopy. All water that eventually reaches the root zone is either stored there (X_1), runs off, or seeps downward into the subsoil and eventually reaches the stream.

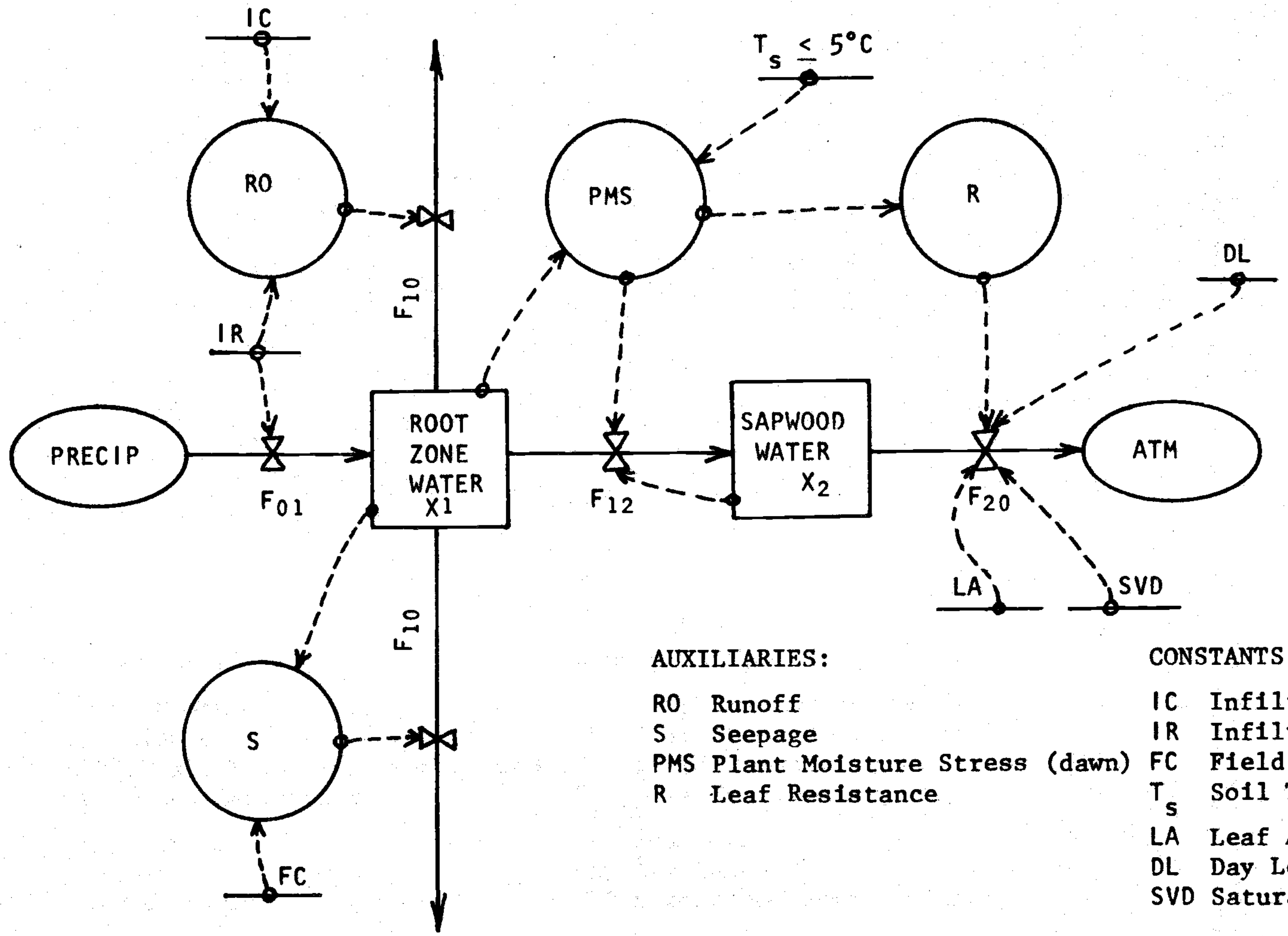
Water in the root zone may be taken up in the sap stream of higher plants (X_2). The flow, F_{12}, is a function of water available in the root zone (X_1) and the plant's ability to extract that water designated by an equilibrium plant moisture stress (PMS).

The sapwood water moves through the plant in the vascular system until it reaches mesophyll cells in the leaves and there evaporates and passes through stomata into the atmosphere. We symbolize the flow of water from the sapwood (X_2) to the atmosphere as being controlled both by meteorological and biological conditions. The major biologic control is through stomatal closure affecting resistance (R) of water vapor diffusion through leaves. The meteorological control can be modeled as part of the energy budget or simply as the water vapor concentration gradient between the air and leaf.

This model was developed from information gathered at the Oregon and Washington Intensive Sites and from analysis performed at Argonne National Laboratory in Illinois. It is applicable to individual trees as well as watersheds. Model components warrant separate discussion before indicating how water uptake applies to other ecosystem processes.

ATMOSPHERIC SOURCE

Generally, the atmosphere is the source of water, although a particular ecosystem may be supplied from ground water or by irrigation. The amount of water reaching the root zone, (X_1), can generally be considered equal to infiltration rates, (IR), which is designated in the model as a forcing function. At the Oregon Site, precipitation is monitored both in the open



AUXILIARIES:

RO	Runoff
S	Seepage
PMS	Plant Moisture Stress (dawn)
R	Leaf Resistance

CONSTANTS:

IC	Infiltration Capacity
IR	Infiltration Rate
FC	Field Capacity
T_s	Soil Temperature
LA	Leaf Area
DL	Day Length
SVD	Saturated Vapor Deficit

Fig. 1. General structure of water uptake model now programmed in Dynamo.

and under forest stands. Storage as snow is recorded on a transect across the intensively monitored Watershed 10. Precipitation is totaled daily on the climatic record from the Oregon Intensive Site.

