
A Simulation Model of the Role of Belowground Dynamics in a Florida Pine Plantation

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ABSTRACT. A model of a 29-yr-old slash pine (*Pinus elliottii*) plantation on a typical flatwoods site in north Florida evaluates the importance and magnitude of belowground processes in a forest. The model, which comprised 22 differential equations, most of them nonlinear, was parameterized with three sets of climate data and validated with measurements of soil moisture, soil CO₂ evolution, root production, and root biomass.

Simulated gross primary productivity (GPP) in a year with normal rainfall was 29.5 Mg ha⁻¹ yr⁻¹ (C), which is consistent with measurements of GPP in a variety of north Florida sites. In the model, one-third of GPP was translocated to the roots, where more than 75% was spent on respiration. Root respiration varied little among the three simulations. Root turnover times were more variable. In the low rainfall simulation, root turnover time was 21% longer than in the other two simulations, which were nearly the same. Simulated P concentration in the soil and plant had much less effect on plant processes than soil moisture did. General agreement of transpiration rates with other studies indicated that evapotranspiration is the only major water loss in slash pine flatwoods. Simulated water-borne P losses from the site were therefore insignificant. Simulated foliage biomass varied considerably during the year, decreasing to less than half its maximum biomass during an annual cycle in one of the simulations.

Comparison of the few sites with comparable estimates of C fixation and allocation suggests that 22%–43% of C fixed is used by roots, and that the proportion allocated to roots may be higher on nutrient-poor sites and sites with low temperatures. FOR. SCI. 37(1):397–438.

ADDITIONAL KEY WORDS. *Pinus elliottii*, carbon budget, water budget, P budget, root dynamics, carbon allocation.

STUDIES OF ENERGY FLOW AND NUTRIENT CYCLING in terrestrial ecosystems usually concentrate on aboveground structure and function, primarily because working with belowground processes is so difficult. It has long been clear, however, that determining the magnitude of belowground material and energy flows and elucidating the physical and biological factors that control them are critical not only to achieving a basic understanding of ecosystem function but also to formulating meaningful long-term management guidelines. This paper presents an ecosystem-level model that summarizes our current understanding about interactions among carbon (C), water, phosphorus (P), and major environmental controls in a forest. The purpose of the model is to estimate the relative importance of belowground processes to the functioning of a mature stand and to identify research areas that are particularly important for further elucidation.

The model simulates above- and belowground processes for 1 year in a mature

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slash pine (*Pinus elliottii*) plantation on a typical, poorly drained coastal plain (flatwood) site in Florida. Slash pine plantations on flatwood sites are common in southeastern United States and comprise 15% of the land area in Florida. Sandy, nutrient-poor soils and low plant species diversity are characteristic of both plantations and natural flatwoods, suggesting that the plantations closely resemble the ecosystems they have replaced.

The relative simplicity of slash pine plantations, both above- and belowground, has made them ideal subjects for evaluating belowground processes and for model development. At our main study site, a 29-yr-old plantation in Bradford County, FL (29°N,82°W), the canopy is slash pine, the shrub layer consists primarily of saw palmetto (*Sereona repens*), and there is an herbaceous layer of scattered grasses and forbs. The Ultic Haplaquod soils (Pomona and Wauchula series: sandy, silicious, hyperthermic) contain two distinct mineral layers, a shallow A horizon and an E + Bh horizon, underlain by a kaolinitic clay (Btg) horizon at approximately 1 m. Patterns of biomass accumulation, nutrient storage, and soil and root respiration in slash pine plantations have been described (e.g., Gholz and Fisher 1982, Gholz et al. 1985a, Ewel et al. 1987a, 1987b), and a model that accurately reproduces aboveground changes in biomass over a 30-yr rotation has been developed (Golkin and Ewel 1984).

The model described in this paper focuses on C, P, and water flows during a 1-yr period in a mature plantation (Figure 1). We elected to include P rather than N in the model both for ecological reasons and for ease of modeling. Both nutri-

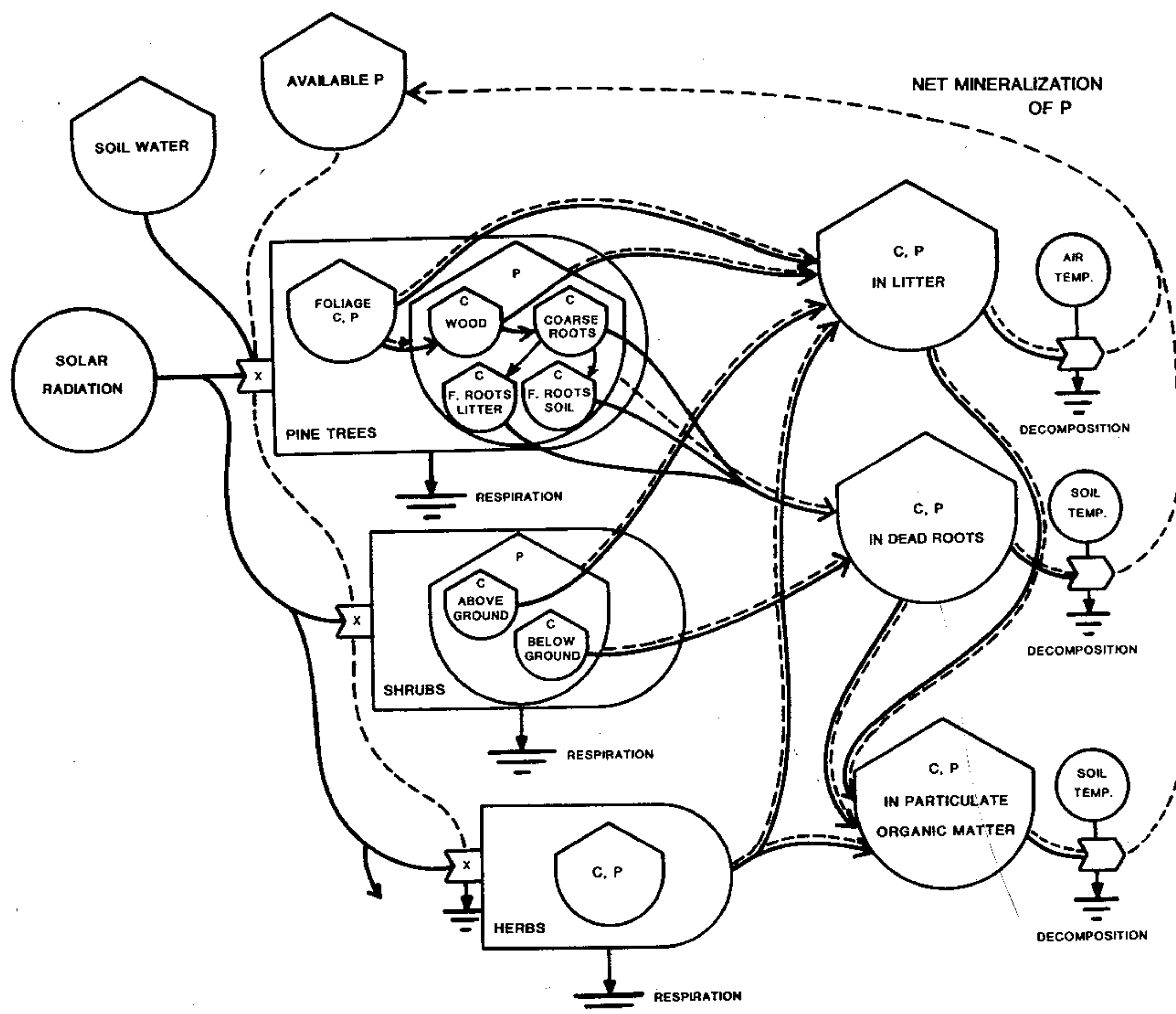


FIGURE 1a. Interactions between C (solid lines) and P (dashed lines) in the model. Equations for state variables are listed in Table 1; further details are available in the appendix.

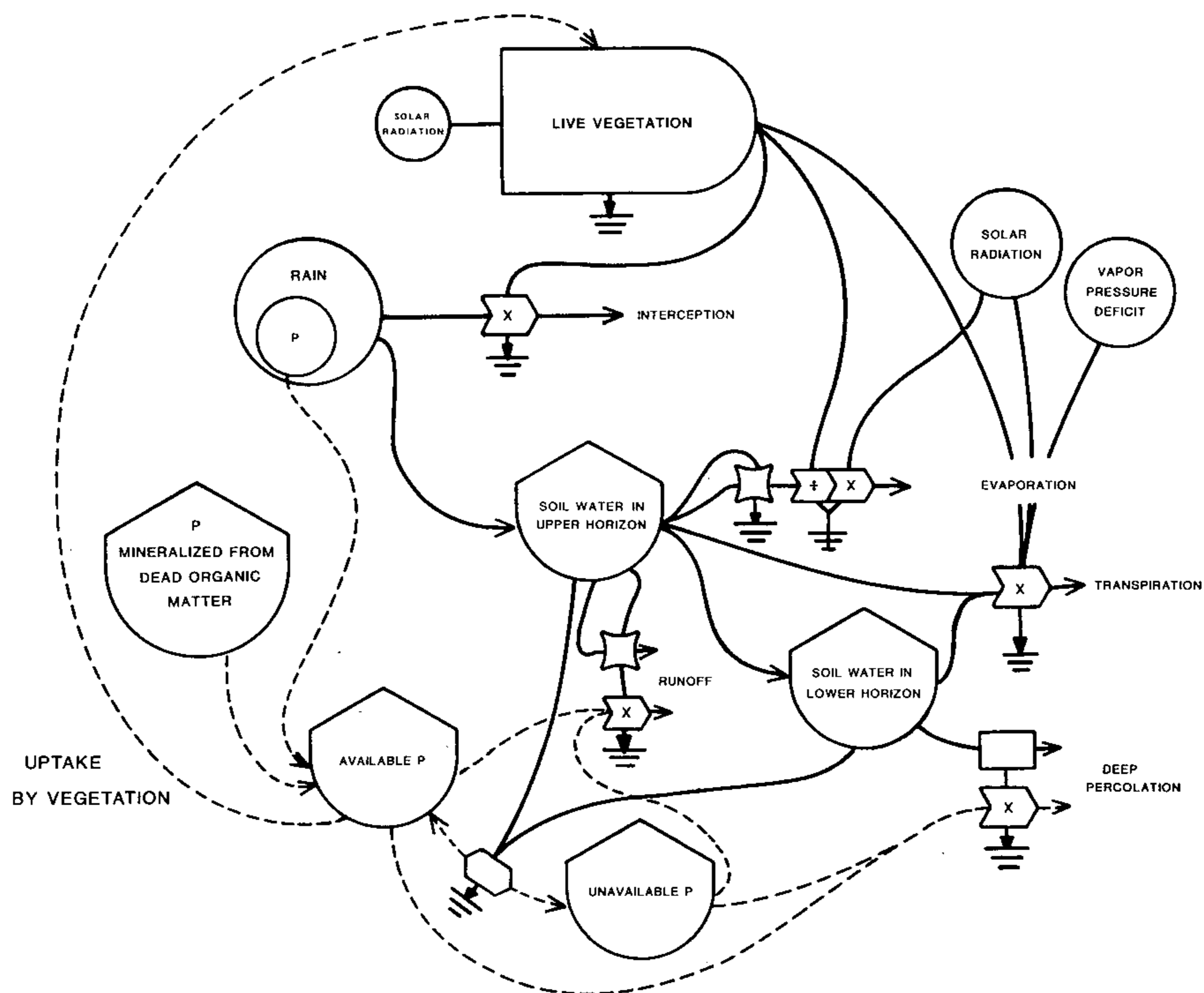


FIGURE 1b. Interactions between water (solid lines) and P (dashed lines) in the model. Equations for state variables are listed in Table 1; further details are available in the appendix.

ents are considered critical to slash pine growth, and response to fertilization with one or the other may vary from site to site depending on wetness and the capacity of the soil to hold P in less soluble forms (Pritchett and Comerford 1983). Focusing on N rather than P would require modeling the dynamics of at least two active inorganic forms in addition to N fixation and denitrification. Although these processes are moderately well understood, there are insufficient data to parameterize this cycle adequately. Modeling both N and P would require formulations for N-P interactions as well, introducing even more uncertainty. Consequently, we selected P, for which we have a larger proportion of useful data.

Time-varying, simultaneous differential equations were driven by three climate data sets, each containing weekly averages for 1 year. The data sets spanned the normal range of variation in rainfall in north Florida during the years for which complete climate data sets were available. We were particularly constrained in our selection of data sets by the fact that comparable solar radiation data were not available before July 1967. Many of our field measurements were made during a year of high rainfall (1407 mm). Although higher rainfall was recorded twice during the previous 10 yr, we considered this a rainy year because of unusually high rainfall in the spring months. Data for a year of average rainfall (1318 mm) and a dry year (837 mm) were also used. In addition, the impact of fertilization was tested by adding 50 kg/ha to the available P pool at the beginning of one of the simulations.

TABLE 1.

General formulations of the differential equations that comprise the model. Mathematical formulations for each term are listed in Appendix A-1. Initial conditions for each state variable are listed in Appendix A-2.

Q_1	= Pine foliage
dQ_1/dt	= Gross primary productivity–Respiration–Translocation to stem and branches–Litterfall
Q_2	= Pine stem and branches
dQ_2/dt	= Translocation from foliage–Translocation to roots–Respiration–Litterfall
Q_3	= Coarse pine roots (>10 mm)
dQ_3/dt	= Translocation from stem–Translocation to fine roots in soil–Translocation to fine roots in litter–Respiration–Mortality
Q_4	= Fine pine roots (<10 mm) in mineral soil
dQ_4/dt	= Translocation from coarse roots–Respiration–Mortality
Q_5	= Fine pine roots (<10 mm) in litter layer
dQ_5/dt	= Translocation from coarse roots–Respiration–Mortality
Q_6	= Shrubs
dQ_6/dt	= Gross primary productivity–Respiration–Translocation to roots–Litterfall
Q_7	= Shrub roots
dQ_7/dt	= Translocation–Respiration–Mortality
Q_8	= Herbs
dQ_8/dt	= Gross primary productivity–Respiration–Mortality
Q_9	= Litter
dQ_9/dt	= Pine foliage litterfall + Pine wood litterfall + Shrub litterfall + Herb litterfall (half)–Decomposition–Comminution
Q_{10}	= Dead roots
dQ_{10}/dt	= Coarse root mortality + Soil fine root mortality + Litter fine root mortality + Shrub root mortality–Decomposition–Comminution
Q_{11}	= Dead particulate soil organic matter
dQ_{11}/dt	= Herb litterfall (half) + Litter comminution + Dead root comminution–Decomposition
Q_{12}	= Phosphorus in pine wood
dQ_{12}/dt	= Uptake–Net translocation to foliage–Litterfall–Root mortality
Q_{13}	= Phosphorus in pine foliage
dQ_{13}/dt	= Translocation from wood–Translocation to wood–Litterfall
Q_{14}	= Phosphorus in shrubs
dQ_{14}/dt	= Uptake–Litterfall–Root mortality
Q_{15}	= Phosphorus in herbs
dQ_{15}/dt	= Uptake–Litterfall
Q_{16}	= Phosphorus in litter
dQ_{16}/dt	= Litterfall + Mortality of fine roots in litter–Comminution–Decomposition–Phosphorus leached away in runoff
Q_{17}	= Phosphorus in dead roots
dQ_{17}/dt	= Pine root mortality + Shrub root mortality–Decomposition–Comminution
Q_{18}	= Phosphorus in soil particulate organic matter
dQ_{18}/dt	= Litter comminution + Dead root comminution + Herb litterfall–Decomposition
Q_{19}	= Available inorganic phosphorus
dQ_{19}/dt	= Throughfall + Release from unavailable P + Litterfall decomposition + Particulate organic matter decomposition + Dead root decomposition–Plant uptake–Conversion to unavailable P–Loss with runoff–Loss to deep aquifer
Q_{20}	= Unavailable inorganic phosphorus
dQ_{20}/dt	= Release from available–Conversion to available P–Loss with runoff
Q_{21}	= Soil water in upper layer
dQ_{21}/dt	= Throughfall–Evaporation–Pine transpiration–Shrub transpiration–Herb transpiration–Runoff–Percolation to lower water layer
Q_{22}	= Soil water in lower layer
dQ_{22}/dt	= Percolation from upper water layer–Pine transpiration–Shrub transpiration–Deep percolation

MODEL STRUCTURE

This model integrates current concepts about how three major cycles in a slash pine forest operate and interact. Our goal at this stage was to reproduce monthly and seasonal changes within a mature stand for a year. We hoped that this model would identify major data gaps and suggest ecological and physiological relationships that might not be obvious from field studies alone. Our strategy has been to alternate between simulating models and conducting field studies with the long-term goal of developing a model that simulates changes in biotic and abiotic compartments throughout a full rotation, in order to understand ecological implications of management practices and climate change.

The model consists of 22 differential equations, many of them nonlinear, that were solved using CSMP (Continuous Simulation Modeling Program) with the trapezoidal method of integration and a time-step of 0.001 yr. The state variables and major interactions are shown in Figure 1; Table 1 describes the rates affecting each variable in greater detail. Each equation was formulated to incorporate as mechanistic a representation as possible of the component processes. Consequently, the limits to production, transpiration, and other flows are imposed by interactions among state variables and not by maximum rates established by the modeler. The advantage to this approach is realism; the disadvantage is that many of the interactions among state variables are not well understood, and the formulations used in the model must be treated as hypotheses to be tested in further field work. The model was developed from an earlier model that simulated changes in aboveground C and P storages in trees, understory, and forest floor, as well as the basic processes in the hydrologic cycle, over a 30-year rotation (Golkin and Ewel 1984). The earlier model was modified by substantially expanding the belowground portion and rewriting formulations for photosynthesis, respiration, and transpiration based on more recent research. Run time was shortened to 1 yr, so the model described in this paper simulates annual processes in a mature (29-yr-old) stand only.

