

INTERNAL REPORT 38

TERRESTRIAL PRIMARY PRODUCTION MODEL

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INTRODUCTION

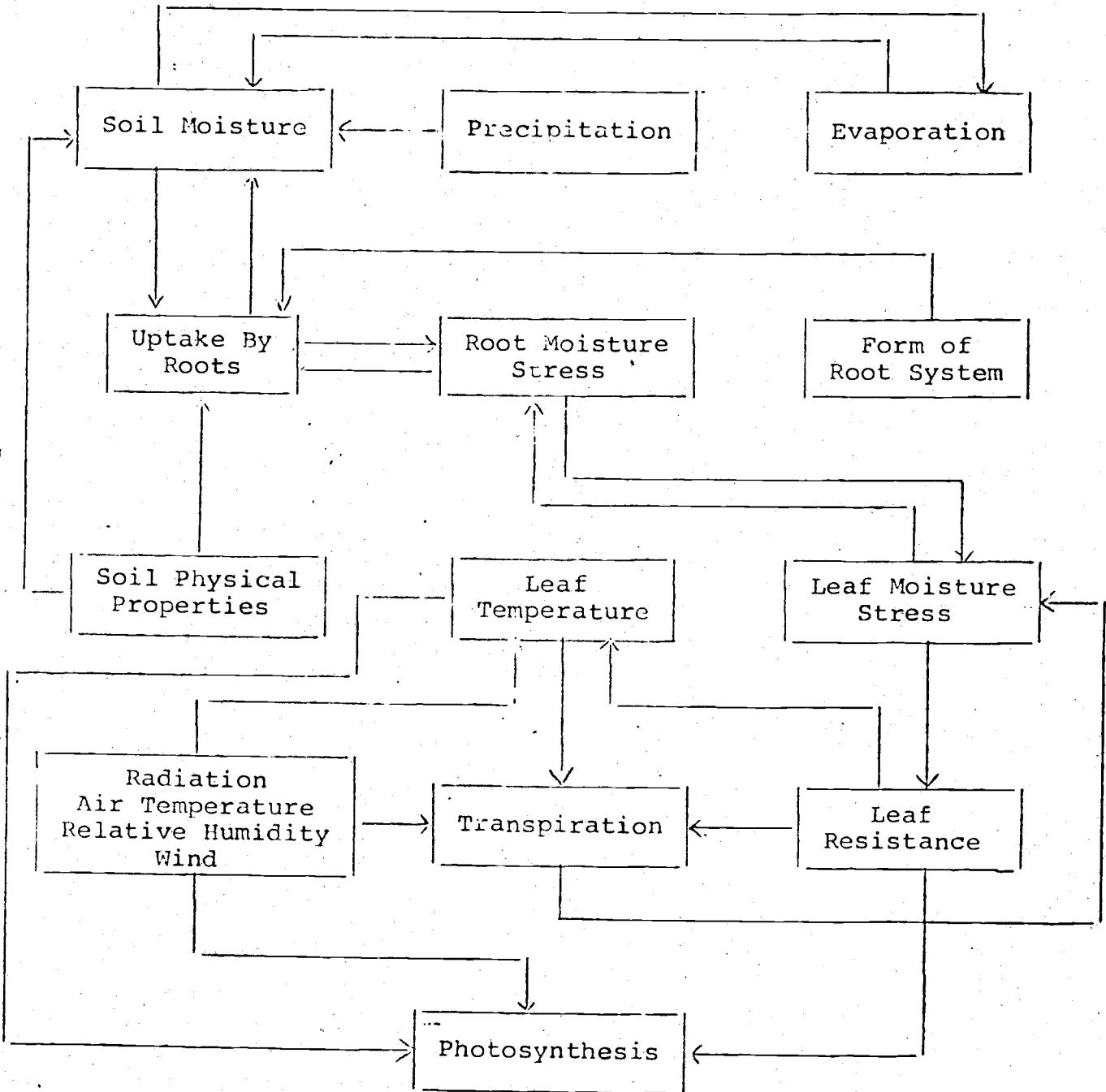
Working in consultation with experimental scientists concerned with primary production, we are developing and linking submodels to simulate photosynthesis and the movement of water through the soil-plant-atmosphere system in a stand of coniferous trees. The primary processes in the model and their linkages are summarized in Figure 1. Principal input variables for the computer simulation include direct and diffuse shortwave radiation; profiles of air temperature, relative humidity, and CO₂ concentration; and an initial profile of soil moisture content. The model predicts total and net photosynthesis, respiration, root and leaf moisture stress, transpiration, and leaf temperatures over several hours or a few days and on a per-unit-area basis.