ROOT ZONE WATER COMPARTMENT (X_1)

Although the uptake of water by roots affects the amount flowing to the subsoil and the stream, our discussion will be restricted to the rooting zone. Capillary rise of water from below the rooting zone initially will be overlooked by accepting a shallow definition of the root zone. That is, the root zone will be to a depth encompassing 90 percent of root biomass. On Watershed 10, the rooting depth varies from about 40 cm near the ridges or by rock outcrops to 100 cm in the lower portions of the watershed.

Water in the root zone can be expressed in three kinds of units: (1) on a percent by weight; (2) on a percent by soil volume; and (3) on the basis of its chemical potential. Differences in the chemical potential of water in the soil, plant, and atmosphere determine the direction of flow but does not relate directly to the flow of water as we shall demonstrate. The percentage by weight expression is not comparable among sites with different soil textures, organic matter and rock content. For hydrologic purposes, expression on a volume basis is required. Soil water volume is being estimated on Watershed 10 with a calibrated neutron probe (Fig. 2). Gravimetric measurements on reference stand 2 were taken by Fogel at 5 cm intervals to a depth of 1 meter in May, August, and November. With knowledge of bulk densities, gravimetric measurements may be converted to volumetric.

The soil water content in the root zone is never reduced to zero. Long before this could happen, all roots would die. After saturation, water drains to a condition called "field capacity" (FC). This state can be approximated by allowing soils to reach equilibrium under 0.1 or 0.3 atm tension on a ceramic plate. Finer textural soils, as found on Watershed 10, hold gravitational water at lower tensions than coarser soils.

When water content in the root zone exceeds field capacity, additional water reaching the zone will infiltrate to lower levels in the soil or run directly to the stream via surface or subsurface runoff. On watershed 10, only when daily rainfall exceeds about 12 cm, does interflow occurs. Subsoil seepage is the major route water follows to the stream.

In our initial model, we combine runoff interflow and seepage into a water loss from the soil root zone with the equation:

$$F_{10} = F_{01}-(FC-X_1)$$

To simplify our calculations, we treat field capacity(FC) as the amount of available water held in the root zone between 0.1 -15 atm tension, rather than the total water content.

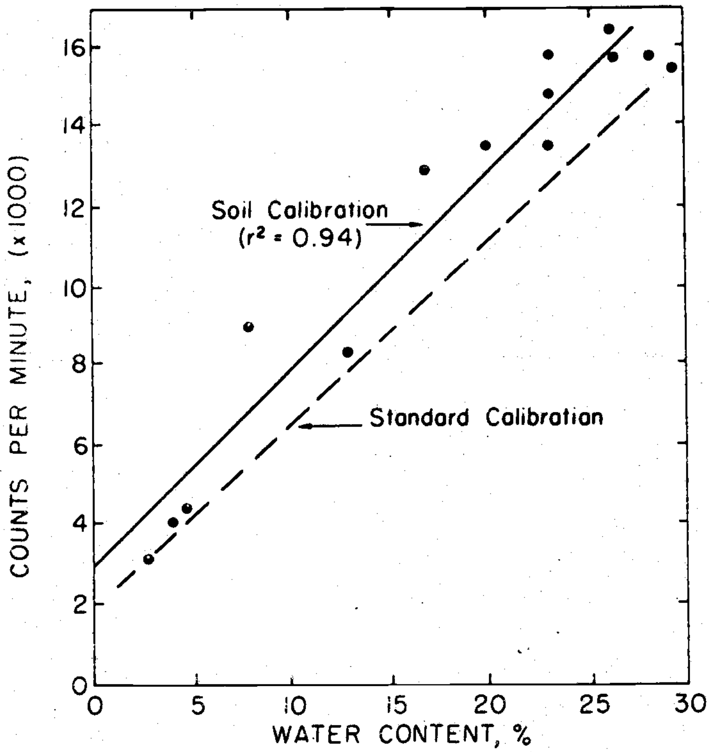


Fig. 2. The relation between volumetric water content and counts per minute by the neutron meter in the plantation soil. The dashed line is the standard calibration obtained by submerging the probe in cadmium chloride solutions. After Waggoner and Turner (1971).

PLANT MOISTURE STRESS AUXILIARY

In figure 1, the level of water in the root zone was monitored to determine two flows from that compartment: first, to determine whether the soil exceeded field capacity and seepage (saturated flow) occurred; and secondly, to determine indirectly the flow of water into sapwood. The latter indirect coupling goes through the plant in order to translate volume of water into equivalents of plant water potential or plant moisture stress (PMS). Fortunately, this coupling is no longer just theoretical, but practical.

If a nontranspiring conifer is permitted to equilibrate in soils with moisture conditions at field capacity, its water potential will be -2 to -3 atmospheres. This assumes the soils are not high in salt concentration, a safe assumption in our region. A living plant, thus, always has some tension on the water column in its vascular system. The larger the plant, the greater the minimum stress because of a hydrostatic gradient of 1 atm/ 10 meters. Tobiessen et al. (1971) suggest from studies on a 90 meter Giant Sequoia that the gradient may be only .8 atm/10 meter, possibly we surmise from use of sapwood water. The tension can be measured by placing a severed twig into