When simulating differential equations, the time step chosen to approximate instantaneous change should be smaller than the smallest rate constant. However, rounding error increases with number of time steps. The time step we chose, 0.001 yr, is smaller than most of our rate constants and allows us to examine seasonal (but not diurnal) changes.

Our model was first run with site-specific weather data. Annual rates of soil C losses (Ewel et al. 1987a), litterfall and litter decomposition rates (Gholz et al. 1985b), and measurements of C and P contents (Gholz and Fisher 1982, Gholz et al. 1986) were used to calculate rate constants and initial conditions. The model was then fine-tuned with weather data from the normal rainfall year. Because the site is a mature plantation, and most aboveground components have stopped accumulating biomass, constants controlling production, translocation, and respiration rates were adjusted slightly so that final values of all live biomass state variables were within 5% of initial values for simulation of the normal rainfall year only. Seasonal changes in the normal rainfall year simulation were not constrained, nor were final values in the other simulations. The simulations with weather data from the dry year and with added fertilizer were conducted primarily as sensitivity analyses.

The differential equations are listed in Appendix A-1. The initial value of each

rate can be calculated using these equations, the initial conditions of the state variables (Appendix A-2), the appropriate values of the functions (Appendix A-3), the initial values of the forcing functions (Figures 2 and 3), and the rate constants (Appendix A-4).

FORCING FUNCTIONS

Average daily soil (5 cm) and air temperatures, weekly rainfall, average daily relative humidity, and belowground biomass and productivity data were collected at the site from March 1983 to March 1984. Data for the dry year (March 1977 to March 1978) and the normal rainfall year (March 1967 to March 1968) were obtained from the University of Florida's Agricultural Experiment Station in Gainesville, FL; Dr. E. Farber (pers. comm.) provided solar radiation data for part of 1967 from another station near Gainesville (Table 2). Weekly averages for all meteorological variables were provided to the CSMP function generator, which calculated values at each time step by linear interpolation. We did not use daily values because many of them were approximated, and not all were taken at the same site. We felt that weekly averaging would smooth the discrepancies sufficiently.

Relative humidity and air temperature were used to calculate vapor pressure deficit (VPD). Soil temperatures ($^{\circ}\text{C}$) were determined from a regression equation relating air temperatures (T_a) and soil temperatures (T_s) measured during the 1-yr study period ($r^2 = 0.83$):

$$T_s = 8.71 + 0.533 * T_a$$

The three sets of weather data differed not only in average conditions but in seasonal patterns as well. Although total rainfall in 1977 was near the 70-year average, early summer and early winter were wetter than normal, and spring and fall were drier than normal (Figure 2). Rainfall differed most among the three simulations in 3 months: May, when a prolonged spring drought can slow rapidly

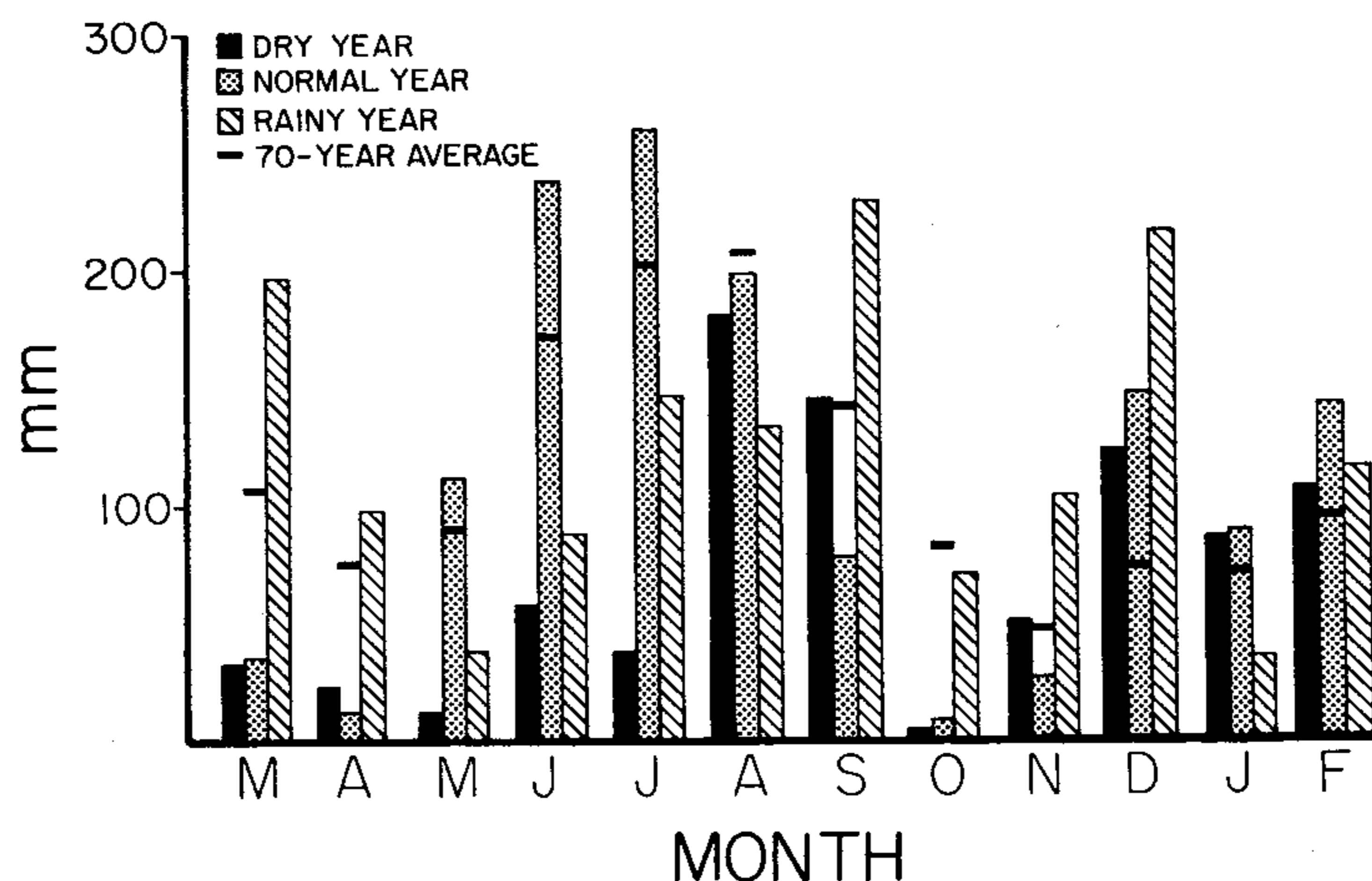


FIGURE 2. Monthly rainfall during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm. Vertical bars over the center column indicate long-term (70 yr) average rainfall amounts.

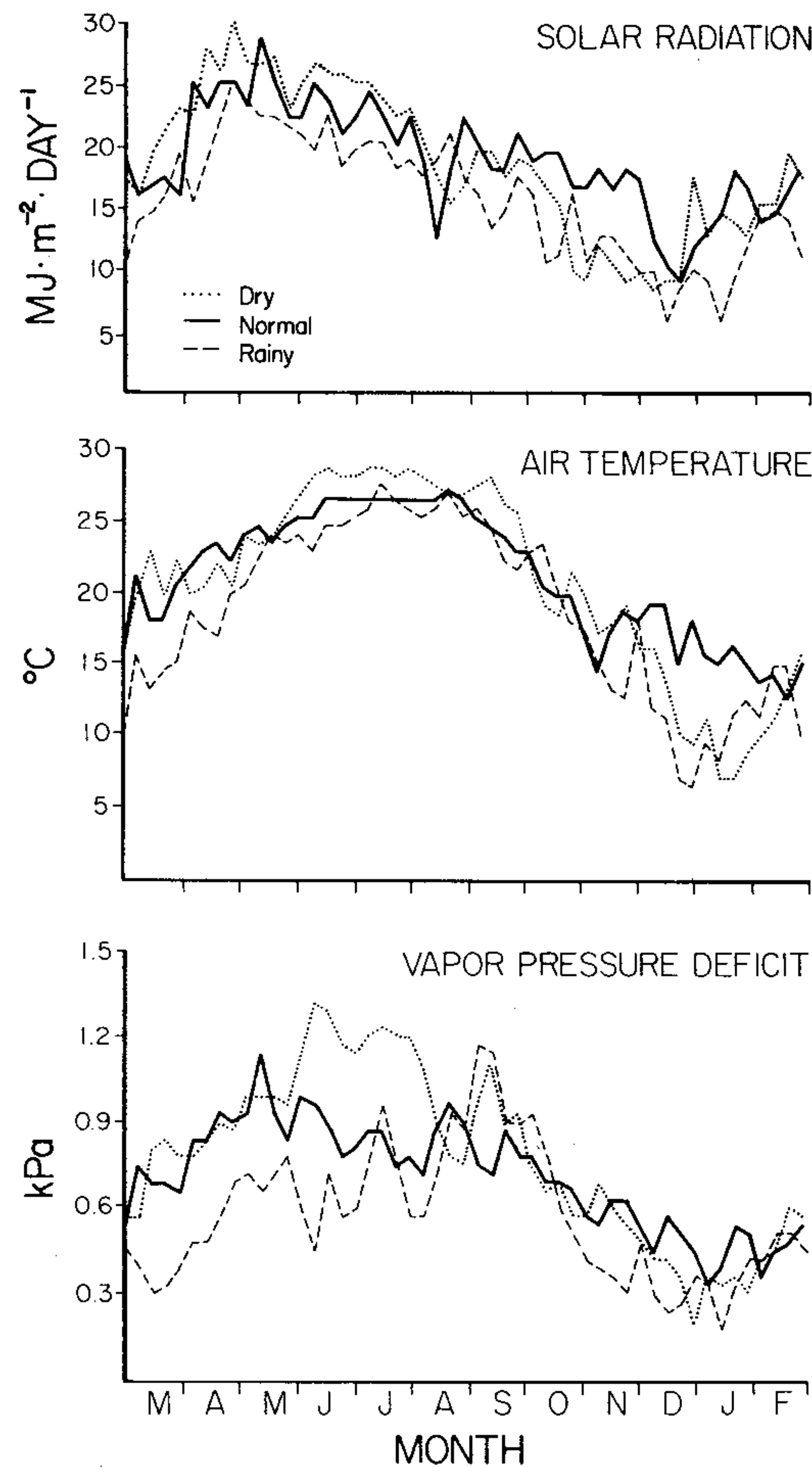


FIGURE 3. Patterns of change in total solar radiation, air temperature, and vapor pressure deficit during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

increasing productivity rates; July, when lack of rain is accompanied by greatly increased solar radiation, temperature, and VPD; and September, when additional rainfall may extend the growing season. Differences in solar radiation among the three years were most pronounced in mid-summer and late fall (Figure 3). Solar

TABLE 2.

Annual rainfall, total solar radiation, average air temperature, and average vapor pressure deficit during each of three simulations with different sets of climate data.

	Dry year (1977)	Normal year (1967)	Wet year (1983-84)
Rainfall (mm)	837	1318	1407
Solar radiation (MJ m ⁻² yr ⁻¹)	6955	7092	5847
Temperature (°C)	21.2	21.5	19.0
Vapor pressure deficit (kPa)	0.79	0.73	0.59

radiation for the rainy year simulation was consistently low for the entire year. Air temperatures in the three simulation years differed most in spring, when the rainy year was cooler than the other two, and in early winter, when the normal year was warmer (Figure 3). Differences in VPD among the three simulation years were much more dramatic (Figure 3), reflecting the exponential relationship between VPD and air temperature. VPD was markedly low in the first 3 months of the rainy year simulation when temperatures were also low. It was particularly high in the dry year simulation during the summer, when temperatures were higher and rainfall less than in the other two simulation years.

We would have liked to have used a set of long-term weekly averages for our average year simulation rather than the 1977 data set. However, solar radiation data were available only from mid-1967, making it impossible to calculate such averages. The fact that the differences among the three sets of weather data occurred during the critical parts of the growing season gives us confidence that we have examined a realistic spectrum of responses.

CARBON STORAGE AND FLOWS

Three major plant groups were included in the model: pine trees, shrubs, and herbs. In all cases, biomass is expressed as C, which we assumed to be 50% of dry weight. Pine tree biomass was separated into foliage, stems, and branches, coarse roots (>10 mm in diameter), and fine roots, which we defined as all roots <10 mm. Fine roots were further divided into those in the litter layer and those in the mineral soil. Many consider fine roots to be no larger than 1 mm in diameter (e.g., *Pinus radiata*; Santantonio and Santantonio 1987). We have chosen to define a broader range, because although we have biomass and turnover estimates for roots in several smaller diameter categories down to <1 mm (Gholz et al. 1986), we do not have respiration and translocation data for each category. Most roots in the litter are in fact <1 mm in diameter, so the model simulates the carbon dynamics of very fine roots in the litter by default. Not subdividing fine roots in the mineral soil may damp the simulated seasonal biomass fluctuations, such as are observed for smaller diameter roots, but roots <1 mm in this lower layer comprise only 22% of the biomass of all roots <10 mm. The total carbon fluxes in our model should therefore characterize the pool of <10 mm roots adequately.

Shrub biomass was divided into one aboveground pool and one root pool. Herbaceous vegetation was aggregated into one pool.

Gross Primary Productivity

Pine trees—GPP in pine trees was simulated as a function of total incident radiation (MJ/m²), soil water availability, P content of the foliage, and biomass (C content) of the foliage. The formulation for the effect of light (Odum 1983) was:

$$GPP \approx \frac{S}{1 + (K_2 * Q_1)}$$

where

S = incident sunlight at the top of the canopy

K_2 = rate constant (estimated) related to proportion of incident sunlight utilized

Q_1 = pine foliage biomass (C).

If biomass remains constant, *GPP* is proportional to *S*. However, the rate of increase of *GPP* decreases as biomass increases.

Hydraulic conductivity data suggested that soil water availability might begin to limit *GPP* below 45% of capacity in the upper soil layer (A horizon, 12.6 cm deep) and below 63% of capacity in the lower soil layer (E + Bh horizon, 12.6–100 cm). Because the lower layer holds so much more water than the upper layer and its water potentials are generally higher, and because it contains a preponderance of coarse roots as well as the tap root, we assumed that less than 10% of the effect of soil water on pine *GPP* could be attributed to the top soil water layer, and more than 90% of the effect was attributed to the bottom soil water layer.

The effects of foliage P on *GPP* were expressed by a Michaelis-Menten formulation, using the ratio of P to C rather than the absolute amount:

$$GPP \approx \frac{Q_{13}/Q_1}{K_3 + (Q_{13}/Q_1)}$$

or

$$\frac{Q_{13}}{(K_3 * Q_1) + Q_{13}}$$

where

Q_1 = pine foliage biomass (C)

Q_{13} = P content of pine foliage

K_3 = half-saturation constant, estimated

Finally, *GPP* is also proportional to pine foliage biomass.

The magnitude of *GPP* is difficult to estimate because of unresolved uncertainties in determining daytime respiration rates. Our *GPP* estimates early in model development were based on *in situ* measurements with an infrared gas analyzer in an old second-growth pine forest during a dry year, and they were calculated with the assumption that daytime and nighttime foliage respiration rates were equal (Golkin 1981). The aboveground *GPP* rate we used in this model was higher, because the rate based on the earlier study was too low to account for the rates of belowground productivity and respiration that we measured in subsequent studies. The annual pine *GPP* rate was therefore the sum of the amount of C that should be translocated to meet the measured demands of belowground biomass (Gholz et al. 1986, Ewel et al. 1987b), litter fall (Gholz et al. 1985b), and estimated aboveground respiration. The value of the rate constant *K* was calculated by dividing the annual estimate of *GPP* by the equation for *GPP*, with each state variable and forcing function set equal to its initial condition.

Shrubs and herbs—Calculation of *GPP* in shrubs differed only slightly from the calculation for pines. The light relationship incorporated the shading effect of pines by adding a simple function (Beer's Law):

$$e^{-F_5}$$

Because of a greater concentration of shrub roots in the top soil horizon, we

assumed that each soil layer would have the same impact on *GPP*. Finally, *GPP* was proportional to aboveground biomass (C) of shrubs, because foliage was not broken out as a separate state variable.

The formulation for calculating herb *GPP* incorporated the shading effects of shrubs; only the top layer of soil water affected this vegetation group; and *GPP* was proportional to total herb biomass (C).

The magnitudes of shrub and herb *GPP* were based on earlier measurements reported in Golkin and Ewel (1984).

Respiration

Pine trees—In establishing the magnitudes of respiration rates, we assumed that annual pine foliage respiration rates were approximately 25% of *GPP* (Golkin and Ewel 1984) and that respiration of pine stems and branches was approximately 10% of average biomass, double the rate in the earlier simulation. Simulated respiration of all aboveground biomass was proportional to temperature with a Q-10 of 3 (c.f., Kinerson 1975). Although this value is high, its use is warranted by the damping of extreme high and low temperatures by input data that are weekly averages. The base temperature used for the calculation is 25°C, and weekly average air temperatures ranged from 29.3°C in the summer of the dry year simulation to 6.2°C in the winter of the normal year simulation. Consequently, the effect of this temperature formulation on the magnitude of respiration varied from 1.6 at the highest temperature to 0.16 at the lowest temperature. These rates were also proportional to biomass.