Our objectives in developing this model are: (1) to study the ways in which interaction and linkages between key processes (such as transpiration and photosynthesis) affect the growth and productivity of trees; (2) to provide a fine-resolution model of primary production in a Douglas-fir or other homogeneous conifer stand (the model is intended to serve as a theory that complements the detailed process studies at the Thompson IBP site); and (3) to develop the terrestrial primary production component of a total ecosystem model. We recognize that the present model--and the experimental studies with which it is based--are more detailed than would be necessary if an overall ecosystem model were our only objective.

Our model, which is written in Fortran IV, is being developed on the University of Washington's CDC 6400 system. All submodels are written in modular form as subroutines that can be changed if necessary without seriously affecting the performance of the rest of the program. This flexibility is important, because it allows us to take quick advantage of new submodels as they become available. Primary production modeling is in a state of extremely rapid development. For example, three new micrometeorological models, which were completed almost simultaneously, have recently come to our attention. Obviously, any new work that we might do in this field would duplicate at least part of this work. In fact, considerable duplication already exists, for apparently none of the three modelers was aware of the others' work. Our strategy, then, has been to write simple working submodels, however crude, that will enable us to follow the whole soil-plant-atmosphere system on the computer. As better submodels become available, developed by ourselves or by others, they are substituted for existing ones. This strategy permits us to concentrate our own modeling efforts in areas in which we have special competence and where existing submodels are, to the best of our knowledge, inadequate. One area of interest includes water transport of nutrient ions through the soil, uptake by roots, and subsequent movement of the solution through the vascular system of the tree to the leaves.

Figure 1

Diagram Summarizing Primary Production Movement Model



PHOTOSYNTHESIS

We have been fortunate to be able to take advantage of an existing model, which describes the attenuation of light moving through a leafy canopy, developed by D. J. Connor (1970), based on work of Warren Wilson and Reeves (1960), H. Anderson (1966), deWit (1965), and others. We have modified Connor's model to include certain suggestions set out in Miller (1969) and have corrected some formulas.

Following Connor, we assume that we need be concerned only with the passage of direct and diffuse short-wave radiation through the forest canopy. The effects of reflected light are not considered, nor are those of light transmitted through the foliage elements. Net photosynthesis is calculated every hour over a 24-hour period. For this calculation areas of foliage illuminated by direct and diffuse radiation in several canopy layers must be determined. Also required is extinction coefficient (K), which is related to foliage area index (F) in each layer; inclination and orientation of foliage in each layer (α); and angle of elevation of sun (β). Then,

$$\text{Percentage of direct sunlight} = e^{-KF} \quad (\text{Anderson, 1966})$$

$$\text{or} = (1-K)^F \quad (\text{Miller, 1969})$$

Subroutine ASSML

Gross photosynthesis for each layer is calculated from a relation suggested by Monteith (1965) and Brown (1969)

$$P = \frac{(CO_2)I}{1/K + I\epsilon r} \quad (1)$$

Here, P is measured in mg CO_2 fixed (per square meter per hour), I is the intensity of direct and diffuse radiation falling on the foliage element, and ϵr and $1/K$ are related to the resistance of the leaf to diffusion of CO_2 and water vapor and to leaf temperature. We have linked our models for photosynthesis and plant moisture stress through these parameters.

Net assimilation, not gross photosynthesis, is measured in leaf chambers by the field research team. We define net photosynthesis (N) as equal to gross photosynthesis (P) less respiration (R_s). In our models for rate of respiration (R_s), we have used a generalization of the Q_{10} relation developed by Arrhenius (see Eyring and Urry, 1965):

$$\frac{d \ln(R_s)}{dt} = \mu/RT^2, \quad (2)$$

where R is the gas constant ($\text{cal gm}^{-1} (\text{°K})^{-1}$),
 μ is the "activation energy" (cal gm^{-1}), and
 T is the Kelvin temperature (°K).

Then, net assimilation is given by

$$N = \frac{1}{1/k + I\epsilon r} ([CO_2]I - R_s/k). \quad (3)$$

As we have noted already, much of the work we initiated in photosynthesis is now obsolete. We are now comparing unpublished models developed by Miller, Stewart, and Murphy, all of which may be superceded in part by a model describing photosynthesis, transpiration, and leaf temperatures of Lommen *et al.* (1971).

MOVEMENT OF WATER THROUGH THE SOIL-PLANT-ATMOSPHERE SYSTEM

The water relations model is summarized in Figure 1. Linkage to photosynthesis is through leaf resistance, leaf temperature, and their common dependence on radiation, air temperature, relative humidity, and wind speed. Water relations components receiving separate descriptions here are: the vertical flow of water through the soil, the uptake of water by roots, the changes in water deficits in the roots and leaves, and the loss of water by transpiration.