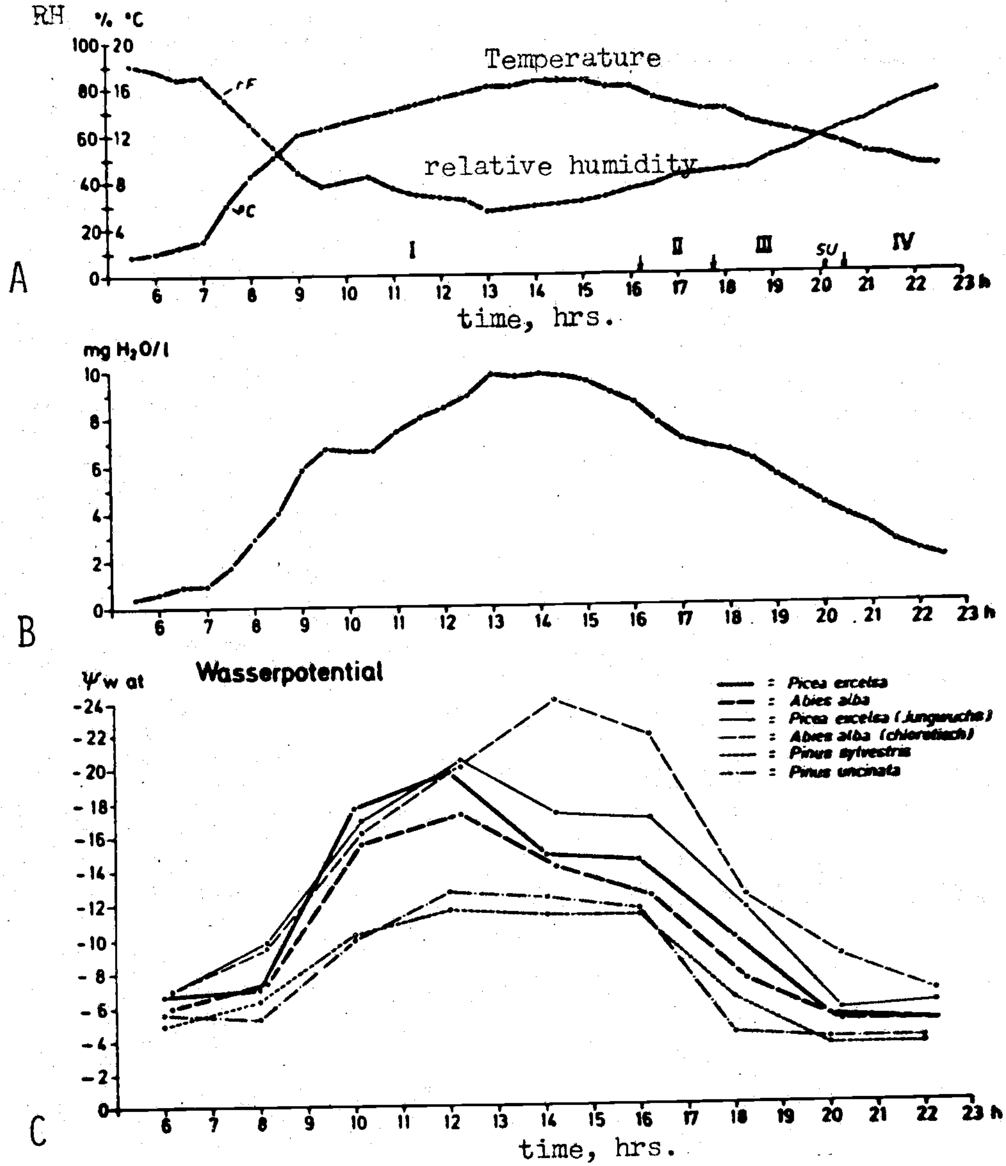


Fig. 3. Daily course of plant water potential, Ψ, of different species of conifers growing in the open (Benecke 1970).

a pressure chamber with the cut surface extruding through an airtight seal. The pressure necessary to force the severed water column back to the cut surface represents the original tension on the column (Scholander, et al. 1965, Scholander 1972).

Fortunately, many different species of conifers reach similar equilibrium tensions with their root water status (Fig. 3c). This equilibrium is best measured in the field just before dawn when the foliage is wet (Waring and Cleary 1967). Figure 3c clearly indicates that water potentials measured during the day reflect atmospheric demands (Fig. 3b) and not the water status in the root zone.

As water is taken up by plant roots, soil moisture is depleted from the root zone. Boersma et al. (1973) found Douglas-fir trees obtain water progressively from surface to subsoil horizons with maximum uptake coming from zones with water tension or stress of less than 2 atmospheres. As long as 20 percent of the root system taps a zone of soil with water near field capacity, tension measured in the plant at dawn will not increase (Fig. 3). Once most of the available water in the root zone is removed, however, a rapid increase in plant stress is observed. The texture, stoniness, and rooting depth determine the amount of available water held in a particular soil.

Initially, we will treat the relationship in two steps. When the available soil water is greater than 20 percent of the total, plant moisture stress will be minimum at 2 atm, with a correction for height (1 atm/10 meters): PMS = 2 atm if AWF > 0.2. When the available water fraction (AWF) is equal or less than 0.2, a linear increase in plant moisture stress occurs until at zero, PMS = 30 atm. The linear equation is simply PMS = 30 -140* AWF.

An example of the relationship coupling root zone water to plant water stress is presented in Figure 4. Data are from three 7-8 meter tall *Pinus resinosa* trees (Sucoff 1972). They represent the first direct, published validation of Hendrickson and Veihmeyer's (1942) statement that water to tree roots is equally available over a wide range in soil moisture. Veihmeyer (1972) summarized more than 30 year's data indicating similar growth and yields could be obtained from orchard trees under different irrigation schedules, but had not measured and, thus, could not demonstrate plant water stresses were comparable. The amount of recharge, F_{12}, is equal to that removed, F_{20}, times a recharge fraction. This recharge fraction decreases linearly as PMS increases from 5 to 30 atmospheres. The equation is $F_{12} = (1.07 - 0.036*PMS)*(X_2Max - X_2)$, where X_2Max represents water available in sapwood at maximum water content and X_2 is the level at present.

In addition to monitoring root zone water, it is desirable to measure the temperature of that water, particularly when plant moisture stress is less than 5 atmospheres. When root temperatures fall below 5°C, changes in viscosity and membrane permeability reduce water uptake and increase plant stress, at least during the day. On some species, such as Monterey pine (*Pinus radiata*) temperatures above 10°C still inhibit water uptake (Fig. 5). The graph indicates however, that temperature is not effective once water becomes at all limiting to the entire root system.