Although a distinction is often made between growth respiration and maintenance respiration (e.g., Waring and Schlesinger 1985), we did not incorporate this in this model. Such an approach might be warranted in modeling respiration in a developing forest stand, but it is less likely to be important in a model of a mature stand with little net accumulation of biomass.

Pine root respiration rates (as well as all belowground decomposition processes) also incorporated a Q-10 of 3, based on temperatures and soil respiration rates measured at the study site. The base temperature for calculation of Q-10 for root respiration was 20°C. The effect of temperature on the magnitude of root respiration ranged from 1.6 at the highest temperature to 0.42 at the lowest temperature. Respiration rates of both fine root categories were proportional to the square of the biomass, a technique that allows growth rates of highly aggregated state variables with few feedbacks to approximate a logistic pattern (e.g., Odum 1983). We assumed that high water tables would not affect root respiration rates (Ewel et al. 1987a).

Shrubs and herbs—Respiration of aboveground shrub biomass was 20% of *GPP*, a smaller percentage than for pine foliage, reflecting the incorporation of woody biomass in this state variable. Respiration was affected by a Q-10 of 3 and by the square of biomass, as described above. The magnitude of shrub respiration was calculated as the difference between gross primary productivity and root respiration and turnover estimates. The formulation for shrub root respiration was similar to that for coarse pine root respiration.

Simulated herb respiration was approximately 60% of *GPP*. We used a smaller value than Golkin and Ewel (1984) in order to take root turnover into account, although we had no data to document this estimate. Simulated herb respiration depended on a Q-10 of 3 and on the square of biomass.

Translocation

Translocation was generally modeled as a donor-controlled process, in some cases with scalars that controlled relative rates within the year. This approach was taken in the absence of data documenting physiological mechanisms in mature individuals of the species on our study sites. For pine trees, C was translocated from foliage to stem and branches, and then to roots. The magnitudes of the rates fluctuated with foliage biomass. The pattern was established by a scalar that is maximum from mid-April to mid-October (Figure 4a). This pattern reflects a general understanding of carbohydrate movement in trees, although relatively little work has been done specifically on mature slash pine trees. Early growth of foliage in the spring depends in large part on mobilization from reserves in both root and shoot, but subsequent growth depends more on current photosynthesis (summarized in Kozłowski and Keller 1966, and Kramer and Kozłowski 1979). Although translocation peaks in early spring and mid-fall have been reported for many species (e.g., Nelson 1963), needle growth in Florida slash pine continues

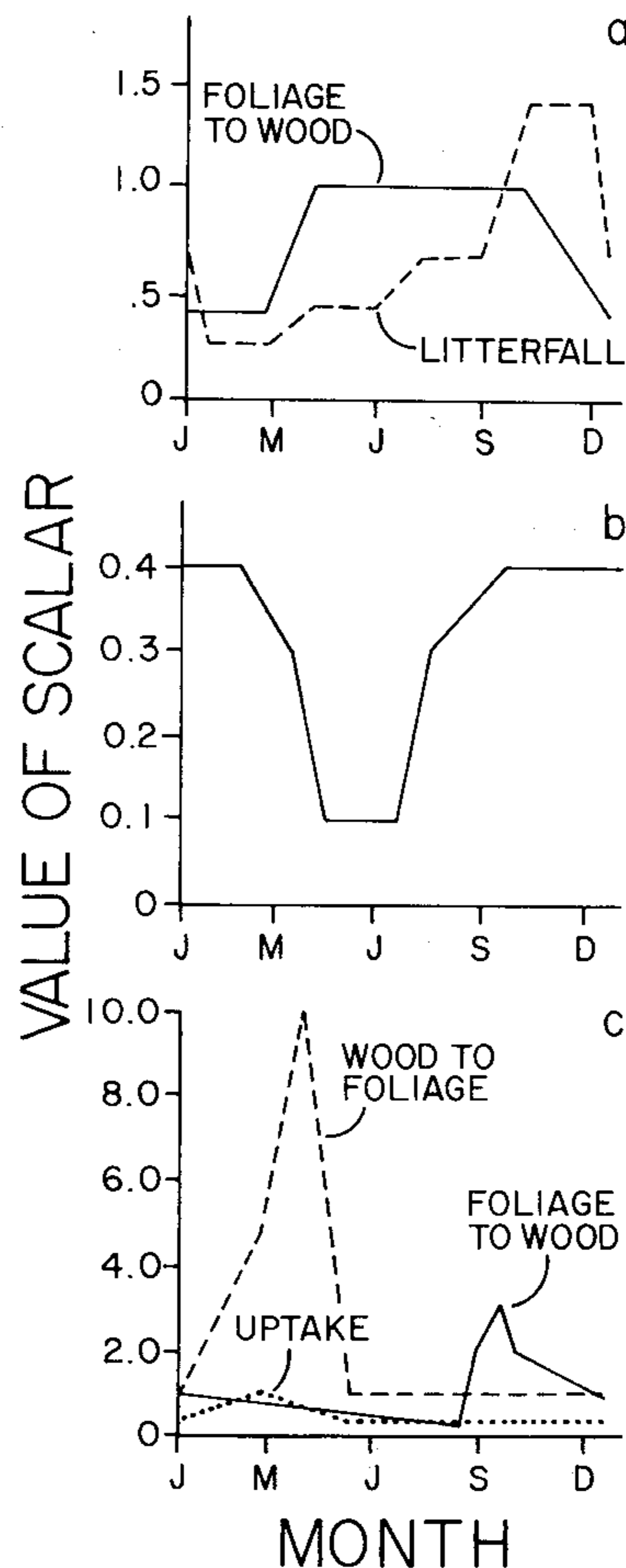


FIGURE 4. Scalars for C and P flows in plant populations. (a) Patterns of C translocation from pine foliage to pine stems and branches and to roots, and of litterfall in pines and shrubs. (b) Pattern of C translocation from above-ground shrub biomass to roots. (c) Patterns of P uptake and translocation in pines.

through the summer (Hendry and Gholz 1986). We assumed that both needle growth and translocation are proportional to *GPP* during this entire period. The scalar for translocation from aboveground shrub components to roots decreased in mid-summer (Figure 4b).

The simulated translocation rate from coarse to fine roots was proportional to coarse root biomass. Translocation from coarse roots to fine roots in the litter layer was also affected by the amount of litter present.

Dynamics of Dead Organic Matter

Total litterfall from each aboveground component was proportional to biomass. A scalar (Figure 4a) forced phenology of litterfall to follow the pattern described by Gholz et al. (1985b) for pine foliage and shrubs, with peak litterfall between mid-October and mid-December. Their study demonstrated that the seasonal pattern of needlefall did not differ significantly in this stand from a dry year (1980–81) to a wet year (1981–82). In the model, moisture availability affected the magnitude of seasonal litterfall by reducing photosynthesis and therefore foliar biomass when soil water became limiting. No explicit delayed effects were included. Simulated herbaceous litterfall occurred between mid-December and late February, when frosts are most likely.

Initial amounts of litter and soil organic matter were estimated from values reported by Gholz and Fisher (1982). The simulated litter layer included litter from pine foliage, pine stems and branches, shrubs, and half of the herbaceous litterfall (the other half became soil organic matter). Dead root biomass was reported by Gholz et al. (1986). Decomposition of litter and dead roots averaged 15%/yr (Gholz et al. 1985b). Soil organic matter in the model was derived from comminution of particles of litter, dead roots, and roots of herbaceous plants. Decomposition of soil organic matter was approximately 2.8%/yr (Cropper and Ewel 1983).

WATER BUDGET

Two layers of soil water were included in the model. The upper layer comprised the A horizon, which is 12.6 cm deep, and the lower layer comprised the E + Bh horizon, which terminates at a relatively impenetrable clay layer at 1 m. Throughfall replenished soil water; it was the difference between rainfall and simulated interception, which was proportional to rainfall and to biomass of pine foliage and shrubs. Movement between the two water layers was based on hydraulic conductivity of the upper layer. Above 38% of saturation in the top layer, flow increased 2–4× for every 10–15% increase in percent of saturation. When the bottom layer reached saturation, inflow ceased. Soil water losses included evaporation and runoff from the upper layer when it was saturated, transpiration from both layers, and percolation downward and laterally from the lower layer. Runoff was proportional to the amount of water that accumulated on the surface. Recharge to lower aquifers is generally very low in this area (Conover et al. 1984); Riekerk et al. (1978) estimated 3% for a nearby site. The rate of percolation from the lower layer was proportional to the amount of water in the lower soil water layer and to the gradient between the upper and lower layers. This damping factor allowed water to flow slowly when the landscape, like the simulated soil column,

was saturated, but quickly when a wetting front moved down under unsaturated conditions.

Simulated transpiration rates from pine foliage were proportional to foliage biomass and VPD. Like GPP, simulated transpiration slowed dramatically below 45% of saturation in the upper soil layer and below 65% of saturation in the lower soil layer. VPD was considered to be a more important control on transpiration than solar radiation for the tree canopy because of the importance of turbulent exchange in aerodynamically rough canopies (McNaughton and Black 1973, Tan et al. 1978). Shrub transpiration was also proportional to aboveground biomass and depended on sufficient water availability in the two soil layers, but, because the shrub layer is well below the canopy and turbulent exchange is minimal, we assumed that transpiration would respond to incident sunlight rather than to VPD. Herb transpiration was affected by availability of water in the top layer, total biomass, and incident sunlight.

The formulations for transpiration in our model were intermediate in complexity between canopy and watershed models. Canopy models can include estimates not only of leaf area, relative humidity, and solar radiation but also temperature, canopy roughness, and/or stomatal resistance (e.g., Running et al. 1975, Tan et al. 1978, Halldin et al. 1980, Kaufmann 1984). Watershed models, at the other extreme, may perform well with as few climate variables as daily precipitation and maximum and minimum air temperatures (e.g., Riha and Campbell 1985).

Transpiration rates in our model were limited at low soil water potentials as described above for *GPP*. The thresholds (45% for the top layer and 63% for the bottom layer) were higher than the value of 20% used by Running et al. (1975) as the inflection point for abrupt change in plant water potential, but they more accurately describe the hydraulic characteristics of our sandy soils.

All water intercepted by plants and not transmitted as throughfall was assumed to evaporate, and evaporation of any standing water at the soil surface was proportional to solar radiation reaching the forest floor. Evaporation ceased when soil moisture in the upper layer dropped below saturation.

PHOSPHORUS BUDGET

State variables were also included for P in pine foliage, pine stems and branches, pine roots, all shrub biomass, all herbaceous biomass, and each of the dead organic matter components. Initial P concentrations in the major biomass components were based on field measurements at the site (Gholz et al. 1985a).

Two categories of inorganic soil P were included. Available P was the fraction obtained from a weak acid (0.05 N HCl + 0.025 N H₂SO₄; Nelson et al. 1953) extraction of the soil; it is composed of phosphate radicals that are weakly sorbed to clay particles and large organic molecules. The remainder was classified as unavailable P and was very much the larger storage. Exchanges between the two groups were proportional to the difference in their amounts; in addition, low soil moisture in the lower layer limited the rate at which unavailable P became available.

The estimates of initial amounts of available and unavailable P were based on previous measurements at a nearby site, where concentrations in runoff provided verification for simulation of the earlier model (Golkin and Ewel 1984). However, because our studies did not include measurements of inorganic P fluxes in soil water, the values simulated in this model could not be validated.

Simulated available P was replenished by rainfall and mineralization from decomposing litter, dead roots, and soil organic matter. Both available and unavailable P were lost from the site via runoff, and available P was lost with the flow of water to deeper aquifers. In one set of simulations, the potential effects of fertilization were tested by adding 50 kg ha^{-1} to the available P pool at the beginning of the simulation.

Simulated P uptake rates in plants were affected by Michaelis-Menten dynamics, biomass (foliage biomass for pines, total biomass for shrubs and herbs), soil water (primarily in the lower layer, using the same weighting for each layer as in the transpiration equations), and, for pines, a scalar that increased slightly in spring when growth rates increase (Figure 4c). Translocation rates of P within the pine trees were controlled by scalars (Figure 4c) and by the magnitude of the donor state variable. The translocation scalar controlling P flow to the foliage increased from January to mid-April.

VALIDATION

Measurements of fine root biomass in March and annual rates of soil C release (as CO_2) were used to establish initial conditions and to set rate constants for the model, respectively. Because seasonal patterns were not explicitly programmed into the model, monthly fine root biomass values (Gholz et al. 1986) and estimates of soil C release (Ewel et al. 1987a) were used to validate the belowground portion of the C cycle. Annual root production values measured at the site were also used for validation.

Monthly soil moisture measurements were used to validate the simulated hydrologic cycle for the wet year. Gravimetric soil moisture content of the top 5 cm was measured monthly during that year (Ewel et al. 1987a). Neutron probe measurements were also made 23 times at 5 depths: 15, 30, 45, 60 and 75 cm. The average value for each time was calculated by weighting each value by the relevant depth.

RESULTS OF SIMULATIONS

VALIDATION

Carbon Dynamics

Total measured C losses from the forest floor and mineral soil were 4.2 and 8.8 $\text{Mg ha}^{-1} \text{ yr}^{-1}$, respectively (Ewel et al. 1987a); simulated losses agreed closely: 4.0 and 8.3 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ (Figure 5).

Soil coring yielded a unimodal seasonal pattern for surface roots $<1 \text{ mm}$ in diameter (Gholz et al. 1986), which is reflected in the simulation of fine root biomass ($<10 \text{ mm}$ in diameter) in the forest floor (where most roots are in fact $<1 \text{ mm}$ in diameter) (Figure 6). The simulation results fall within one standard error of only 4 of the 13 observed means. However, 7 of the simulated values corresponding to measurement times fall within one standard deviation, and only 2 (December and February) are not included within two standard deviations of the measured values.

Simulated biomass fluctuations were more damped than the monthly core data.

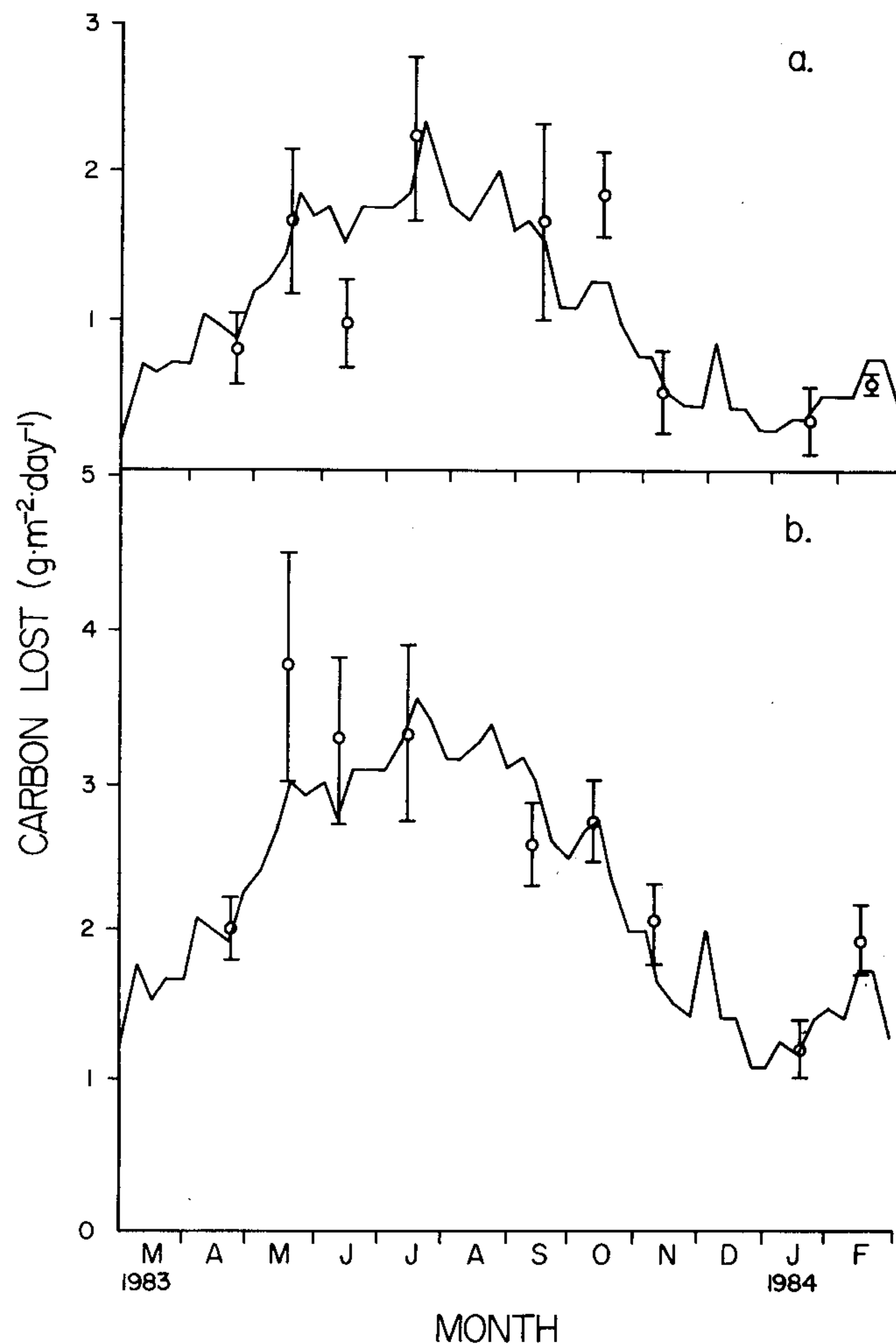


FIGURE 5. Simulated and measured C efflux from (a) the forest floor (litter and humus layer) and (b) the underlying mineral soil during 1983–1984. Data points are means and standard errors that were measured at the study site (Ewel et al., 1987a).