The profile now consists of 10 layers, each 30 cm deep; roots occur in the top four. Moisture content of each layer is calculated sequentially, beginning with the top layer. The moisture content of the lower boundary of the top layer becomes the new upper boundary for the next layer. The lowest layer is assumed to be in contact with the ground water table. Changes in moisture content of the upper boundary require special procedures to take account of evaporation, runoff, and infiltration during and after storms. Our simple method needs evaluation by field work before it can be judged to be fully satisfactory.

Vertical Flow of Soil Water

The general equation for the vertical liquid flow of soil water developed by Philip (1954, 1957) is given by Rose (1966) as

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial \theta}{\partial z} \right) + \frac{\partial k}{\partial z}, \quad (4)$$

where θ = moisture content at the point considered,
 z = vertical distance from some reference point,
 k = hydraulic conductivity of the soil,
 D = soil water diffusivity, and
 t = time.

This equation assumes

(1) That liquid water in the absence of differentially permeable membranes tends to move in response to gradients in hydraulic potential.

(2) Whatever the state of saturation, the volume of water crossing a unit area per unit time is proportional to the gradient of hydraulic potential in the direction of the flux.

Philip (1954, 1957) shows that if the dependence on water content of soil water suction and hydraulic conductivity are known for a given soil, the progress of moisture into and across a soil profile can be determined by solving equation (4).

Because exact solutions of this equation are not possible, numerical methods are used. Our strategy has been to approximate the flow equation with a finite difference form and to solve this numerically. The finite difference form is that used by Remson, Drake, McNeary, and Wallow (1965), which is

$$\frac{\theta_{t+1} - \theta_t}{\Delta t} = \frac{\left(\frac{D_j + D_k}{2}\right) \left(\frac{\theta_k - \theta_j}{\Delta z}\right) - \left(\frac{D_i + D_j}{2}\right) \left(\frac{\theta_j - \theta_i}{\Delta z}\right) + \frac{k_k - k_i}{2\Delta z}}{\Delta z}, \quad (5)$$

where θ = moisture content as before,
 t = time, and
 i, j, k = points in the soil profile.

Beginning with an initial profile of soil moisture contents, the computer program FILTER provides a numerical iterative solution of equation (5) to give a new moisture profile at the end of each time period.

Modification of Moisture at the Upper Soil Boundary

For soil water flow when there is no flux of water across the upper boundary, some procedure must be adopted for representing the change in moisture content of this boundary. Our method is simple but needs evaluation by field work before it can be judged satisfactory.

In conditions of no liquid flux across the soil surface, the loss from it is by drainage and evaporation.

To represent the drainage we have made the moisture content of the surface boundary at time $t+1$ the average of its content at time t and the content of the second boundary layer at $t+1$.

To represent evaporation, we have first used this average moisture content and the depth of the first layer to calculate the moisture content of that layer. Then the potential evaporation from the first layer has been calculated using Penman's (1948) combination method. In general form, this is

$$E = [\Delta R_n + \beta E_a] / \Delta + \beta,$$

where E = potential evapotranspiration,
 Δ = the slope of the saturation vapour pressure curve at the bulk air temperature T_a ,
 R_n = net radiation at soil surface,
 β = the psychrometric constant, and
 $E_a = f(u) [e^{\circ}(T_a) - e_a]$,
 where $e^{\circ}(T_a) - e_a$ = the saturation deficit at the bulk air temperature,
 e_a = air vapour pressure, and
 u = windspeed.

The modified moisture content of the boundary layer is then expressed as

$$\theta_{t+1}^1 = \left[\left(\frac{\theta_t^1 + \theta_{t+1}^2}{2} \right) \Delta z - KE \right] / \Delta z, \quad (6)$$

where θ = moisture content
 superscripts refer to soil boundary layer, ¹ representing the surface,
 K = proportionality constant, and
 ΔZ = thickness of first soil layer.

Water Uptake by Roots

We assume with Gardner (1960) and Cowan (1965) that in the neighborhood of a root, water moves in response to gradients in matric potential according to a diffusion-type flow equation. In cylindrical coordinates, this is

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \cdot \frac{\partial}{\partial r} (rD \frac{\partial \theta}{\partial r}), \quad (7)$$

where θ is the volume concentration of soil water,
 D is the diffusivity,
 t is the time, and
 r is the radial distance from the root.