Cold root temperatures force partial stomatal closure in leaves so information concerning root temperature as well as predawn PMS must be passed along to another auxiliary in the model, leaf resistance, R (fig. 1). Root temperature at 20 cm depth are recorded continously underneath forest on Watershed 10 and at other sites on the H.J. Andrews Experimental Forest. For modeling purposes, we will assume a linear increase in stress from 2 - 30 atm as soil temperatures decrease from 5° to -2°C. The equation is $PMS = -3.85*T_s+22.3$.

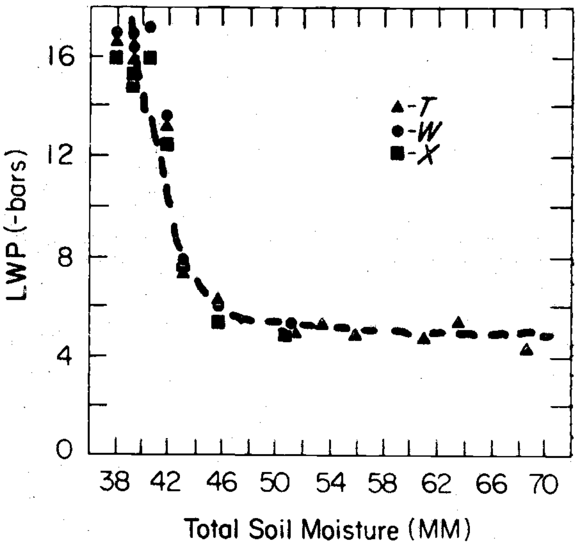


Fig. 4. Determination of available water in soil by monitoring predawn water stress in Pinus resinosa (Sucoff, 1972).

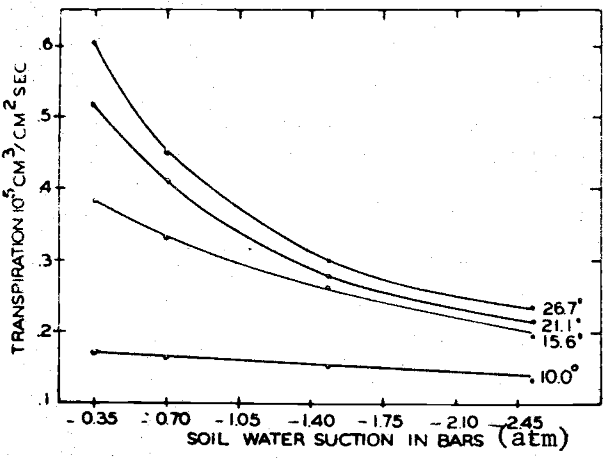


Fig. 5. Rates of transpiration in Monterey pine seedlings as a function of soil temperature and soil water potential. (Babalola, et al. 1968).

SAPWOOD WATER (X_2)

We have only recently identified sapwood as being important in the modeling of water uptake, although the timber and pulpwood industry have long recognized that fresh cut wood varies seasonally in water content. Rough calculations indicate that old growth forest of Douglas-fir may represent at least 300 metric tons/hectare of sapwood. With a maximum change of 100 percent in moisture content possible, this means sapwood stores at the beginning of the summer at least 3 cm of water/hectare available for transpiration. Normally, sapwood water will be withdrawn during the day and recharged at night from the root zone (Doley 1967).

The amount of sapwood in comparison with heartwood, which is nonfunctional, varies with the diameter, crown size, and species of tree. In general, pines have a greater proportion of sapwood to heartwood than does Douglas-fir or western redcedar, which is notable for its small amount of sapwood (Fig. 6).

The entire sapwood of most conifers can be considered equally efficient for water transport (Vite 1959). Bordered pits in the wood cells seal off each cell when ever the wood is frozen and air is introduced into the conducting system. When thawing occurs, pressure is maintained within the cell until all air is redissolved and then the bordered pit opens to permit wood conduction between cells (Hammel, 1967). Our tritiated water studies on Douglas-fir confirmed that all sapwood was equally efficient in transporting water.

From our field experiments with tritiated water, Kline found a linear relationship between the cross sectional area of sapwood in Douglas-fir and the amount of water transpired over a 10 to 30 day period, when soil water was not limiting in the root zone and similar meteorological conditions existed. His rate of conduction through sapwood was 3.8 $\mathrm{ml/cm^2/hr}$ averaged for 24 hrs.

Differences existed even among plantation trees at the Thompson Site in Washington, reflecting differences in the foliage area. All destructive biomass sampling should thus, include sapwood volume as a part of the analysis. This knowledge permits indirect estimation of foliage weight as well as stand transpiration. Initial comparisons by Dr. C.C. Grier give $R^2 = .96$ for the linear regression between sapwood cross sectional area at DBH and foliage weight for Douglas-fir.

Because tritiated water experiments were conducted in the same stand as the lysimeter tree, the possibility exists of estimating daily transpiration for the stand with knowledge of the sapwood cross sectional area at breast height of the lysimeter tree. This technique has ready application on the watershed, also through foliage sampling.

ATMOSPHERIC SINK

The driving force to water movement through the soil-plant-atmosphere system is the atmosphere, for unless precipitation is occurring, a demand exists. The amount of water vapor that can be held in a gaseous form is a function of temperature and pressure. At 0°C, the air is saturated when it has 4.85 g H_2O $\mathrm{cm^{-3}} \times 10^{-6}$; whereas at 25°C, air can hold 23.05 g $\mathrm{cm^{-3}} \times 10^{-6}$ of water (from table 1.II, p.11, Slatyer 1967). The saturation deficit from the leaf to the atmosphere, together with wind produced mixing of the air is one expression of the demand function driving transpiration.