No seasonality was detected in biomass changes of larger, deeper roots in the monthly cores; simulated coarse root biomass changed only 15%, increasing from early spring to early summer.

Simulated net production of all roots averaged $3.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in the rainy year (1983–1984) and $2.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in the normal year; measured production from April 1983 through March 1984 (when total rainfall was 1337 mm) was $3.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Gholz et al. 1986). Simulated and measured values for the wet year differed only slightly for pines (1.9 and $2.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively) and nonpine vegetation (1.2 and $1.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively). Simulated and measured C losses via root respiration in the forest floor and mineral soil were both $8.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Ewel et al. 1987b). Simulated specific respiration rate of all roots combined for the rainy year was $0.38 \text{ g g}^{-1} \text{ yr}^{-1}$; the rate calculated from field data was $0.40 \text{ g g}^{-1} \text{ yr}^{-1}$.

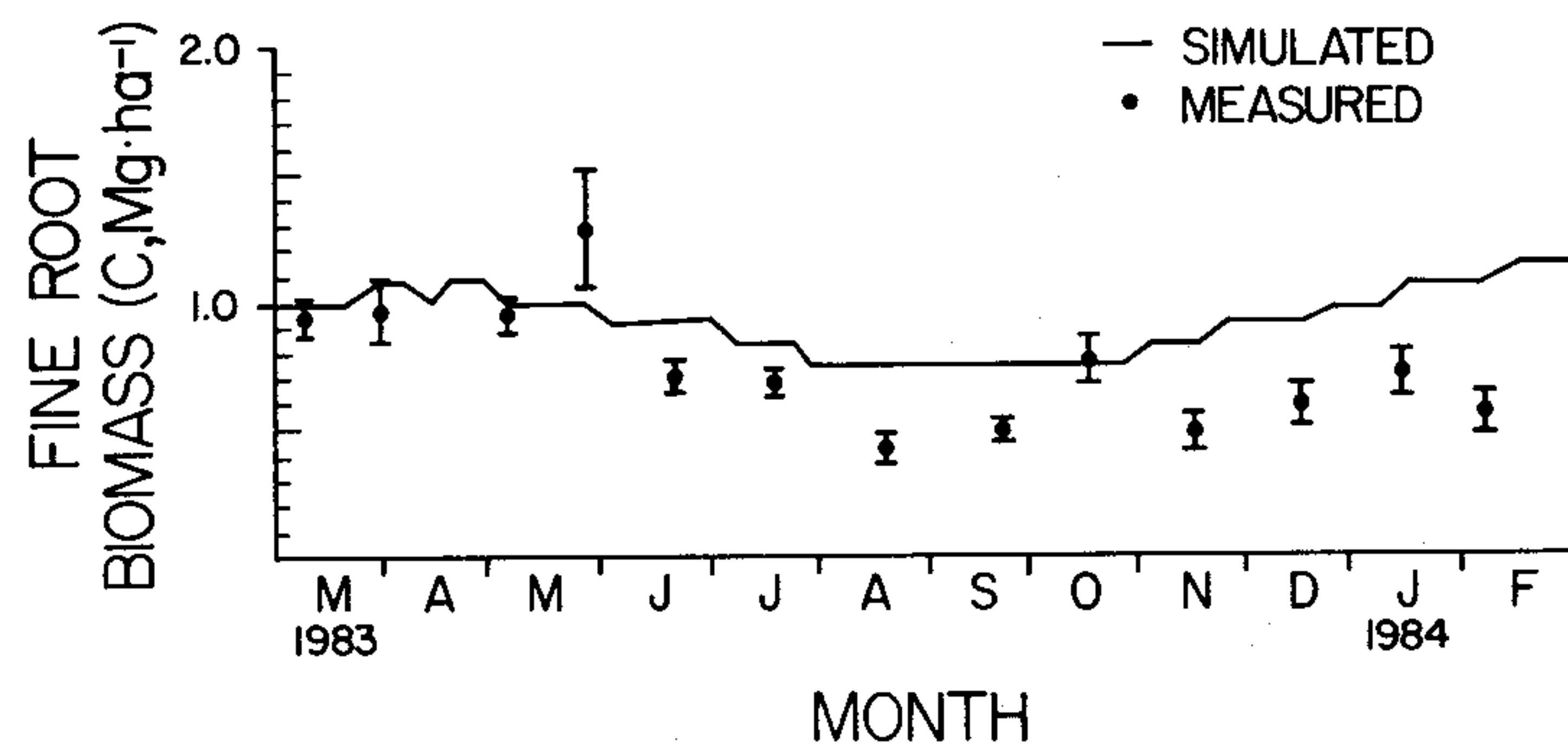


FIGURE 6. Biomass (± 1 SE) of live pine fine roots (< 1 mm) and simulated biomass of roots < 10 mm in the forest floor of a mature pine plantation.

Soil Moisture

The water table at the study site fluctuated between saturated and drought conditions several times during the study year (Figure 7). This pattern is reflected in the changes in soil water in the lower layer, reproducing neutron probe measurements accurately (Figure 8). However, simulation of soil water in the top layer did not reproduce relatively transient saturation peaks in the spring, because the weekly averages used for input distributed the rainfall peaks too broadly at a time when simulated ET was high.

SIMULATED CARBON BUDGET

Carbon Allocation

Simulated overall *GPP* during the normal rainfall year was $29.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, of which 36% was translocated to belowground components (Figure 9). These values changed only slightly in the rainy year simulation. Although *GPP* in the dry year simulation was considerably lower than in the other 2 years, the same percentage of C was allocated to roots. Pine *GPP* and translocation rates followed the same pattern; 31–34% of *GPP* was allocated to roots in this species. Total net primary productivity of the stand in the normal rainfall year was $5.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, and total aboveground net primary productivity (*ANPP*) was $2.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; pines accounted for 82% of this. Root respiration rates were slightly higher

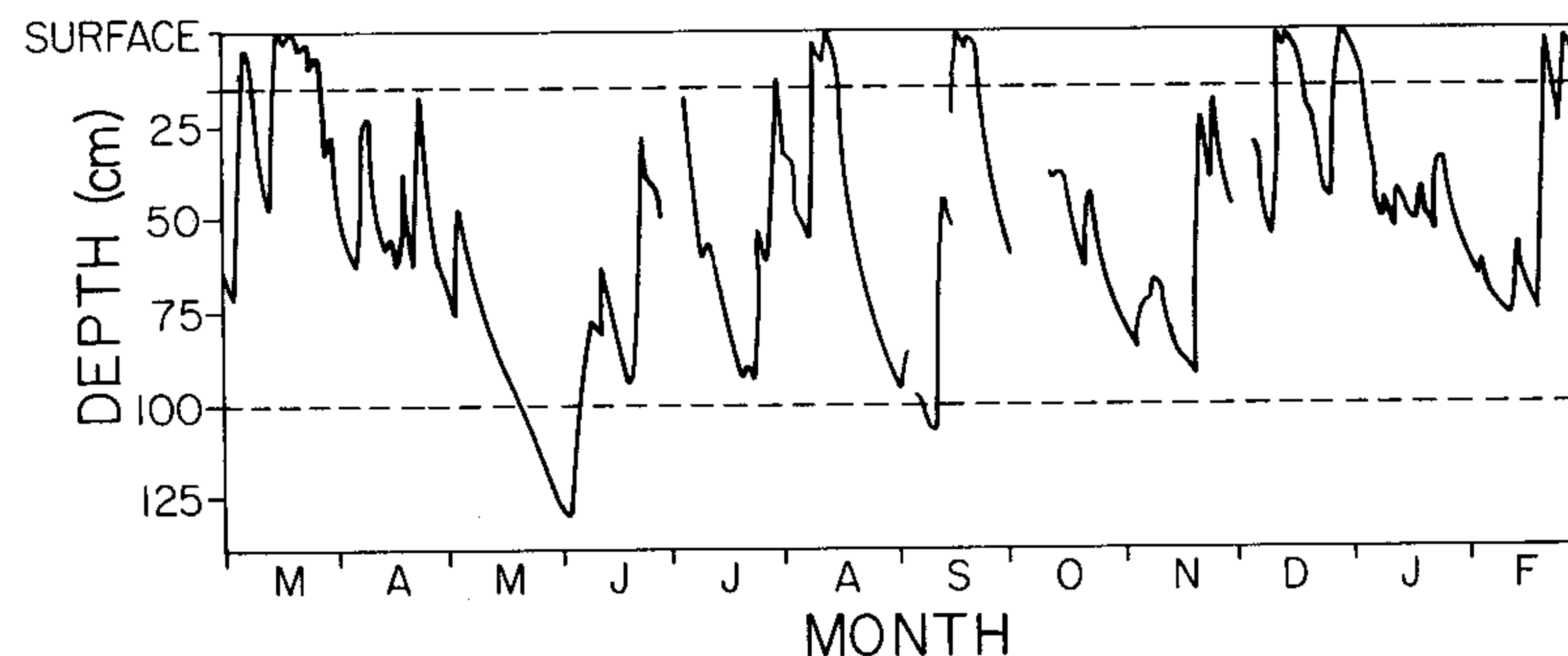


FIGURE 7. Water table fluctuations at the study site during 1983–1984. Dotted lines mark the boundaries of the A and the E + Bh horizons.

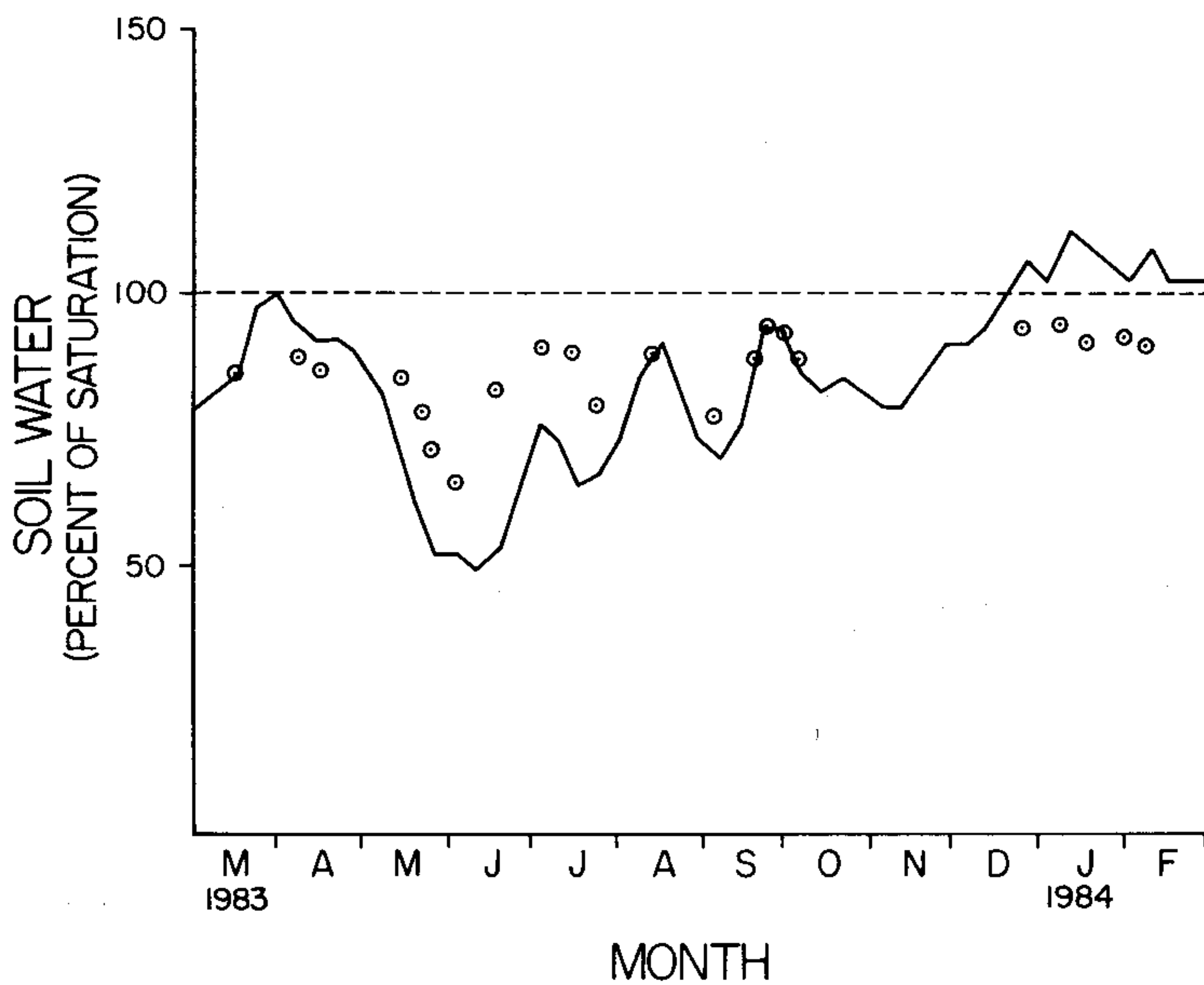


FIGURE 8. Simulated and measured changes in soil water contents in the E + Bh horizons. Data points are weighted averages of neutron probe measurements at 5 depths.

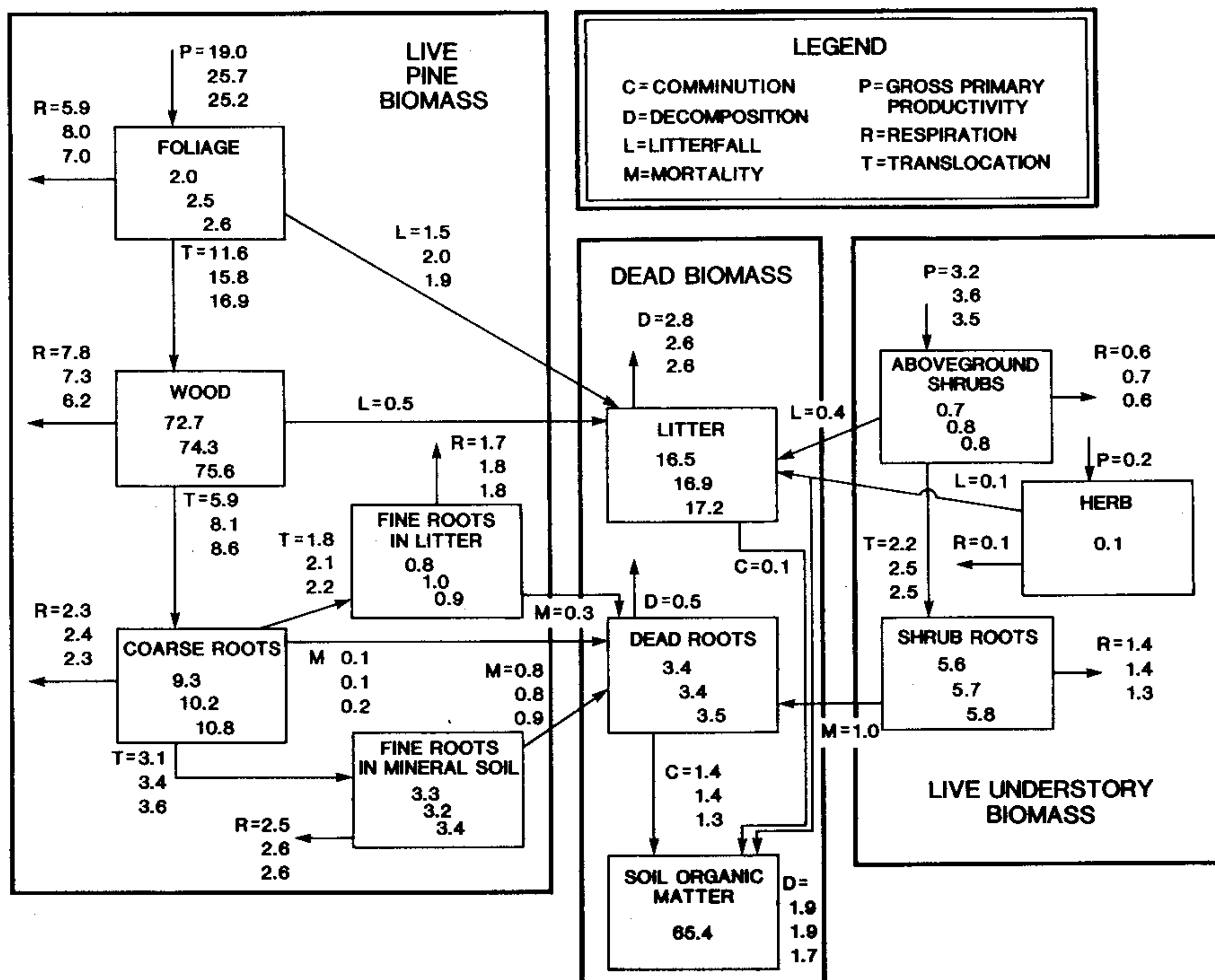


FIGURE 9. Simulated carbon budgets for a mature slash pine plantation during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm. Values are listed in increasing order of rainfall. If all three values are the same, the value is listed only once. Numbers in the boxes are averages (Mg/ha) calculated over the simulation year; rates are $\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.

during the normal rainfall year, primarily because of higher levels of coarse root biomass during the warm late summer months. Turnover times for both pine and shrub roots were 21% longer than in the other two simulations, which differed by only 1%.