We also assume that the flow of water is radial (perpendicular to a single root), and that the root behaves as an infinitely long cylinder with uniform radius and water-absorbing properties. The assumed initial and boundary conditions are (Gardner, 1960):

$\theta = \theta_0$, uniformly throughout the medium and corresponding to a soil potential or suction τ_0 at the soil-root interface sufficient to maintain a constant flow of water to the plant. Also,

$$\tau = \tau_0$$

$$t = 0$$

$$q = 2\pi aD \left(\frac{d\theta}{dr} \right) = 2\pi ak \left(\frac{d\tau}{dr} \right)$$

where q is the rate of water uptake by the root (volume of water per unit length of root per unit time),

k is the capillary conductivity of the soil, and
 a is the radius of the root.

Following Gardner, we assume that the diffusivity, D , and conductivity, k , are constant and hence proportional to each other. In fact, however, both vary greatly with soil water content and soil potential. This unrealistic assumption, however, does permit a closed form solution to (7),

$$\Delta \tau = \frac{q}{4\pi k} \left(\ln \frac{4Dt}{r^2} - \gamma \right), \quad (8)$$

where $\gamma = 0.5772\dots$ (Euler's constant).

In the present state of development of this submodel, the root is regarded merely as a sink for soil water (of strength q ml per day per unit length). As water moves from the soil to the root, the soil moisture potential changes, affecting internal plant water deficits. Although at present we do not attempt to keep track of the amount of water that moves through the tree, a submodel that describes water fluxes across unit areas of roots, stems, and branches is an important objective in our primary production modeling.

Several possible improvements of the present model have been considered. A very simple one adopts the approach used in obtaining solutions to (1), where D is not a constant but instead a function of soil water potential and water content. We have decided, however, that it may be more fruitful first to look into the distribution of tree roots. In Douglas-fir, water uptake is perhaps better modeled as if it occurred across the outer surface of a thin cylindrical slab or hemisphere rather than through a large number of linear roots, as in the Gardner (1960) model, which we now follow. This change clearly would require a formulation somewhat different from equation (7).

Internal Plant Water Deficits

In developing a model to describe these changes, two assumptions were made:

(1) The driving forces for water movement inside the tree are gradients of water potential.

(2) For water movement from leaves to air, the driving forces are not wholly determined by gradients of water potential.

Assumption (2) is made explicit by the model for transpiration that is described below.

Two simple, simultaneous ordinary differential equations have been used to represent changes in root and leaf water stress.

$$\frac{d\psi_R}{dt} = K_1 (\psi_S - \psi_R) + K_2 (\psi_R - \psi_L) \quad (9)$$

$$\frac{d\psi_L}{dt} = K_2 (\psi_R - \psi_L) + K_3 (\text{TNSP}), \quad (10)$$

where ψ_R = root moisture stress,
 ψ_S = soil water potential,
 ψ_L = leaf moisture stress,
 K_1 = constant of proportionality,
 K_2 = permeability of whole stem,
 K_3 = constant of proportionality, and
 TNSP = transpirational loss.

Equations (9) and (10) are integrated numerically for each crown layer to give new values for root and leaf moisture stress. These operations are carried out in subroutine UPTAK.

This submodel is, frankly, a very provisional stopgap. As we have emphasized already, we intend to develop a model that will describe the flow of water in the vascular system of a tree from the roots to the leaves. This flow is interpreted as a response to a gradient of potential maintained by loss of water from the leaves (cohesion theory). Rate of water movement will depend on resistance to flow, and this clearly is related to the anatomy of the vascular system. A possible first approximation might be a relation like (1), which combines continuity with response to a matric potential in an isotropic medium. A better model will take into account the preferred directions of flow inside the tree.

Loss of Water through Transpiration

Transpiration from plant leaves involves water vapor transfer along a concentration gradient from the evaporating surfaces within the leaf, to the natural leaf surface, and then from leaf surface to bulk air.

In the second part of the gradient, we assume that latent heat flow encounters the same boundary layer resistance as sensible heat flow. This assumption allows the use of the equation described by Slatyer (1967):

$$TNSP = \frac{(C_i - C_a)}{r_a} = \frac{273 \rho_v (e_i - e_a)}{RT r_a}, \quad (11)$$

where E = evaporation in $\text{gcm}^{-1}\text{sec}^{-1}$,

$\Delta C = C_i - C_a$ = difference between water vapor concentration of the air at the leaf surface and in the bulk air,

$\Delta e = e_i - e_a$ = corresponding difference in vapor pressure,

P = atmospheric pressure in the same units as e ,

ρ_v = density of water vapor in air,

r^v = diffusive resistance to water vapor transfer in air,

T^a = leaf temperature, and

R = gas constant.

In normal transpiration, the evaporating surfaces are inside the leaves, so an internal resistance, r_i , is added to the external resistance. Equation (11) becomes

$$TNSP = \frac{273 \rho_v}{RT} \frac{(e_w - e_a)}{RL}, \quad (12)$$

where $RL = r_a + r_i$ and

$e_w = e_w^a$ = saturation vapor pressure.