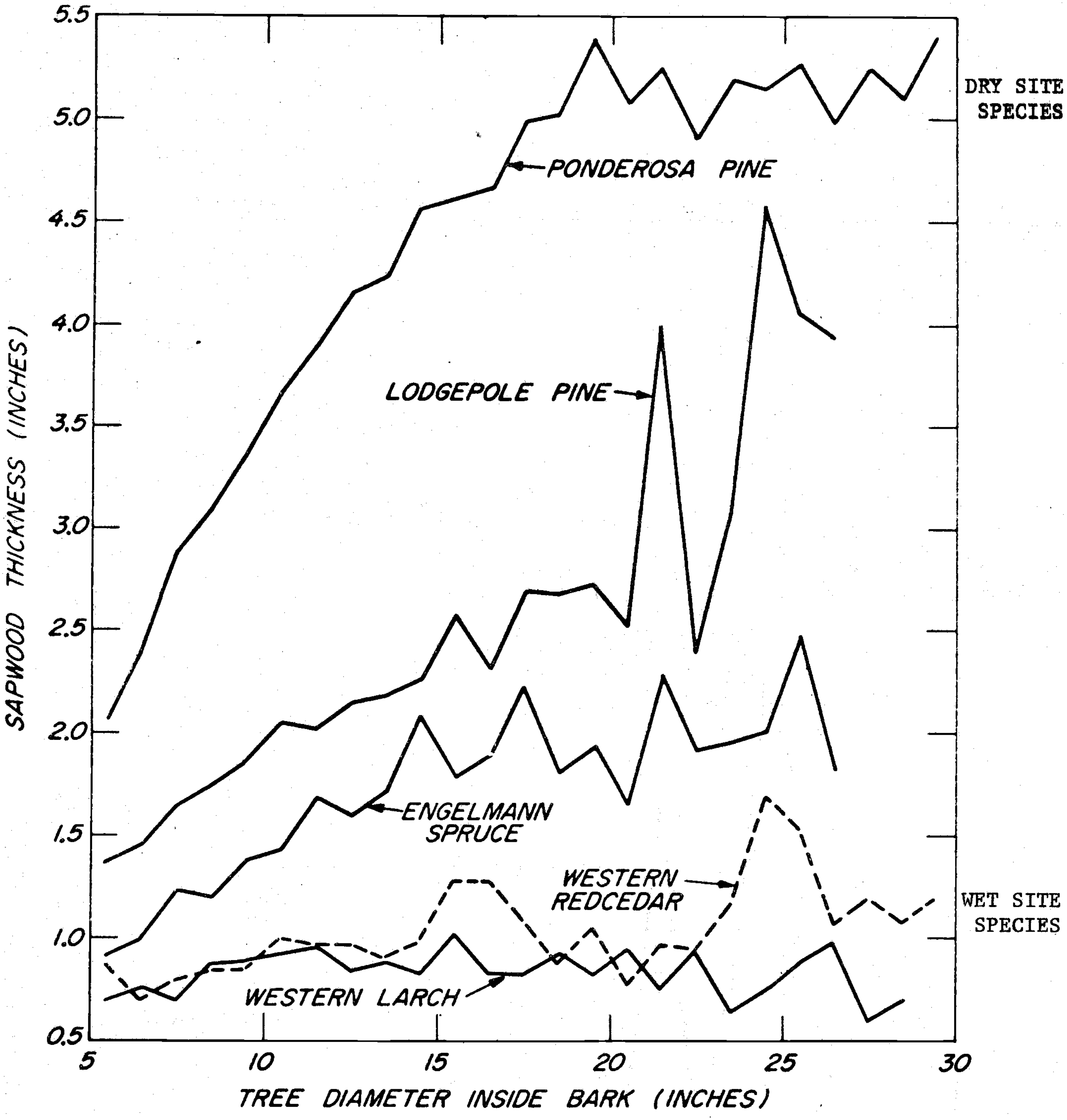


Fig. 6. Relationship of sapwood thickness of five western softwood species to tree diameter (Lassen and Okkonen 1969).

In terms of water potential gradients, the atmosphere generally represents a steep increase from even the most desiccated conifer needle (death occurs at -50 to -60 atm). At 15°C, a relative humidity of 98.9 represents a water potential of -15 atm, whereas a humidity of 89.5 % is equivalent to -150 atm of water potential.

Water uptake in a saturated atmosphere has been demonstrated (Slatyer 1956, Stone et al. 1950). Also, on the Andrews, tritiated water appeared more concentrated in the twigs than in the foliage, suggesting that uptake of dew could have diluted the concentration of tritiated water in the needles. For modeling purposes, however, we recommend treating the condition of saturated foliage as "zero", rather than "negative" transpiration.

On the Oregon Intensive Site, atmospheric vapor concentration and temperature are recorded continuously and averaged over hourly intervals. More intensive meteorologic data are available at the Thompson Site in Washington, where energy budget studies have been conducted and the lysimeter tree is located. In our initial model, the saturated water vapor deficit (SVD) is a Table value provided hourly or averaged for the daylight hours.

LEAF RESISTANCE (R)

Controlling the flow of water from the plant to the atmosphere is the leaf resistance auxiliary (R), (Fig. 1). Regardless of the hydration state of the soil or sapwood, the resistance through the plant is always greater than from a free water surface. Resistance is a term with units of sec cm^{-1} which may be calculated from experiments where transpiration is measured and the water vapor concentration gradient between air and leaf is known. The equation is:

$$T = \frac{e_s - e_o}{R}$$

Where T is transpiration in cm^3 H_2O cm^{-2} leaf area sec^{-1}

e_s is saturated water vapor concentration at temperature of leaf in cm^3 H_2O cm^{-3} air

e_o is water vapor concentration of the air

R is total resistance in sec cm^{-1}

Units cancel to leave sec cm^{-1}

$$R = \frac{e\ (cm^3\ cm^{-2}\ sec^{-1})}{T\ (cm^3\ cm^{-3})} = sec\ cm^{-1}$$

The leaf resistance, as the equation shows, requires knowledge of transpiration to calculate, but is not directly dependent upon the rate of water loss. Transpiration, thus, may vary with constant leaf resistance depending upon the vapor concentration gradient (e_s-e_o).

Wet filter paper with the shape of a needle would represent zero leaf resistance. With wind speeds above 2 miles an hour, the boundary layer resistanc decreases to about 0.5 sec cm^{-1}. The resistance of Douglas-fir needles with wide open stomata is always much greater, at a minimum of 4-5 sec cm^{-1}. When stomata are completely closed and the only water loss is through the cuticle of the leaf, resistances reach 250-300 sec cm^{-1} (Running, personal communication).