Seasonal Patterns

Of all the pine biomass components, foliage changed the most dramatically during the simulations (Figure 10). Following rapid growth during early spring, foliage biomass declined again, particularly in the dry year simulation, but returned to moderate levels by early summer. Both dry and normal simulations showed a second decline in the fall. The rapid growth phase in the spring was extended by 2 months in the rainy year simulation.

Differences in simulated *GPP* were most marked during the first 5 months of the simulations, March through July, when *GPP* reached both highest and lowest values in each simulation (Figure 11a). The most uniform response was in the late fall and early winter, when *GPP* maintained moderate levels in all three simulations.

Variation in *ANPP* of pines was similar (Figure 11b). *ANPP* was highly variable in the late spring and early summer months, moderate but still variable in the later summer and fall, and consistently positive in the winter months. Litterfall accounted for most of *ANPP*. Although stem biomass in this mature stand of pines actually increased in the rainy year simulation, it was still within 3% of the initial biomass.

Seasonal changes in root respiration varied little among the three sets of weather data (Figure 12), reflecting the damping effect of soil on temperature fluctuations. Although differences were most pronounced in winter and spring, the same pattern of high summer and low winter respiration rates was followed in all three simulations.

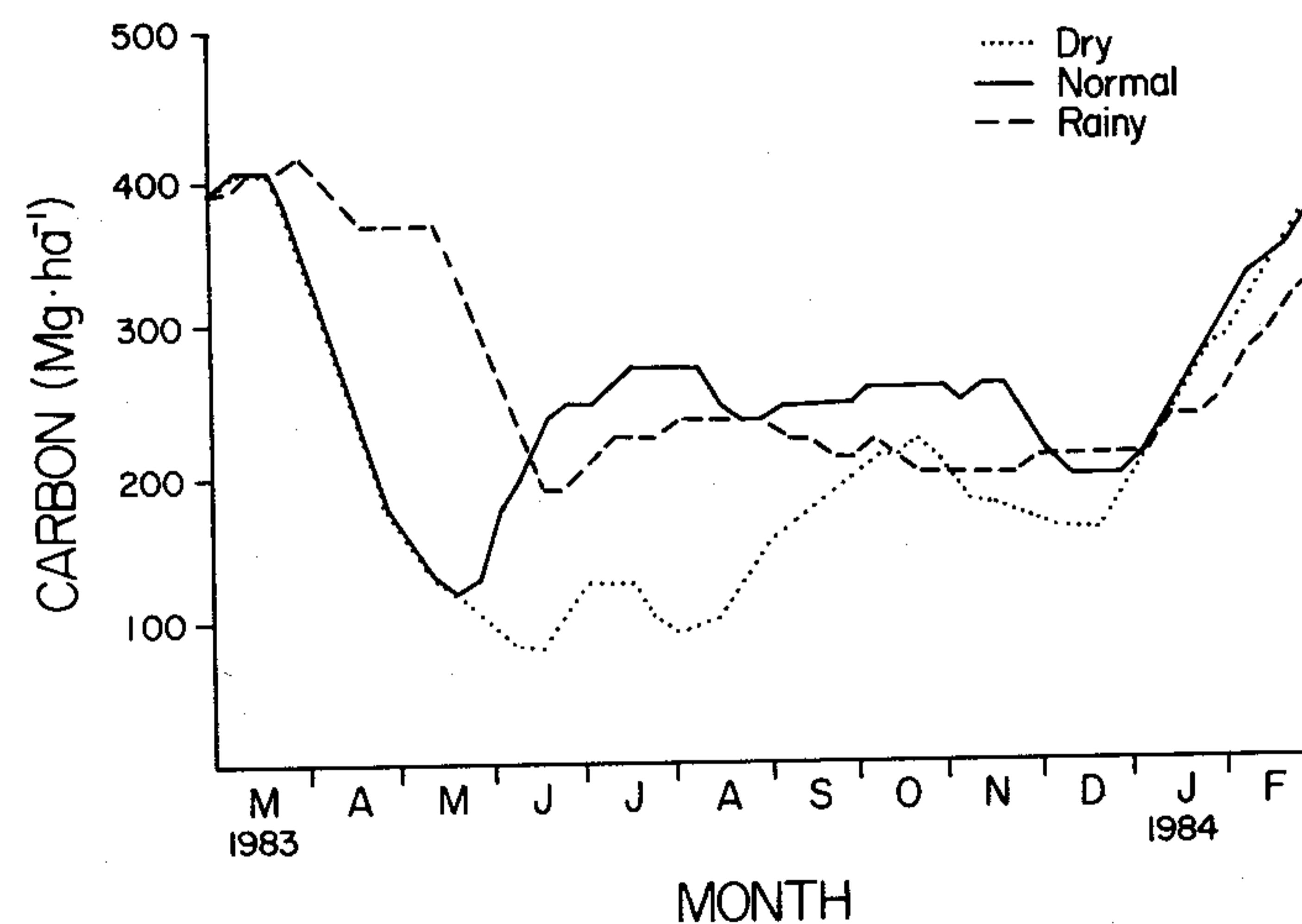


FIGURE 10. Simulated changes in pine foliage C during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

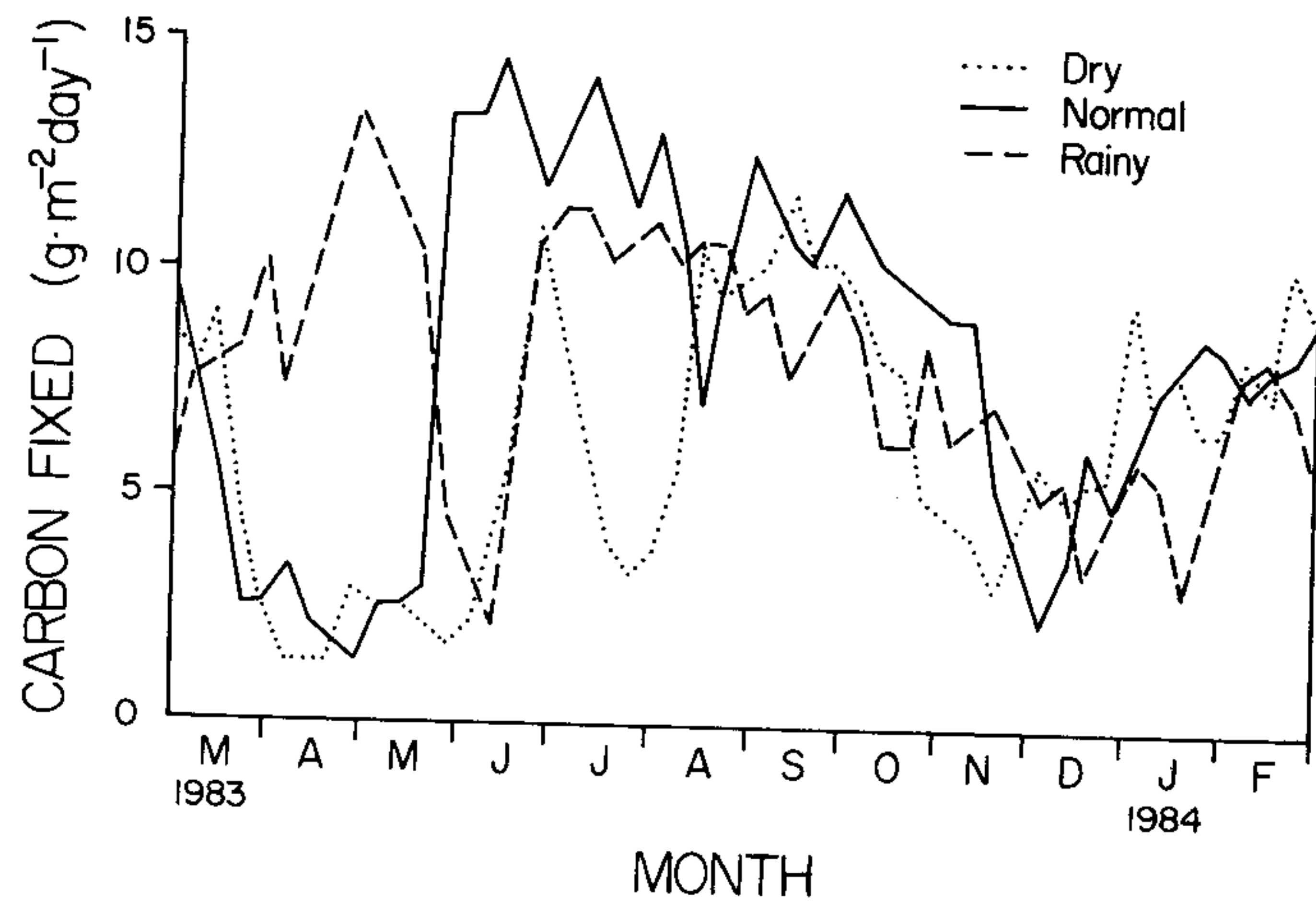


FIGURE 11a. Simulated changes in gross primary productivity of all plants during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

SIMULATED WATER BUDGET

Simulated *ET* averaged 99% of rainfall in the dry year simulation, 97% in the normal year simulation, and 91% in the rainy year simulation (Figure 13). Seasonal *ET* patterns resembled *GPP* patterns closely, with the least variation in the winter months and the greatest variation in the spring and summer (Figure 14). The highest *ET* rate simulated was 6.7 mm/day in late summer of the rainy year simulation.

Soil saturation occurred in late summer in the normal year simulation and in winter in the rainy year simulation (Figure 15a). Soil moisture fluctuations in the lower horizon tracked *ET* except for the late fall and winter months in the rainy

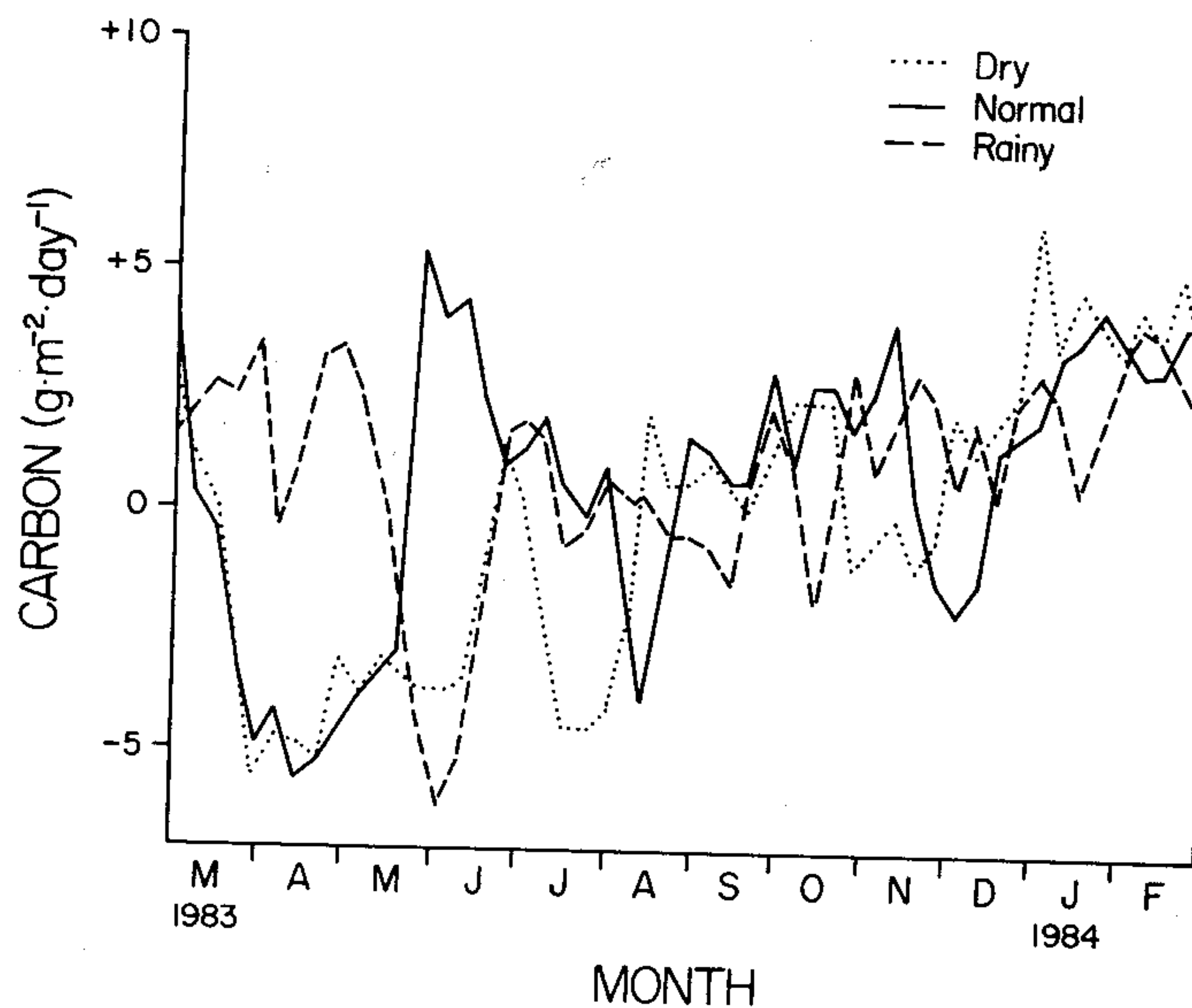


FIGURE 11b. Simulated changes in aboveground net primary productivity of pines during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

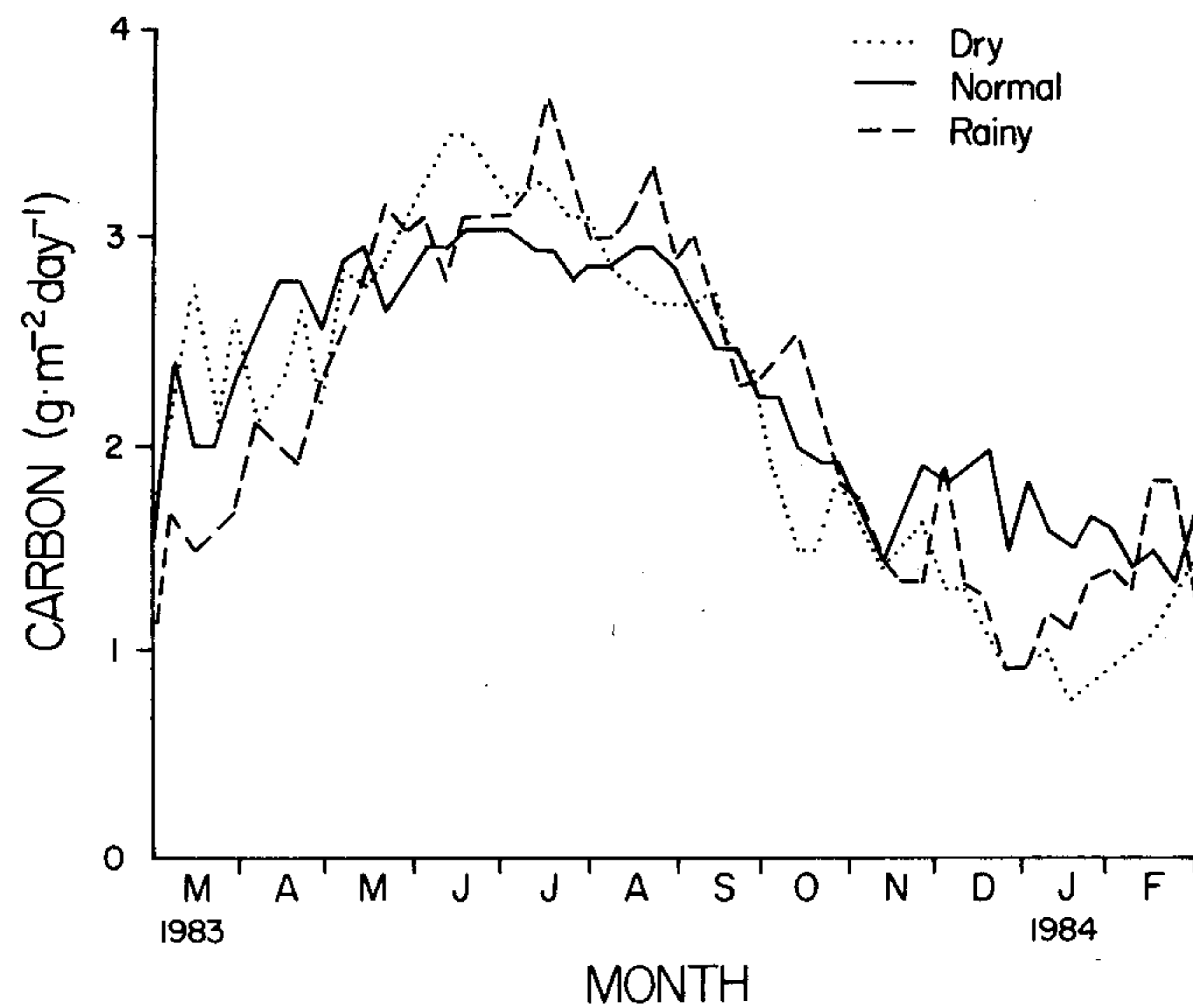


FIGURE 12. Simulated changes in root respiration in a mature pine stand during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

year simulation when the soil remained saturated after unusually high late fall rainfall (Figure 15b). Runoff and percolation losses were negligible and low, respectively (Figure 13), reflecting the assumption that downward and lateral belowground water movements were limited by the flat topography and clay subsoil horizon that characterize the study site.