Besides assuming sensible and latent heat flow to be analogous, other assumptions implicit in equation (12) are:

(1) Convective transfer of water vapor occurs along gradients of water vapor concentration from leaf to air and vice versa.

(2) The vapor pressure at the evaporating surface is that of saturated air.

(3) r_a remains constant.

Calculation of Leaf Diffusive Resistance

In Douglas-fir, leaf diffusive resistance is assumed to vary with leaf moisture stress according to

$$RL = a + b \cdot \ln(\psi_L), \quad (13)$$

where $a = r_a$ + cuticular resistance and

b = constant of proportionality.

Leaf resistance is calculated for each crown layer at each time period.

Our submodels for transpiration, leaf temperature, and stomatal aperture and closure are also very provisional. As we indicated above, a number of models describing canopy processes have been developed recently. Those of Miller and Lommen, *et al.* (1971) are being studied to determine the degree to which they may be applied to the Douglas-fir system. Miller's model describes primary production in a canopy of red mangrove, a broadleaved evergreen species. We have reason to suspect important differences in stomatal behavior and leaf temperature response to infrared radiation in the two species. In most respects, however, these new models seem to generalize readily to our system, and we intend to substitute them, with suitable modifications, for our existing submodels.

COMPUTER PROGRAMS

Our computer programs are best summarized by the series of simplified flow charts that follows this description.

OUTPUT

All system variables are calculated at one-hour intervals. Normal runs are for 20 hours (from 2 a.m. to 4 p.m.), but one run of 72 hours has been completed. Some characteristic results are exhibited in Figures 2-5.

In Figure 2, diffuse, direct, and total radiation are positive after 4 a.m. and rise to a maximum at noon. Direct radiation declines somewhat at 1 p.m. but increases at 2 p.m., after which it and diffuse radiation decrease steadily until nightfall, at 9 p.m. Net assimilation in the top layer of the canopy follows total radiation closely. In the lowest canopy layer, where light intensity is much reduced, net assimilation is negative from midmorning until midafternoon, when air temperature, leaf temperature, and rate of respiration are high. We wish to emphasize that we have no direct estimates of net assimilation or respiration in several layers of a Douglas-fir canopy. Accordingly, differences between net assimilation in the top and bottom layers may be exaggerated.

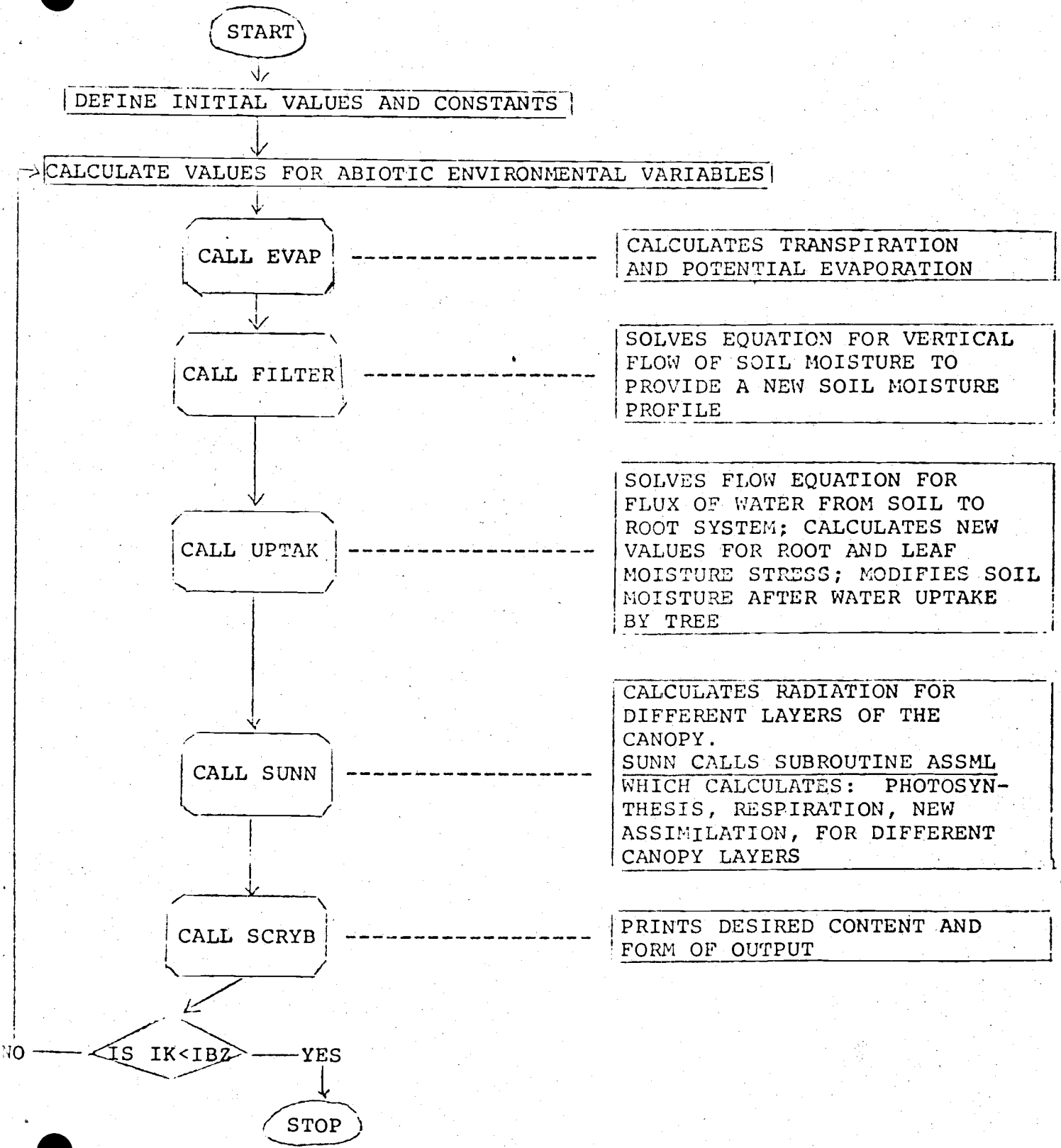
Changes in soil moisture in several soil layers are shown in Figure 3. Moisture in the top layer of the soil is reduced, but uptake by the root system of trees and evaporation from the soil surface increase during the day. During the night, uptake and evaporation are reduced, and a net upward movement of soil moisture into the top layer takes place.