The effect of increased leaf resistance upon transpiration is illustrated in Figure 7. As shown, a change in leaf resistance between the range of 5 and 15 has the largest effect on transpiration. When resistances are above 100 sec cm^{-1}, proportional changes have little measureable influence upon transpiration. Doubling stomata resistances decreases transpiration by half, unless the atmosphere is saturated.

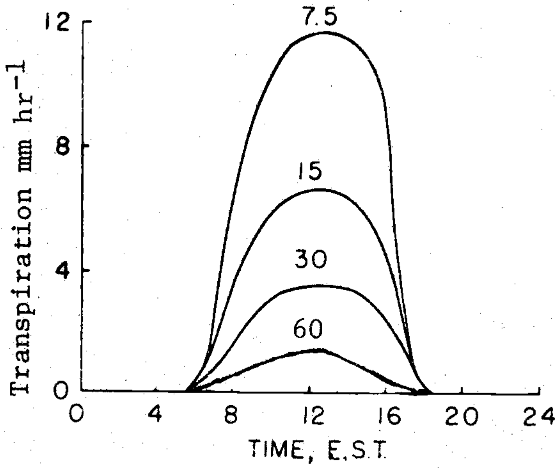


Fig. 7. Reduction in diurnal transpiration as a function of leaf resistance. (Waggoner and Turner 1971).

All of the factors controlling stomata are not completely understood. We know, however, that both light and temperature can trigger a response. Generally, throughout the growing season, stomata remain closed at night. There are some exceptions to this when soils are near saturation and foliar expansion is taking place. For our purposes, we will assume transpiration is predominantly a day time process and that at night leaf resistances increase and that the vapor concentration in the atmosphere approaches saturation, so water loss is neglible.

Temperature influences leaf resistance in two ways: first, by initiating stomatal closure when temperatures of the leaf drop below freezing (Reed 1968, Drew and Fritts 1972); and secondly, by reducing root growth and water uptake from the soil, indirectly leading to a water deficit in the leaves and partial stomatal closure.

The effect of low light and temperature can be treated simply as threshold values in our modeling. Interactions with soil temperature and soil moisture are more difficult. Fortunately, both relationships have been studied in recent years.

Reed (1971) showed that new foliage of Douglas-fir would wilt if root temperatures were lowered below 2°C. This may explain why bud swell has not been observed before temperatures at 20 cm depth have exceeded 4°C (Waring 1969).

Studies with other species have also identified that low soil temperatures affect stomatal resistance and transpiration. European larch and spruce both reduce transpiration by 50 percent at soil temperatures of 2°C as compared to 15°C (Havranek 1972). Benecke (1970) reported similar findings with mugo pine.

From preliminary field studies, Waring and his colleagues have observed partial stomatal closure when soil temperatures reach 2°C and full opening at temperature of 5°C (with vapor concentration gradients of less than 10mb).

Drew and Fritts (1972) reported similar responses in ponderosa pine. For modeling purposes, therefore, we will store a function in the leaf resistance auxiliary (R) that indicates resistances above 250 sec cm^{-1} at freezing temperatures and decreasing to 5 sec cm^{-1} when soil temperatures exceed 5°C at 20 cm depth. These temperatures are being monitored continously under different forest communities at the Oregon Intensive Site.

As mentioned earlier, soil temperature is important mainly when soil moisture is readily available to tree roots. We measure availablility through the plant moisture stress auxiliary (PMS) and relay this information to the leaf resistance auxiliary (R). In Oregon, we generally find limiting conditions may begin to occur after full leaf development has been completed (Fig. 8). Thus, it is only during the dormant season and at the stage of bud swell that low soil temperatures greatly affect water uptake.

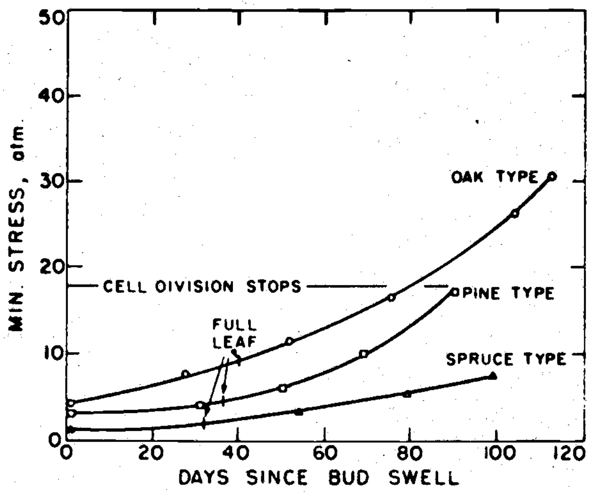


Fig. 8. Seasonal changes in predawn stress of 1-2 m tall Douglas-fir growing in three different Oregon ecosystems. In the oak type, growth begins in April, but cool temperatures lengthen the period between bud swell and full leaf. Note, stress remains below 10 atm until after "full leaf" stage. (Waring 1970).

Reed (1971) first quantified the general relationship between predawn plant moisture stress and leaf resistance. He found with Douglas-fir that minimum resistances of 4-5 sec cm^{-1} occurred with stress below 5 atm and that maximum resistances were reached at about 28 atm predawn stress. Running is more accurately determining the non-linear relationship which is indicated in Figure 9.

We know that extreme vapor concentration gradients may force stomata to close somewhat more than predicted by the predawn stress. However, such conditions are rare and usually occur where leaf resistances are already approaching maximum. Thus, a preliminary model for Douglas-fir need not include an information input from the atmosphere to the leaf resistance auxiliary. With other species of conifers or hardwoods such a link may be desirable.