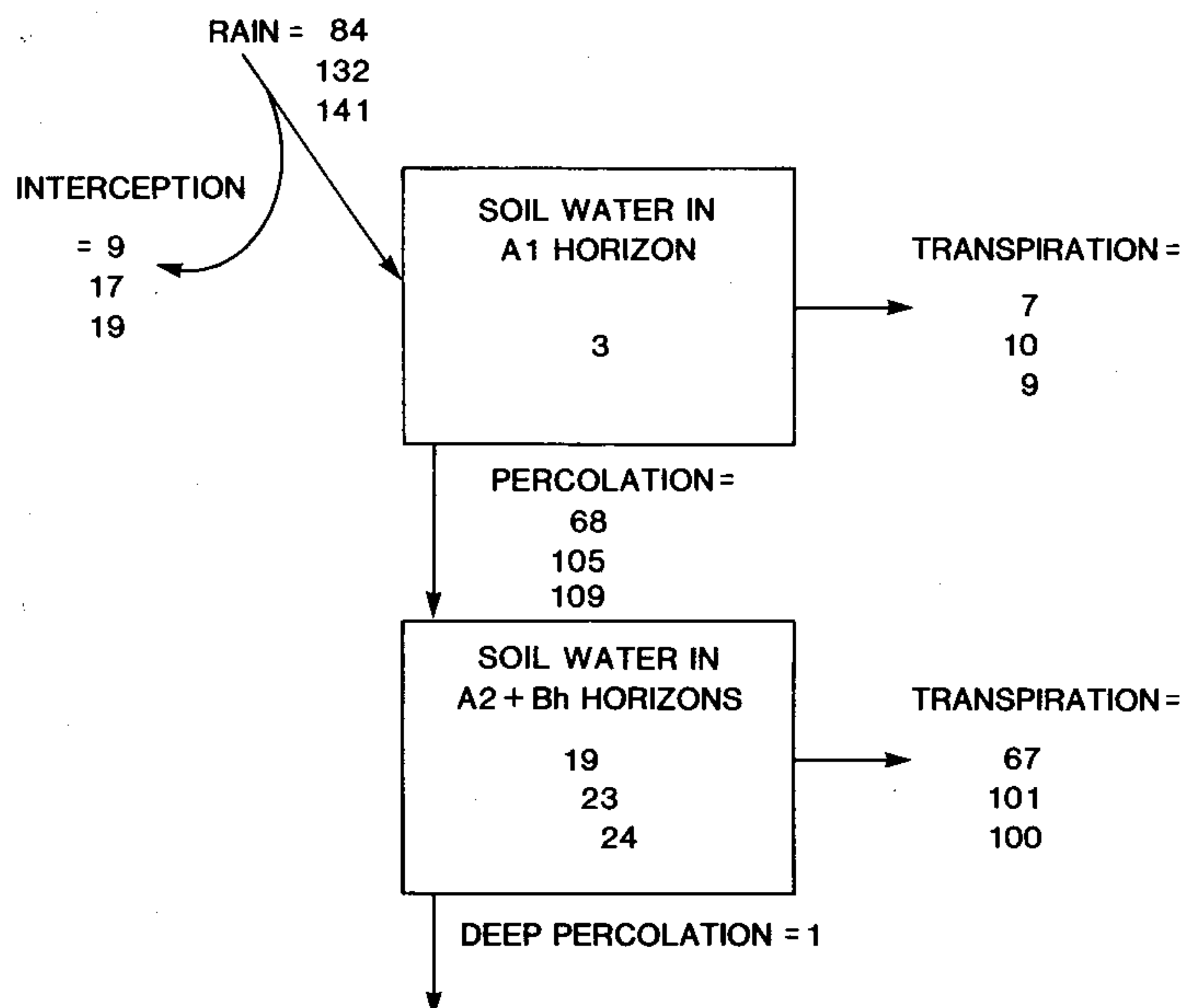


FIGURE 13. Simulated water budgets for a mature slash pine plantation during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm. Values are listed in increasing order of rainfall. If all three values were the same, the value is listed only once. Numbers in the boxes are averages (cm) calculated over the simulation year; rates are in cm/yr.

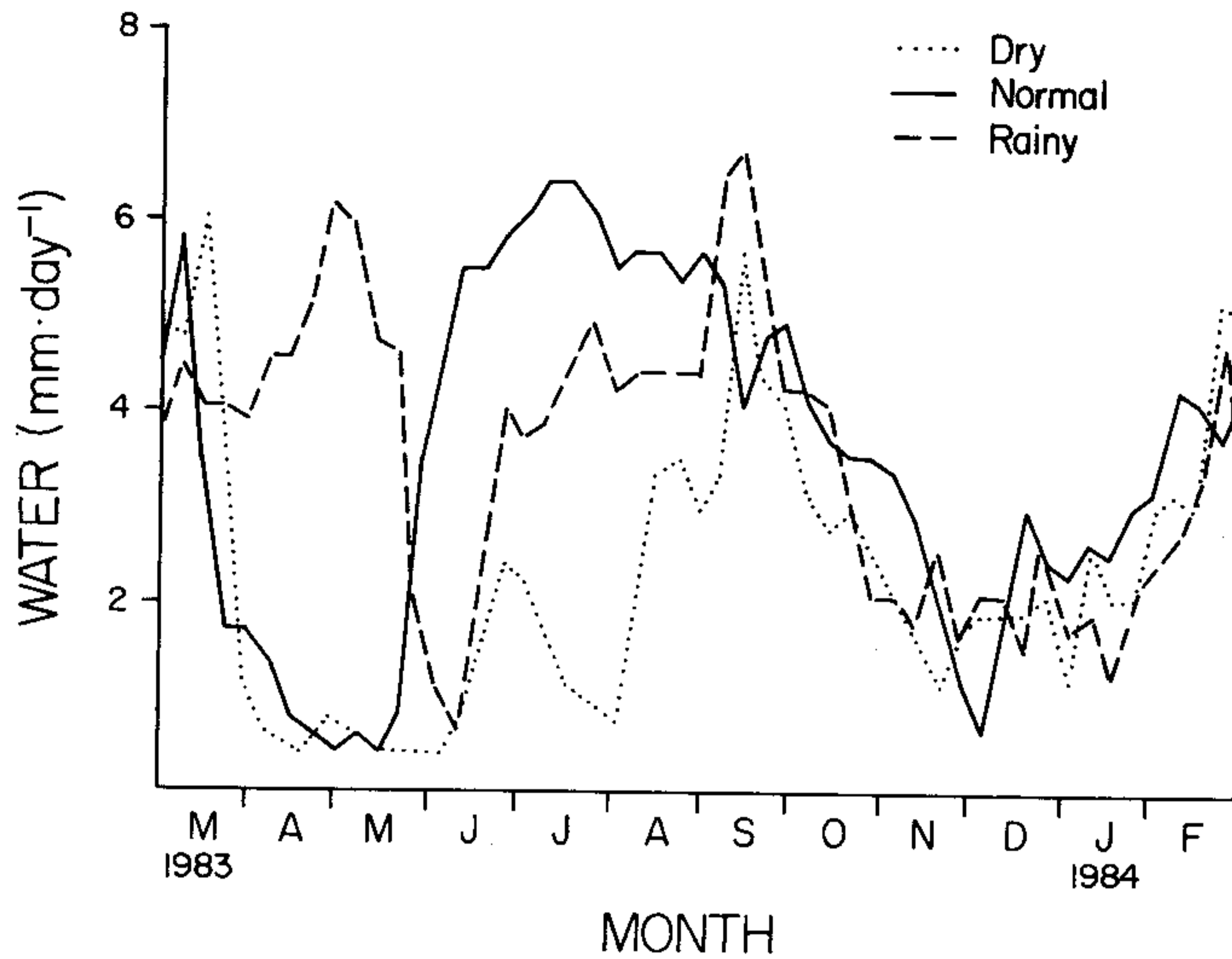


FIGURE 14. Simulated changes in evapotranspiration during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

SIMULATED PHOSPHORUS BUDGET

Changes in Storages and Flows

Mineralization of inorganic P from decomposing litter and fixation of available P in the soil into less available inorganic forms dominated the simulated P budget (Figure 16). Insignificant amounts were lost through runoff and deep drainage.

The average quantity of available P in the soil was not greatly affected by changes in simulated weather conditions. Although more rainfall was associated

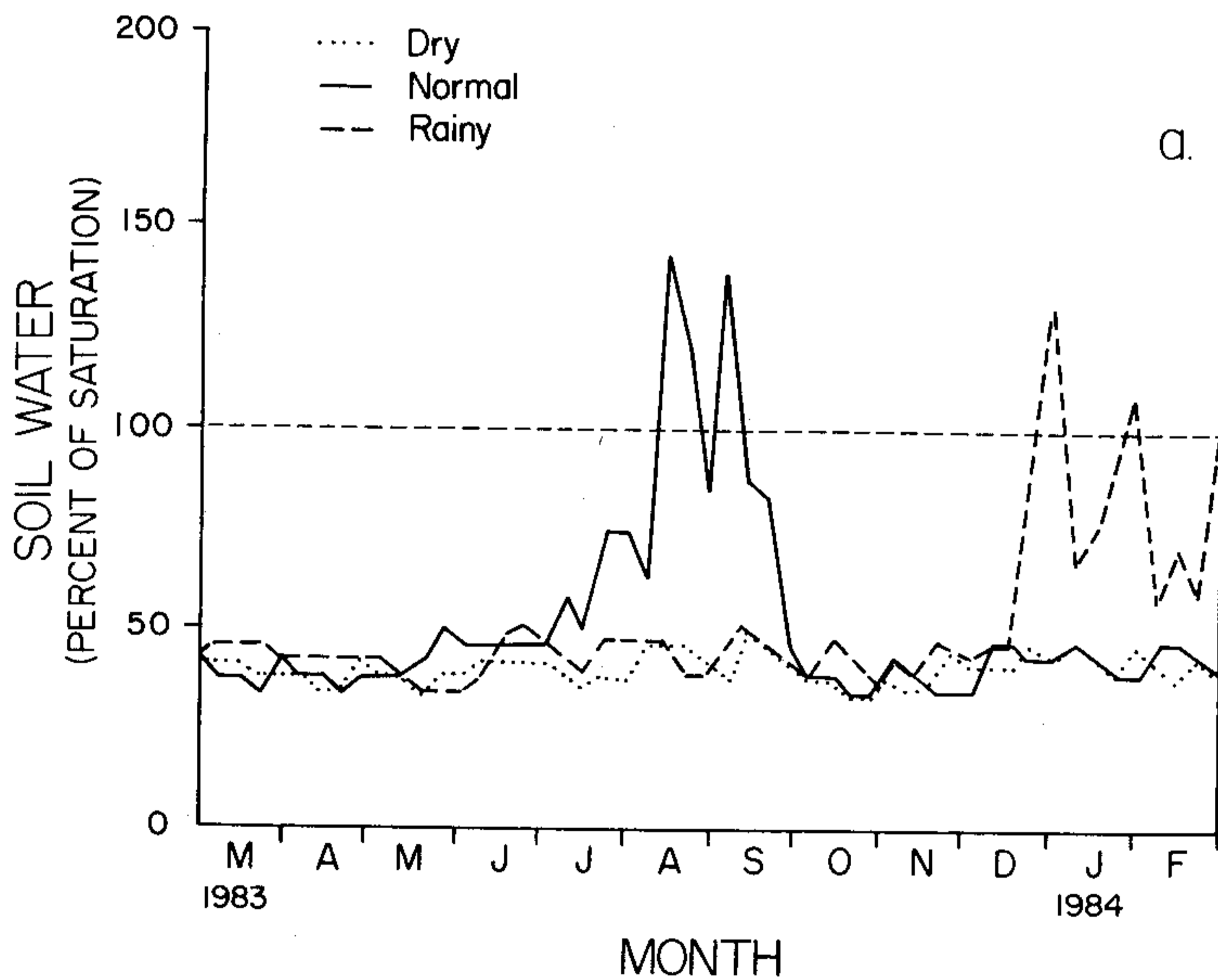


FIGURE 15a. Simulated changes in water content of A horizon during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

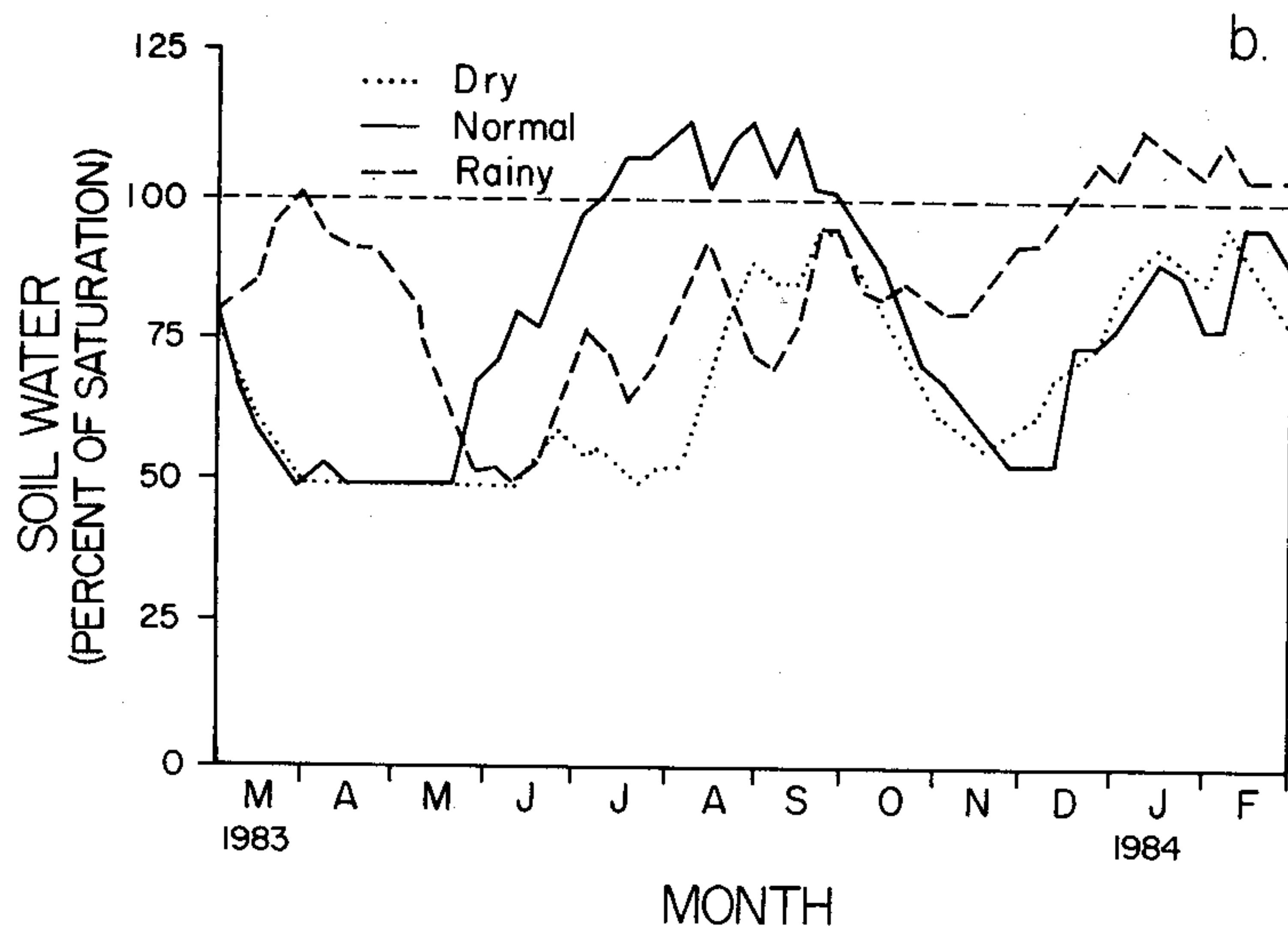


FIGURE 15b. Simulated changes in water content of E + Bh horizon during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

with increased plant uptake and decreased decomposition (due to lower temperatures) and hence decreased mineralization from dead organic matter, net fixation into unavailable forms of P decreased also. Nevertheless, seasonal differences in simulated available P were apparent (Figure 17). In the normal rainfall simulation,