The march of temperature, leaf resistance, and leaf temperature are shown in Figure 2. All increase to a maximum shortly after noon and decline steadily in the afternoon. Similar patterns are exhibited by root and leaf moisture stress in Figure 3.

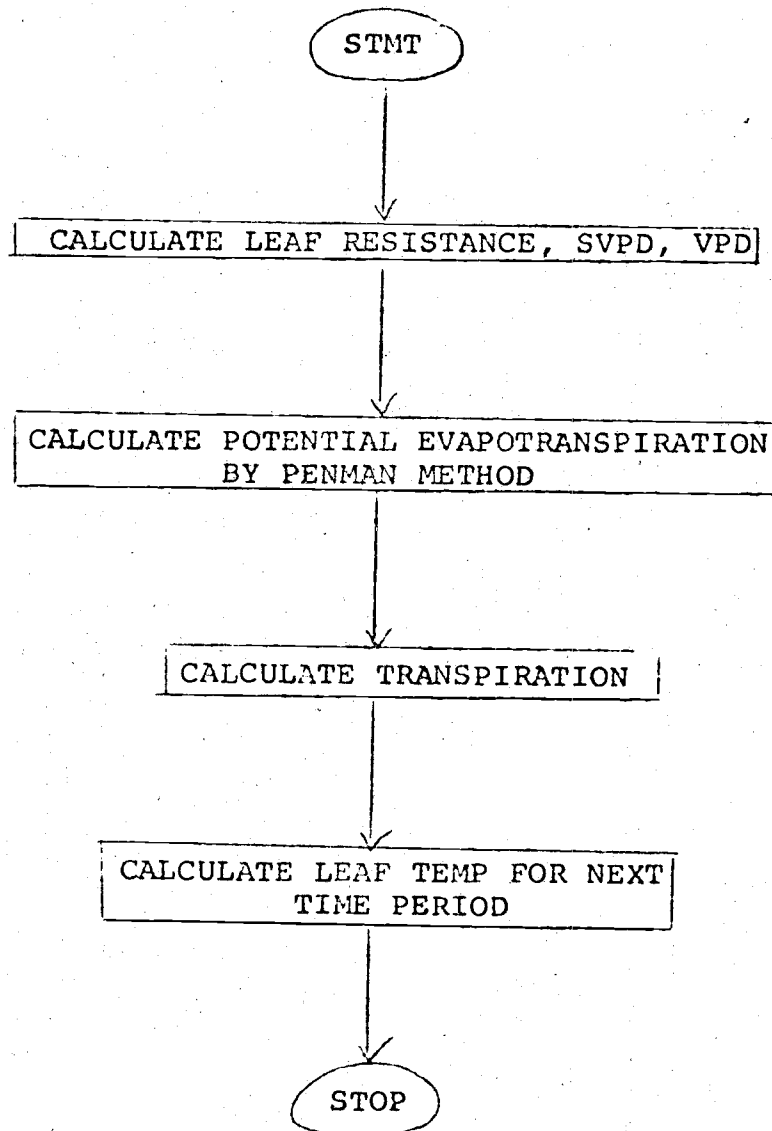
OTHER SUBMODELS

A new model that describes movement of nutrient ions from the forest floor through the soil is being developed with members of the Soils Group. Cations,