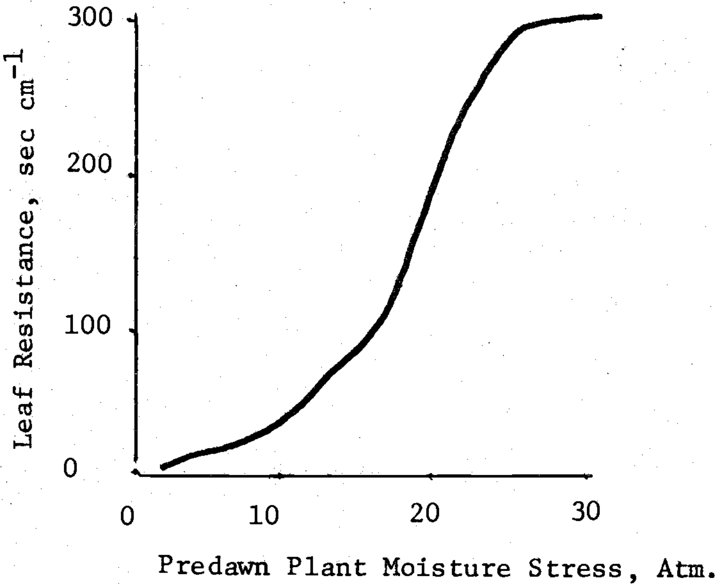


Fig. 9. Relationship between leaf resistance and predawn stress in 1 meter tall Douglas-fir (after Running 1973).

THE ENERGY BUDGET APPROACH

Water transfer can also be derived based upon thermal energy considerations. This is due to the heat of vaporization of water, or latent heat, λ, which is required in the evapotranspiration process. The applicable energy conservation equation for determining the rate of evapotranspiration, ET, from a system is:

$$ET = -(Q^* + H + G) / \lambda.$$

For vegetated surfaces like forests, the amount of evaporation from the soil is usually small, relative to transpiration from plants, so that ET is essentially equal to the transpiration term, T, which was defined earlier. The other terms in the equation are: the radiative heat transfer, Q^*; the convective heat transfer, H; and the conductive heat transfer, G. The apportioning of these energy budget components varies importantly as a function of surface characteristics, season, and the time scale of interest.

Solving the above equation for ET depends upon the availability of suitable expressions for the remaining energy transfers and upon the availability of appropriate meteorological data. The generalized, direct expression for these energy transfers, q, is:

$$q = c\ k\ (dT/dz),$$

where c is a constant of proportionality, k is the thermal conductivity, and dT/dz is the temperature gradient in the direction of transfer. This may be reduced to a finite difference form, in which case the effect of distance, Δz, is incorporated with k, giving:

$$q = c\, k' \, (\Delta T).$$

The problem of evaluating Q*, H, or G, is thus seen to be one of establishing applicable values of k' and ΔT.

The alternative to employing direct expressions for heat transfer is to rely on secondary relationships, or regressions. This is not preferable, but it may be necessary for practical reasons. The main detriment of this alternative is that there is no way to independently validate the estimate. Also, the precision of estimations made in this way tends to be less, although it may be adequate for some purposes.

Considerable effort is being made to develop and apply the energy budget approach to forest water transfer problems. The actual form used in any particular case is dictated by the kind of data that can be made available. Generally, energy budget studies require quite intensive data. When this type of data is lacking, more reliance must be placed on assumptions and secondary relationships. For forest applications, the operational model for ET is most likely to result from a combination of these.

INITIAL TEST OF WATER UPTAKE MODEL

In order to evaluate the water uptake model, IBP data from the Central Oregon Site were utilized. Initial tests were completed on a model programed in DYNAMO II_F simulation language.

The model has the following inputs, initial conditions, constants, and equations:

Program: H_2O TRANS

Environmental Variables

T_s = soil temperature at 20 cm depth, °C

SVD = Saturated water vapor deficit, cm^3 H_2O cm^{-3}

DL = Day Length, seconds

INITIAL CONDITIONS

X_1 = Soil water supply at $t = 0$, cm^3 H_2O

X_2 = Sapwood water supply at $t = 0$, cm^3 H_2O

F_{01} = Infiltration in cm^3 H_2O reaching root zone daily

BIOLOGICAL AND PHYSICAL CONSTANTS

LA = Leaf area, cm^2 = 150 $cm^2 \cdot$ dry wt. in grams

X_2Max = Sapwood capacity, cm^3 H_2O available between 200 and 100% moisture content

FC = Field capacity of root zone, cm^3 H_2O available between 0.1 and 15 atm tension.

AUXILIARY EQUATIONS

AWF = Available water Fraction $= \frac{X_1}{FC}$

PMS_1 = Plant Moisture stress, atm = $f(X_1) = 30 - 140 \cdot AWF$

APMS = Plant moisture stress = 2.0 atm if $AWF > .2$

$= PMS_1$ if $AWF \leq .2$

PMS_2 = Plant moisture stress, atm = $f(T_s)$ if $< 6°C = -3.85 * T_s + 22.3$

BPMS = Plant moisture stress, atm = PMS_1 if $T_s \geq 6°C$

$= PMS_2$ if $T_s < 6°C$

RPMS = Leaf Resistance, sec cm^{-1} = f (PMS)

May be programed as a Table function

FLOW EQUATIONS

(J,K,L refer to time steps = past, present and future)

$F_{10} \cdot KL = F_{01} \cdot JK - (FC - X_1 \cdot K)$

(includes both seepage, runoff and interflow losses)

$F_{12} . KL = (1.07 - .036 * PMS) * (X_2Max - X_2.K)$

(calculates sapwood recharge with complete recovery at 2 atm and none at 30 atm)

$F_{20}.KL = (SVD/R)*LA.K * DL$

(Calculates daily transpiration)

LEVEL EQUATIONS

$X_1.K = X_1.J + DT * (F_{01}.JK - F_{12}.JK)$

$X_2.K = X_2.J + DT * (F_{12}.JK - F_{20}.JK)$

PROGRAM SPECIFICATIONS

SPEC: DT = .1 day/length = x days/print and plot intervals x days

Our specific example concerns a Douglas-fir tree that is 83 meters tall and transpired, on the average, 530 liter/day^{-1} in late June (Kline, tritiated water experiment). The tree has an estimated leaf weight of 346 kg. For the latter part of June the SVD averaged 7×10^{-6} cm^3 H_2O cm^{-3} air. Day length averaged 5.76×10^4 sec. The field capacity or available soil moisture storage was 15 cm in the surface meter. With a radius about the tree of 10 meters, the initial state of soil water supply was set at 4.7×10^7 cm^3 H_2O. The sapwood was estimated from the same tritiated water experiment to be 4.3×10^6 grams, with a maximum moisture content range of 100% this value was assumed the storage supply (X_2 Max).