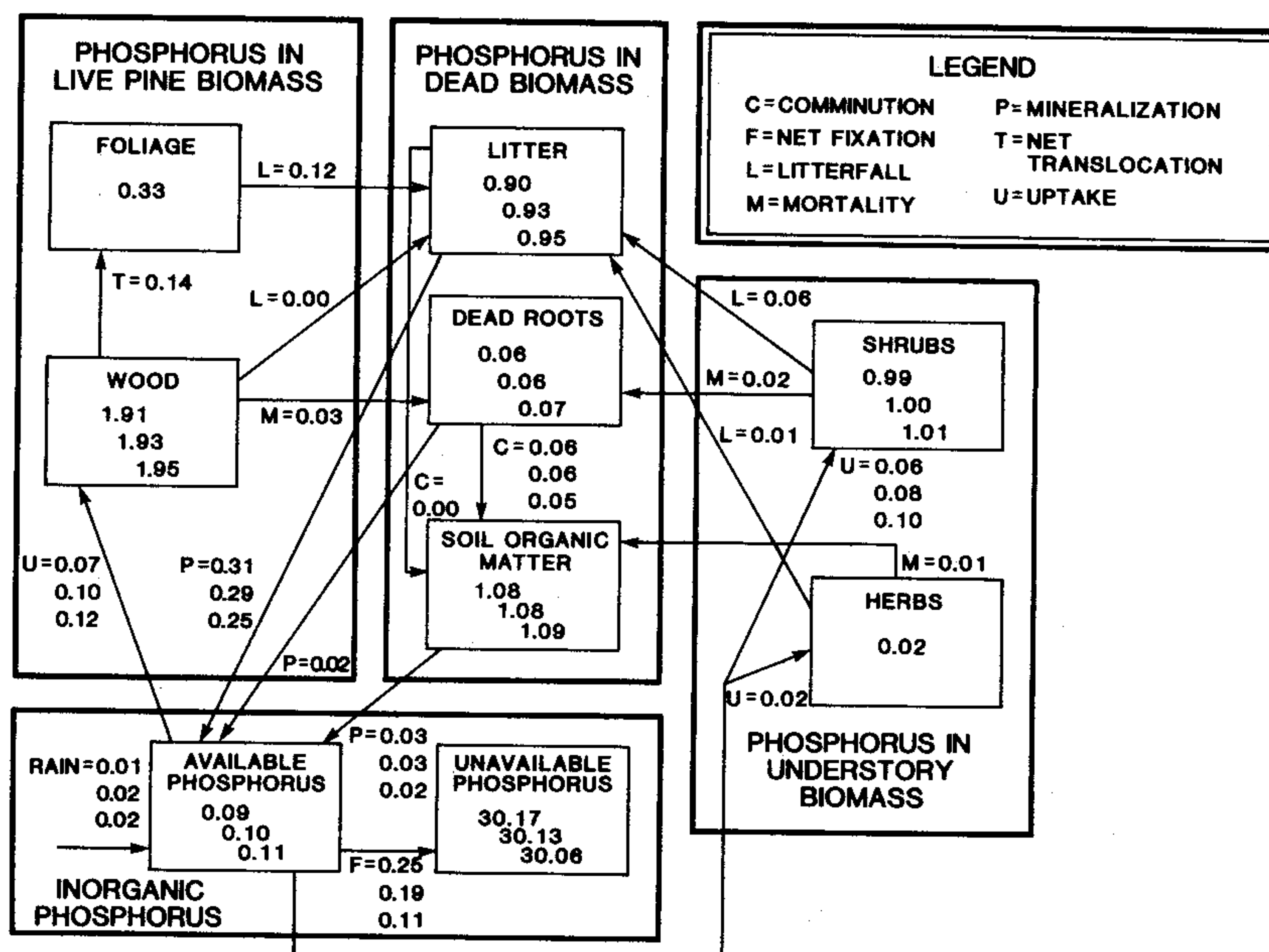


FIGURE 16. Simulated phosphorus budgets for a mature slash pine plantation during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm. Values are listed in increasing order of rainfall. If all three values were the same, the value is listed only once. Numbers in the boxes are averages (g/m^2) calculated over the simulation year; rates are $g \cdot m^{-2} \cdot yr^{-1}$.

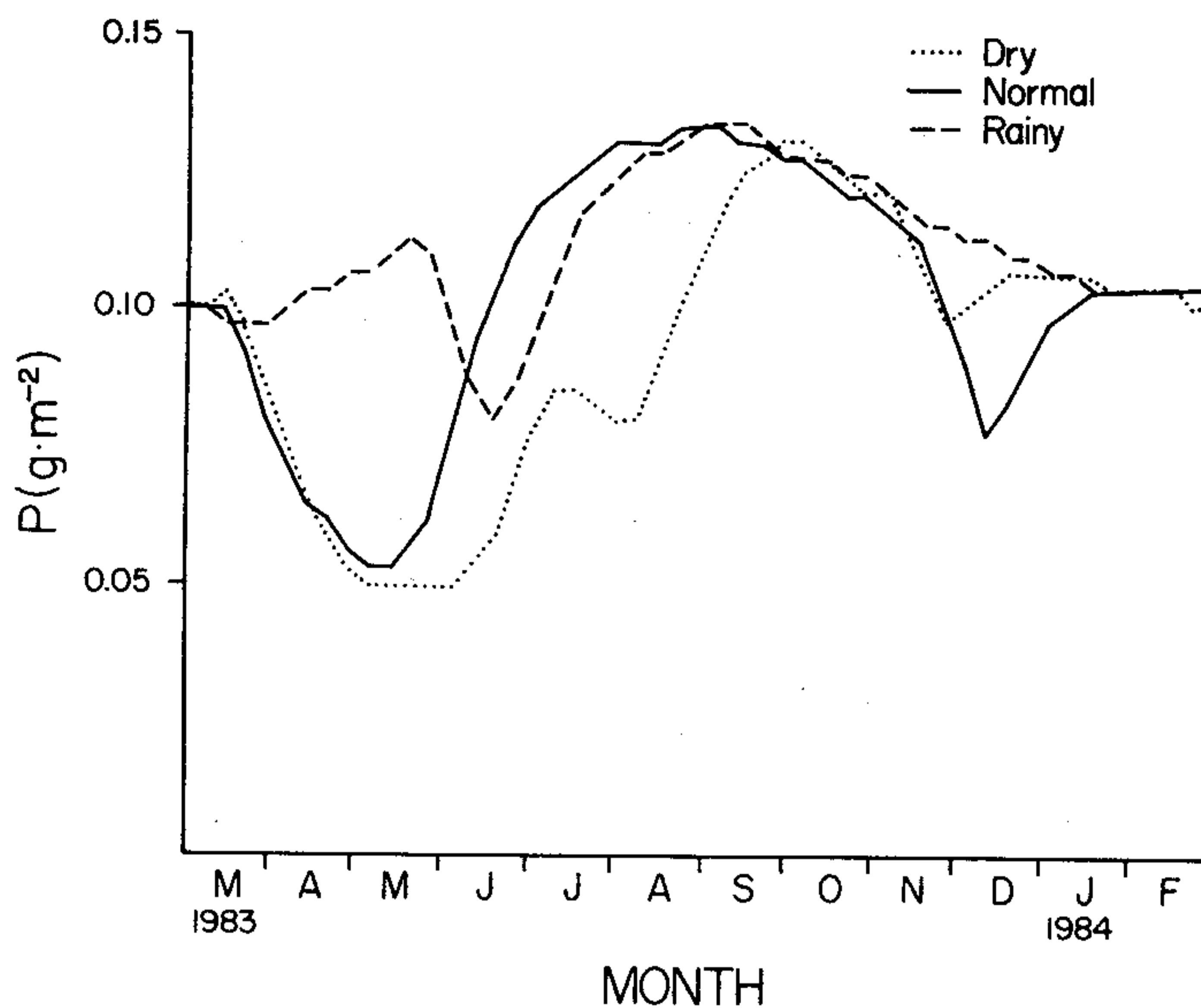


FIGURE 17. Simulated changes in available P in the soil during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

available P was lowest in late spring and early winter. It remained low until the end of the summer under dry conditions. The rainy year simulation was distinctive because of high concentrations of available P in the early spring.

Among live and dead biomass components, only pine foliage showed distinct changes in P concentration throughout the year (Figure 18). Concentrations were highest in the dry year simulation. In all three simulations, maximum concentrations were reached in May or June.

Fertilization

Simulated fertilization in the normal rainfall simulation had virtually no effect on the C budget of the mature pine plantation during the subsequent 12 months. Al-

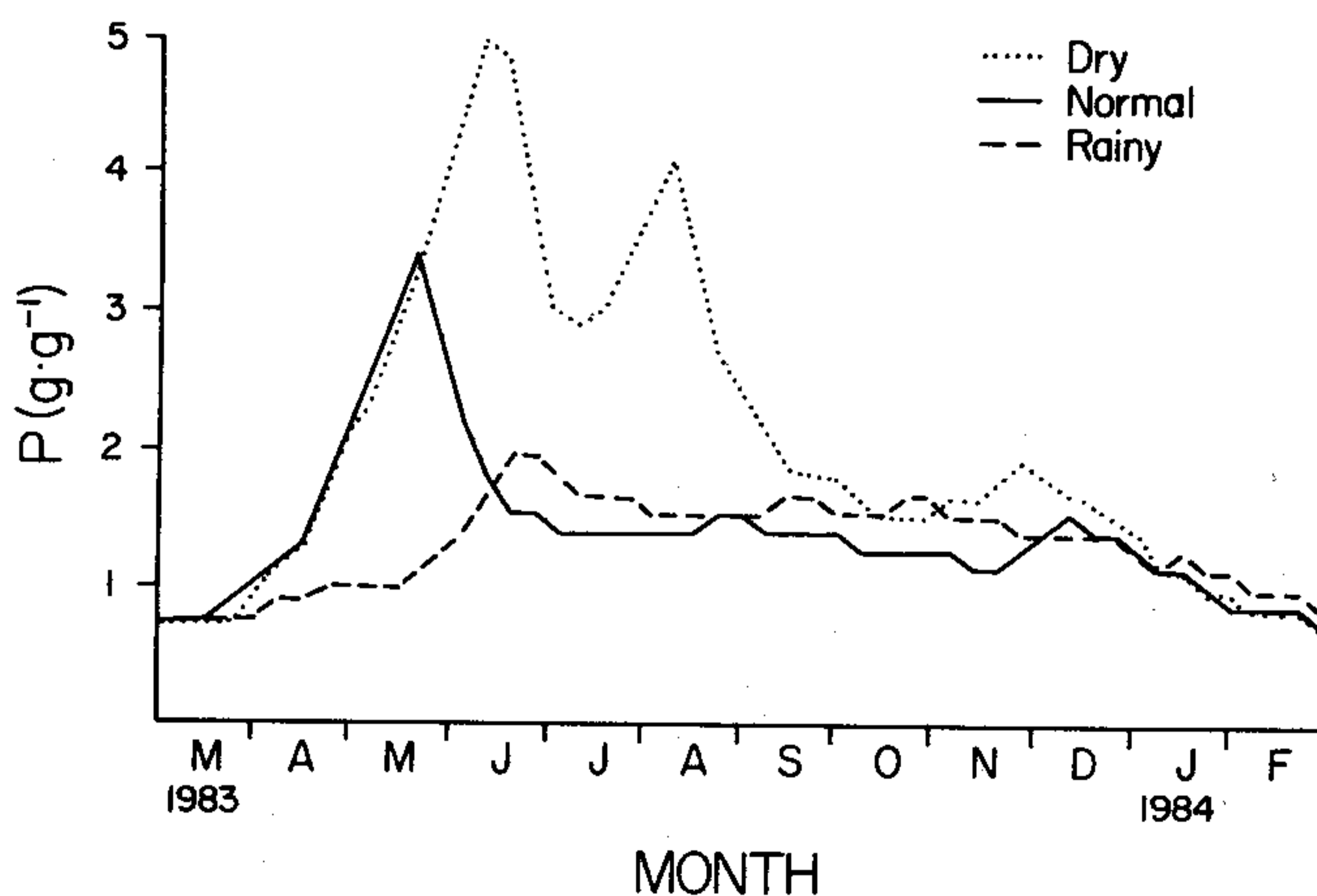


FIGURE 18. Simulated changes in P concentration in pine needles during three simulation years: dry = 837 mm; normal = 1318 mm; rainy = 1407 mm.

Respiration	8.3	8.1	0.1	0.6	4.1	2.1	17.0	3.9	5.6
Net productivity (BNPP)	2.3	3.1	1.0	5.7			1.5	3.7	2.8
% of photosynthate							6.1		
Translocated to roots	36		6	15			23	35	23
Mortality/litterfall (%)	73	60-79		155			86	13	
Productivity/biomass (yr ⁻¹)	0.11	0.15	0.56	0.51	0.14	0.05	0.02	0.45	0.15
BNPP/total NPP (%)	46		63	28	53	23	27	25	17
Fine roots									
Size (mm)	10	10	2	10	2	2	5	5	2
Biomass	4.2	9.8	0.1	2.2	4.2	1.4	5.6	3.8	2.0
Productivity	1.1	2.8	0.9	4.7	2.8	0.7	5.8	4.5	2.0
Productivity/biomass (yr ⁻¹)	0.26	0.29	1.0	2.08	0.67	0.50	0.91	1.18	1.0

^a Normal rainfall simulation

^b Gholz and Fisher 1982, Gholz et al. 1986, Ewel et al. 1987b

^c Persson 1978, Ågren et al. 1980, Albrektson 1980

^d Kinerson et al. 1977

^e Keyes and Grier 1981

^f Grier and Logan 1977

^g Grier et al. 1981

^h Harris et al. 1975, 1977

ⁱ Benecke and Nordmeyer 1982

though foliage P concentrations were slightly elevated, *GPP* rates were not affected. Most of the added P became unavailable inorganic P, and small quantities were lost in runoff and deep percolation.

DISCUSSION

VALIDITY AND SENSITIVITY OF THE MODEL

The purpose of this model was to synthesize existing information and to examine the capability of several major assumptions to describe how the belowground portion of a mature forest operates. We view such a synthesis as an important step in determining the kind of research that should be conducted in order to formulate a useful management model. Even though the model may not be a useful management tool at this stage, validation is still important in generating confidence about the results that are obtained in order to provide a solid basis for progress.

Monthly measurements of soil C losses (Figure 5), fine root biomass (Figure 6), and soil moisture in the lower layer (Figure 8) supported our formulations for such processes as translocation, root respiration, root mortality, and transpiration. They also supported the results of other field studies that suggest that slash pine roots are more conservative in behavior than some other conifer root systems (Gholz et al. 1986), in that they do not demonstrate the rapid turnover described for *P. taeda* (Kinerson et al. 1977), *P. sylvestris* (Persson 1978), *Pseudotsuga menziessii* (Santantonio and Hermann 1985), or *Abies amabilis* (Grier et al. 1981). Moreover, the model's ability to reproduce monthly changes in soil C loss, including the close correspondence between simulated root respiration rates and estimates derived from field measurements, supported the hypothesis that slash pine roots are unaffected by the short-term flooded conditions that can be encountered during any season (Ewel et al. 1987b).

No validation is available for the aboveground trends that we have simulated. Although the general patterns of change in aboveground processes were established in the earlier version of the model (Golkin and Ewel 1984), many rates, especially *GPP*, respiration, and transpiration, have been reformulated. Simulated *GPP* for the normal rainfall year ($29.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) was accordingly 38% higher than estimated *GPP* in the earlier model. However, this estimate was based on field measurements during a dry year, and simulated *GPP* for the dry year in this study was only 4% higher than the earlier estimate. We are therefore confident that this reformulation is accurate.

The relationship between simulated and measured soil moisture in the lower soil layer supports our formulations for transpiration and our assumption that it represents by far the largest component of water loss. Estimates of ET from young pine forests in north Florida include 770 mm during a dry year (86% of 900 mm precipitation), 1060 mm during a slightly wetter year (89% of 1180 mm precipitation), and 1180 mm during a very wet year (72% of 1620 mm precipitation) (Riekerk 1985). Our estimates were higher (averaging 96% of precipitation compared to 83%), which might be expected from the higher foliage biomass in the simulated stand.

The lack of significant annual amounts of overland flow or downward percolation is consistent with the generally poor drainage that characterizes many of the

flatwoods that have been converted to slash pine plantations. The simulation suggests that less than 10% of the water that falls in the pine stands contributes to recharge of deep aquifers and swamps and to regional streamflow. Although the density of surface water bodies in north Florida appears to contradict this, in fact most of the lakes are small and shallow, and many of the ponds are vegetated by pondcypress trees (*Taxodium distichum* var. *nutans*), which have low *ET* rates (Brown 1981, Ewel 1985). The water levels in most streams fluctuate widely, high water normally corresponding to early spring rainfall events when *ET* rates are low. The rivers in the area are slow-moving and depend on springs from deeper aquifers for a significant proportion of their flow (e.g., Burnson et al. 1984).

Because of the relatively low level of hydrologic connectedness between these uplands and downstream aquatic and wetland ecosystems, nutrient transfers should also be low. The losses attributed in our simulation to runoff and deep drainage were in fact less than the leaching losses recorded from forests with well-drained soils (e.g., *P. nigra*; Miller et al. 1976). There is no information on seasonal changes in available and unavailable soil P pools in pine flatwoods. Nevertheless, the behavior of this portion of the model conformed to generalizations about the behavior of P in forests. For instance, more P was provided in rainfall than was lost in drainage; continued plant uptake depended on organic matter decomposition; and P added as fertilizer rapidly became bound into unavailable forms (Harrison 1985).

Determining the sensitivity of a model is also an important part of evaluating its performance. Simulating a model with a large number of nonlinear differential equations runs the risk of producing unrealistic results, especially when forcing functions with different oscillation patterns interact. Sensitivity analysis of this model was limited primarily to comparisons of the impacts of different patterns of solar radiation, temperature, rainfall, and humidity on C, P, and water budgets. Highest variability is generally expected in the components with fastest turnover. Turnover rates of at least twice per year were programmed for carbon in pine foliage and in fine roots in the litter, carbon in aboveground shrubs and in herbs (Figure 9), the two water compartments (Figure 13), and available phosphorus (Figure 16). The largest differences at the end of the year between the simulation with normal rainfall and either of the other two simulations occurred in the two water compartments. Differences of 10% to 15% were also recorded for carbon in pine foliage, coarse roots, and fine roots in the litter. The interrelationships among the state variables therefore appear to have damped the volatility that might be expected in the more labile compartments while still allowing meaningful variability in the more refractory components.