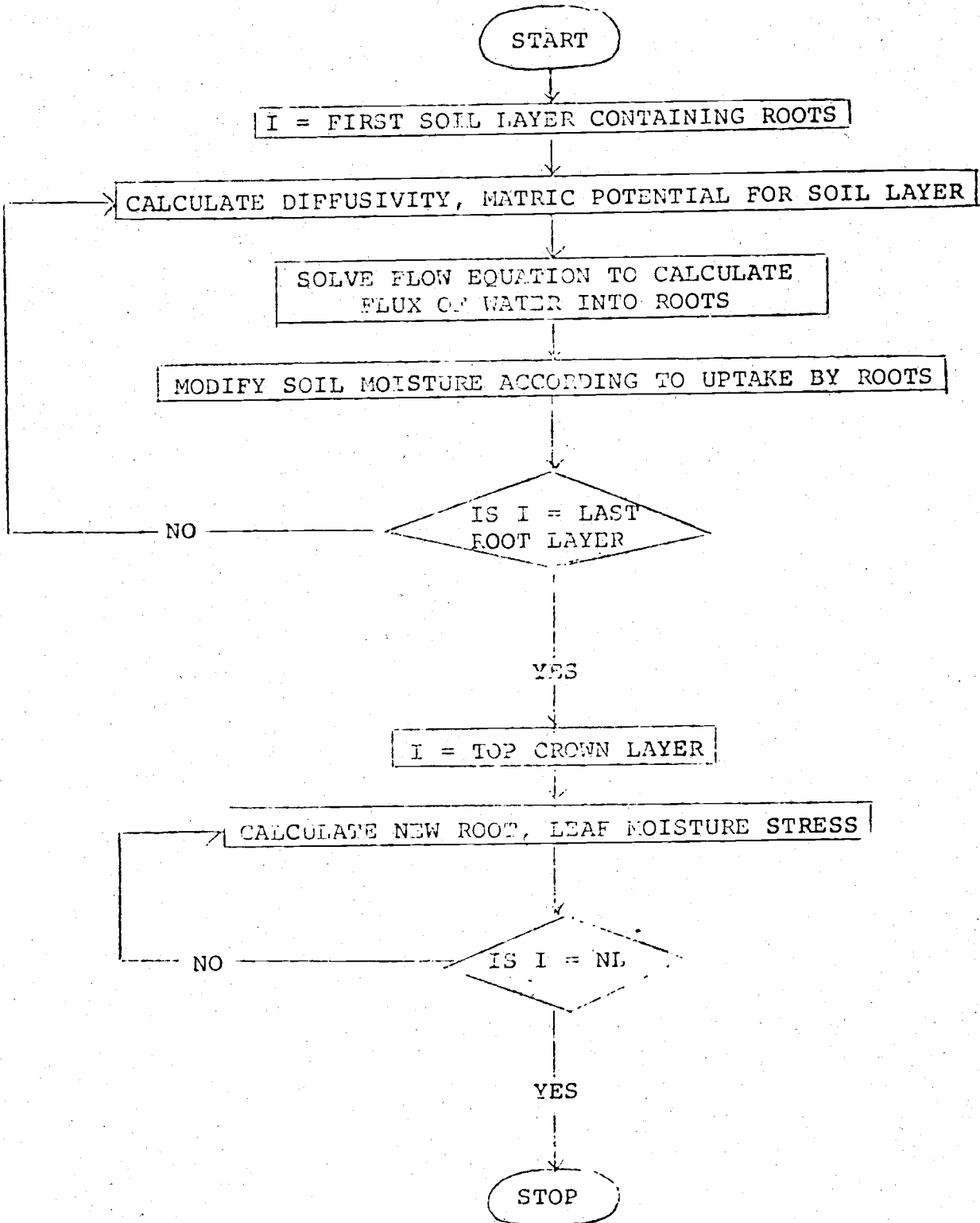
Main Program



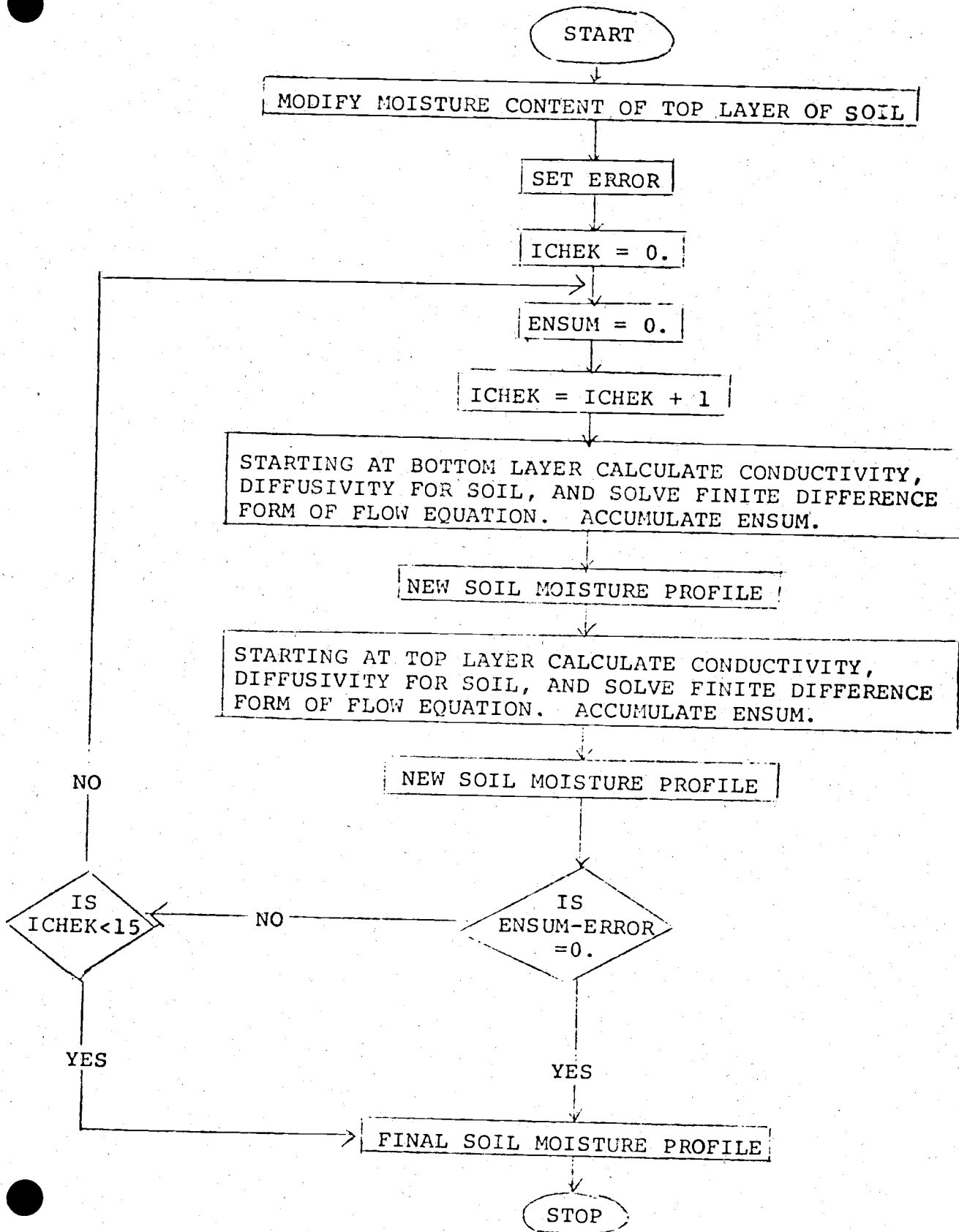
SUBROUTINE EVAP



SUBROUTINE UPTAKE



SUBROUTINE FILTER



released from the forest floor litter and humus together with bicarbonate ions, are transported in the water moving through the several layers of the forest soil. These layers are the components of the soil moisture and wetting front submodel described above. Within each layer, cations (1) may be adsorbed on the clay or organic particles that constitute the exchange complex, (2) be taken up by roots of trees or subordinate vegetation, or (3) pass through to the next layer. Provision also is made for release of cations from the exchange complex as hydrogen ions are discharged into the soil solution by roots. The behavior of potassium, calcium, and ammonium ions is being considered separately.

In consultation with our Plant Physiology Group and with Dr. Philip C. Miller, of the Tundra Biome, we also are developing a model that describes translocation of carbohydrates and protein synthesis in the tree. Depending on the availability of ammonium and other nutrient ions, part of the carbohydrate pool provided by photosynthesis is converted to protein and subsequently to new leaves and other tissues, or is shunted to storage and the formation of wood. Dr. Kenneth Turnbull has developed a growth model that describes diameter and height increase in trees, which we believe can be coupled with this translocation submodel.

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