A number of simulation runs were conducted varying soil temperature and the relationship between leaf resistance and plant moisture stress. Preliminary runs, with leaf resistances initiating at 5 sec cm^{-1}, indicated transpiration values more than eight times that measured, and a depletion of available water to less than 20 percent of capacity within 12 days (Table 1). By 20 days, transpiration was approaching a minimum.

TABLE 1. Simulation Output of Water Uptake Model

TIME E+00 DAYS	X_1 E+03	F_{12} E+03	X_2 E+03	PMS E+00	F_{20} E+03
0	47000	0	4300	2.00	4185
2.00	42311	3674	619	2.00	4185
4.00	34390	4123	169	2.00	4185
6.00	26075	4178	114	2.00	4185
8.00	17711	4184	107	2.00	4185
10.00	9341	4159	107	2.17	4185
12.00	4770	934	2438	15.79	203
14.00	3582	361	3335	19.33	113
16.00	3041	200	3669	20.94	96
18.00	2711	136	3814	21.93	89
20.00	2470	107	3882	22.64	85

Environment: SVD = 7 cm^3 H_2O x 10^{-6} cm^{-3} air; DL = 5.76 x 10^4 seconds;
T_s = 15°C

Initial Conditions: X_1 at field capacity, 47,000 liters
X_2 at capacity 4,300 liters

Biological and Physical Constants: LA = 346 kg foliage x 1.5 x $10^5 cm^2$
FC = 15 cm of water in surface meter with area = Π 10 m^2
X_2 Max = 4,300 liters

Leaf Resistance permitted to change from 5 sec cm^{-1} to 300 sec cm^{-1}

In additional siumlation runs, leaf resistance was maintained constant at 20 sec cm^{-1} and at 40 sec cm^{-1}. At a constant leaf resistance of 20 sec cm^{-1}, transpiration averaged 1046 liters day^{-1} exhausting soil and sapwood water supply in 50 days. The value of 40 sec cm^{-1} is more appropriate to a large tree with at least a 6 atm hydrostatic gradient and a large amount of older foliage. Transpiration was then 523 liter day^{-1} with the water supply lasting 100 days in the soil and sapwood. The 40 sec cm^{-1} of leaf resistance best fits our observation of transpiration and the fact that the soil water supply in the soil is adequate for at least 90 days during the summer. The sapwood held a maximum of 8 days supply but as recharge decreased the reserve dropped to a 2-3 day supply. At conditions when complete stomatal closure occurs and leaf resistances reach 300 sec cm^{-1}, only 70 liter day^{-1} are transpired. However, by this time, all the sapwood reserve has been utilized.

In another simulation, leaf resistances were permitted to change over the range from 20-300 sec cm^{-1}. Soil water supply dropped to 20 percent of the capacity in 40 days with the resistance increasing to about 40 sec cm^{-1} reducing transpiration by half. Continued increase in leaf resistance reduced transpiration to a minimum of 70 liter day^{-1} after 96 days. All available water was removed from the root zone and sapwood in 150 days.

In yet another simulation, soil temperature has held at 2°C, reducing maximum transpiration rates to 258 liters day^{-1} until critical soil moisture levels were reached after 145 days.

CONCLUSIONS

The sapwood is probably more important for damping diurnal changes in plant moisture stress than in providing a major source of water. When stress does develop, the sapwood reservoir is already greatly depleted, although the diurnal demand is also reduced proportionally. The sapwood water has a turnover rate of 10 days in June, again suggesting little water is actually stored. When soil temperatures drop below 6°C, as they do throughout the entire dormant season, transpiration should be reduced at least by half that obtained at the higher soil temperatures. When the weather is cold or raining, this should have little effect upon transpiration, although photosynthesis may be reduced because of increased leaf resistance. When weather is clear, as may the case for more than two months during the dormant season, cold soil temperatures may have important consequences upon water and nutrient uptake as well as photosynthesis.

The observation that 5 sec cm^{-1} leaf resistance gives transpiration values 8 times those observed, encouraged us to apply a correction for the hydrostatic gradient and to consider the possible reduced efficiency of older foliage.

The model is being programmed into Fortran and climatic data for the entire year entered at Table values. Field experiments are underway to assess the simulation results concerning the effect of soil temperature and the hydrostatic gradient

APPLICATION

The water uptake model described, has sufficient reality to provide a link between the soil-plant-atmosphere system and to aid our understanding of other ecosystem processes.

For example, the nutrient uptake by vegetation can be coupled directly to transpiration. Already, we know the concentration of nutrients in the sap is low, representing concentrations of less than 0.5 moles/liter usually. As water content of the sapwood is reduced, the nutrient concentration increases proportionally. The concentration of nutrients in the sap also varies seasonally as they are released from the soil. Meentemeyer (1971) has suggested that decomposition and the activity of soil organisms can be linearly related to actual evapotranspiration. We advise studies of nutrient concentration in sapwood using large pressure chambers to better evaluate these relationships.

The energy budget approach, as discussed by Holbo, does not generally incorporate an estimate of leaf resistance, yet we see through parallel comparisons that these relationships can be established.

Primary production also rests upon a gas exchange process that requires knowledge of leaf resistance generated by our model as a function of PMS and root temperature. The basic data requirements of the model are in hand or are being gathered this year. A more complete report on our computer simulation will be provided at a later date.

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