SIMULATED VARIATION IN SLASH PINE ECOSYSTEM DYNAMICS

Aboveground

Although it is difficult to compare *GPP* values among studies because of extreme differences in techniques and assumptions, several measurements have been made in north Florida that are similar in overall design. Simulated *GPP* in the normal rainfall year ($29.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) was close to the rate reported for a local cypress pond (approx. $27 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Brown 1981), which is also a nutrient-poor ecosystem. Average daily *GPP* for mid-September to mid-October was

slightly more than the rate measured in a young mixed hardwood forest (the upland late successional forest type in north Florida) during the same time period in the early 1970s ($10.4 \text{ g m}^{-2} \text{ day}^{-1}$ vs $9.2 \text{ g m}^{-2} \text{ day}^{-1}$, respectively; Lugo et al. 1978). Average annual simulated *GPP* in the pine flatwoods was half the *GPP* reported for a floodplain forest (approx. $56 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Brown 1981), which is characterized by high nutrient availability and floristic diversity. Rates of slash pine assimilation and respiration now being measured will soon provide data for comparison.

GPP in this model was influenced more by rainfall and solar radiation than by P. Simulated soil moisture (Figure 15) was frequently low enough to limit *GPP*, but relatively low *ET* rates in the fall (due to low temperatures; Figure 14) allowed more rapid recovery of soil moisture content after rainfall, particularly in the upper soil layer than in the spring and summer. Peak solar radiation in all three simulations occurred in the spring (March through May; Figure 3), and high rates of *GPP* were predicted for brief periods during the times when sufficient soil water was available (Figure 11a).

The pattern of change of available P differed considerably among the three simulations (Figure 17) but had little net effect on productivity. The simulated concentrations of P in the foliage of the pines showed much greater response to moisture conditions than has been reported in field studies (Figure 18; Mead and Pritchett 1974). A reasonable expected range is from 0.5 to 2.0 g g^{-1} , indicating that the scalar controlling P translocation from the wood to the foliage in the spring may not be restrictive enough. However, simulated P concentrations were also affected by the amount of foliage biomass and the rate of uptake from the soil, so that dilution effects may also play a role. Unfortunately, data on seasonal changes in whole-canopy chemistry are lacking.

Because P concentrations in pine needles were highest when foliage biomass was lowest and/or when soil moisture was limiting, their potential impact on *GPP* was minimal. Increasing the available P pool by fertilization had only a slight effect on foliage concentration and no effect at all on the annual rate of *GPP*. Mature slash pine stands apparently respond very slowly to increased P availability. Our ongoing research in a 21-yr-old stand found no increase in either LAI or net assimilation rates in the first year after quarterly additions of a complete fertilizer. The more dramatic effects of fertilization of younger plantations may be due to lower levels of available P. In the simulated P cycle in the mature plantation, mineralization associated with litter decomposition is the dominant contributor of available P (Figure 16).

The simulations indicate that Florida slash pine trees are metabolically active year-round and that daily *ANPP* rates (calculated as *GPP* minus aboveground respiration minus translocation to roots) can be substantial at any time of the year, depending on environmental conditions. Periods of negative *ANPP* indicate that an internal carbon storage, which is not a separate component in this version of the model, is being depleted to support respiration and translocation to roots. In the wet year, values were positive most of the year (Figure 11b). However, in the two other years, both characterized by a very dry spring, *ANPP* was consistently high only in the relatively cool fall and winter regardless of rainfall. Even though solar radiation was lowest during the fall and winter, and rainfall was not always abundant, lower temperatures reduced respiration directly and moisture stress indirectly through a reduction in VPD and hence transpiration.

Both *GPP* and *ANPP* of the mature slash pine stand therefore appear to be directly correlated with precipitation (primarily through short-term effects on soil moisture). Simulated productivity appears to be limited primarily by periods of low soil water availability during spring and summer months rather than by foliar P concentrations.

ANPP in a mature pine stand can vary from near 0 under the driest conditions to $3.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ under the wettest conditions. The low *ANPP* rate reflects the maturity of the stand and the accompanying lack of a significant annual biomass increment. Sharp fluctuations in all three simulations are caused by the sensitivity of *GPP* to changes in soil moisture and solar radiation (Figure 11a). The degree of fluctuation suggests that drainage systems, which may facilitate manipulation of heavy equipment during logging, site preparation, and planting activities, could decrease productivity during years of normal to low precipitation. Although the differences in stem productivity among the three simulations were negligible, a more substantial difference should appear in younger stands with larger stem biomass increments.

Changes in foliage biomass are obviously a critical determinant of both *ANPP* and *GPP*. Foliage biomass fluctuations were extreme in these simulations, with the lowest values almost 70% less than the highest (Figure 10). The simulation suggests that foliage biomass may decrease considerably because of both litterfall and internal translocation processes, but if bud phenology were modeled explicitly, some of the variability in both productivity and foliage biomass might be damped. Because no differentiation was made between the development of the typically large buds throughout the winter and emergence and growth of needles in the spring, the simulated large increases in January and February and decreases in April and May (Figure 10) reflect a combination of the buildup of stored carbon over the winter in buds, the depletion of this pool as new foliage emerges and "buds" become "twigs," and the transition of the new foliage from a net sink to a source of translocated carbon. A 16–28% change in the specific needle weight of Scots pine over a year (Flower-Ellis and Persson 1980) and a 23% change for *P. roxburghii* (Ralhan and Singh 1987) may be better representations of changes due to carbohydrate storage. The simulated fluctuations, however, suggest that seasonality in foliage biomass of slash pine stands is significant, and the contrast in climate years indicates that substantial differences may occur from year to year even in closed canopy evergreen stands.

Belowground

Our simulations suggest that C translocation to roots accounted for approximately one-third of slash pine *GPP*, regardless of variation in weather (Figure 9). Because of relatively slow turnover rates in fine roots and warm soil temperatures, fine root respiration accounted for most of the translocated C. The close agreement of our simulated soil respiration with field data (Figure 5) suggests that high water tables often encountered in these plantations have no significant effect on root respiration or mortality. Other research suggests that slash pine roots have very low root bulk density and water-filled volume, obtaining sufficient oxygen from stem lenticels to continue respiring under flooded conditions (Fisher and Stone 1990). Simulated mortality in our pine fine root category ranged from slightly more than 50% to slightly less than 75% of pine needlefall, depending on rainfall.

As with the aboveground rates, simulated translocation rates to roots and respiration and mortality rates of roots were adjusted so that amounts of biomass of all the living components at the end of the normal rainfall simulation were within 10% of the initial values. Measured values for dry weight of live fine roots in the litter in this stand (Gholz et al. 1986) were higher by 80 g/m² in April 1983 than 1984, suggesting that a steady-state assumption, as useful for calibration purposes as it may be, is not generally valid. In simulations for the wet and dry years, total live fine root biomass values (C) in the litter at the beginning and end of the year differed from steady-state values by -8 and +14 g/m², respectively, or about half the change measured in 1983-84 (Figure 6).

Simulated changes in rate (but not pattern) of C allocation in the wet and dry years (Figure 9) may be caused by changes in the state variables that supply the C. Effects of sunlight or P uptake on *GPP* and of temperature on respiration can all impact the amount of C that is fixed in the leaves and translocated to the stem and roots. Nevertheless, differences between simulated and measured net root production rates were generally small, especially for nonpine vegetation. Although simulated pine net root production (for all root sizes) was only 10% less than the field estimate (Gholz et al. 1986), mortality of pine fine roots (<10 mm in diameter) was 35% less. This indicates that the model underestimated pine fine root turnover, perhaps because it did not discriminate among size classes of fine roots. Field estimates suggest that pine roots <1 mm contributed 60% of total pine net root productivity (Gholz et al. 1986). The simulated estimates for nonpine roots may have been more similar to measured values because, although shrubs have fewer coarse roots, palmetto (the major contributor to this group) also has many fewer very fine roots.

Belowground components appeared to be little affected by annual weather differences. Simulated translocation in shrubs was proportional to aboveground biomass, which varied more in timing of fluctuations than in magnitude among the three simulations. Because simulated root respiration was proportional to root biomass, which changed little throughout the year, as well as to soil temperature, which was damped relative to air temperature, respiration and turnover rates were similar among the three simulations. Simulated slash pine root respiration ranged from 78% of the C translocated to roots in the wet year to more than 100% in the dry year.

COMPARISON WITH OTHER STUDIES

Hydrologic Cycle

In many ecosystems, the major link between the hydrologic cycle and other ecosystem functions is via export of nutrients in runoff and downward percolation. In north Florida flatwoods, however, vertical drainage is greatly impeded by clay layers underlying the surface sands, and flat topography precludes significant lateral drainage during high water. Consequently, simulated transpiration rates dominated the water budget (Figure 13), accounting for at least 90% of the water loss in a mature slash pine flatwoods. Water-mediated nutrient losses in the mature stand are therefore relatively low. This has important implications for groundwater relationships among adjacent ecosystems and for off-site nutrient losses in a landscape with low topography and high water tables. Simulated major interactions among the three cycles resulted from dramatic seasonal shifts from droughty to flooded conditions.

Our simulated interception rates of 11–13% were similar to those of pines elsewhere in north Florida: an interception rate of 12% of rainfall was measured in a nearby slash pine stand (Voss 1975), and interception in a variety of pine stands in North America averaged 14% (Helvey 1971, summarized in Waring et al. 1981).

Simulated daily transpiration rates (2.0–3.0 mm/day; maximum = 6.7) were similar to those not only of other slash pine stands (see Validity and Sensitivity of the Model) but of other temperate zone pines as well. For instance, Jarvis et al. (1976) reported pine transpiration rates that averaged approximately 3.4 mm/day, approaching 8 mm/day on occasion. This agreement suggests that the combination of variables we selected was sufficient for a stand-level model.

Carbon Dynamics

Large-scale C budgets outline the pathways of photosynthate through ecosystems over time. They facilitate comparisons of different ecosystems and the subsequent development of general guidelines concerning the effects of different substrates, climates, species, and management practices on ecosystem structure and function. Such budgets are often prepared by integrating both data and estimates in simulation models. The results may then be used as hypotheses to guide further research efforts to strengthen the data base of the model and, accordingly, of the ecosystem type.

Several ecosystem studies with detailed belowground analyses have now been completed on both plantations and natural stands (Table 3), and some estimation can be made of the variability among mature forests within this group. These include three pine plantations, from Sweden to the southern United States; four natural coniferous forests in the northwestern United States; and two midlatitude natural deciduous forests, one in the Atlantic Coastal Plain of the United States and the other in montane New Zealand. Two of the stands in the Pacific Northwest are over 100 years old; the other forests are less than 55 years old.

Aboveground Dynamics

Among the values reported for *GPP* and canopy net photosynthesis, only *GPP* in the old-growth *Pseudotsuga* stands is markedly different. *ANPP* in the stands varied with age, as expected. It was highest in the two hardwood stands and the young North Carolina pine stand. In one of the hardwood stands and the young North Carolina pine stand, *ANPP* represented more than one-third of *GPP*; it was 9% of *GPP* in the *P. elliotii* simulation and only 5% of *GPP* in the old-growth *Pseudotsuga* stand.

Among the few aboveground respiration measurements, the oldest (and most massive) stand had the highest value, which was 72% of estimated *GPP*. Aboveground respiration in the slash pine plantation was 55% of *GPP*, which is closer to the estimates of 49% and 50% for the young *P. taeda* plantation and the *Liriodendron* forest, respectively. Very low respiration at the *P. sylvestris* stand may be due to the short growing season and cold temperatures.

Belowground Biomass

In general, roots represent 15%–25% of total biomass in forests (Harris et al. 1980), but they appear to represent a higher proportion of biomass at sites of lower quality. In coniferous forests with C storages greater than 37.5 Mg/ha, values converge to 22.5% (Bazilevich and Rodin 1968). The studies listed in Table

3 conformed to these generalizations. Among all the stands, root biomass ranged between 9% and 24% of total biomass; in the coniferous stands, the range was between 10% and 21%, and biomass values in the two hardwood stands were among the lowest, even though the New Zealand *Nothofagus* stand was comprised almost entirely of coppice.

Productivity of both fine roots and total roots was much less variable than *ANPP*, differing by less than an order of magnitude. The Swedish pine forest and the 450-year-old *Pseudotsuga* stand had the lowest net root productivity values, but *BNPP* rates at these sites were not based on direct measurements. The percent of total annual *NPP* attributable to roots varied from 17% to 73%. The highest percentages were all from stands on sites with low fertility (Florida, Washington) and/or low average air temperatures (Sweden, subalpine Washington).

An interesting contrast with these stands is a very productive 12-yr-old plantation of *Pinus radiata* in New Zealand (Santantonio and Santantonio 1987). In this case, *ANPP* was estimated as 24 Mg ha⁻¹ yr⁻¹ (assuming 50% C in the biomass), fine root biomass <5 mm as 1.45 Mg ha⁻¹, and fine root production as 1.1 Mg ha⁻¹ yr⁻¹. Because most of the root production is included in this size range, *BNPP/TNPP* can be estimated as 4.4%, one-fourth of the lowest ratio for the other stands, supporting the trend of lower investment in roots on better sites.

Root turnover rates (productivity per unit biomass) showed much more variability. Highest turnover rates for all roots were in the two young pine plantations and the *Liriodendron* forest. Fine root turnover rates among the other stands were all between 0.26 and 1.0, including the *P. radiata* stand cited above. Root mortality was also variable; it was greater than litterfall in three stands, the 180-year-old *Abies* stand, the young *Abies* stand, and the young *P. taeda* plantation.

Root respiration rates represented 28% of GPP in the simulation of the slash pine plantation. Root respiration estimates in the other stands included 23% of GPP in the *Pseudotsuga* stand and 3% in the *P. taeda* plantation; 17% of net photosynthesis was allocated to root respiration in the *Liriodendron* forest and 12% in the *Nothofagus* forest. Our high rates were probably due to the year-long growing season and high average temperature. Root respiration rates per unit biomass were highest in the *P. elliotii* plantation and *Liriodendron* forest (0.40–0.48 g g⁻¹ yr⁻¹), intermediate in the *Nothofagus* forest and *Pseudotsuga* stand (0.22–0.33 g g⁻¹ yr⁻¹), and very low (0.05 and 0.06 g g⁻¹ yr⁻¹) in the *P. taeda* and *P. sylvestris* plantations, respectively.

How much of a C sink do roots in general represent? Among the stands with available data, the proportion of photosynthate that appeared to be translocated to roots (respiration plus net production) was lowest in the two youngest pine plantations. Among the other five sites for which gross or net canopy photosynthesis estimates were available, this proportion varied only from 22% to 43% (Table 3). The very low proportion in the *P. taeda* plantation may be due to serious underestimation of root respiration.

Accurate measurements of *GPP* coincident with measurements of root turnover and respiration are essential to understanding the role of roots in total ecosystem function. Absolute rates of belowground processes provide important and useful information about ecosystem function, but their greatest worth will be realized when they can be put into a larger context, such as a system-wide C budget.

APPENDIX

Table A-1. Differential equations used in the model. (See Table 1 for general formulations.) S = solar radiation, R = rainfall, V = vapor pressure deficit, T_a = air temperature, T_s = soil temperature. See Table A-2 for initial conditions, Table A.3 for functions (F_x), and Table A-4 for constants.

Q_1 = Pine foliage

$$dQ_1/dt = K_1 \cdot \frac{S}{1 + (K_2 \cdot Q_1)} \cdot (0.07 \cdot F_1 + 0.93 \cdot F_2) \cdot \frac{Q_{13}}{(K_3 \cdot Q_1) + Q_{13}} \cdot Q_1 \\ - K_4 \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_1 - K_5 \cdot F_3 \cdot Q_1 - K_6 \cdot F_4 \cdot Q_1$$

Q_2 = Pine stems and branches

$$dQ_2/dt = K_5 \cdot F_3 \cdot Q_1 - K_7 \cdot K_5 \cdot F_3 \cdot Q_1 - K_8 \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_2 - K_9 \cdot Q_2$$

Q_3 = Coarse pine roots

$$dQ_3/dt = K_7 \cdot K_5 \cdot F_3 \cdot Q_1 - K_{10} \cdot Q_3 - K_{11} \cdot Q_3 \cdot Q_9 - K_{12} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_3 \\ - K_{13} \cdot Q_3$$

Q_4 = Fine pine roots in mineral soil

$$dQ_4/dt = K_{10} \cdot Q_3 - K_{14} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_4^2 - K_{15} \cdot Q_4$$

Q_5 = Fine pine roots in litter layer

$$dQ_5/dt = K_{11} \cdot Q_3 \cdot Q_9 - K_{16} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_5^2 - K_{17} \cdot Q_5$$

Q_6 = Shrubs

$$dQ_6/dt = K_{18} \cdot \frac{S \cdot e^{-F_5}}{1 + (K_{19} \cdot Q_6)} \cdot (0.5 \cdot F_1 + 0.5 \cdot F_2) \cdot \frac{Q_{14}}{(K_{13} \cdot Q_6) + Q_{14}} \cdot Q_6 \\ - K_{20} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_6^2 - K_{21} \cdot F_6 \cdot F_7 \cdot Q_6 - K_{22} \cdot F_4 \cdot Q_6$$

Q_7 = Shrub roots

$$dQ_7/dt = K_{21} \cdot F_6 \cdot F_7 \cdot Q_6 - K_{23} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_7 - K_{24} \cdot Q_6$$

Q_8 = Herbs

$$dQ_8/dt = K_{25} \cdot \frac{S \cdot e^{-F_5} \cdot e^{-F_8}}{1 + (K_{26} \cdot Q_8)} \cdot \frac{F_1 \cdot Q_{15}}{(K_3 \cdot Q_8) + Q_{15}} \cdot Q_8 \cdot F_9 \\ - K_{27} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_8^2 - K_{28} \cdot F_{10} \cdot Q_8$$

Q_9 = Litter

$$dQ_9/dt = K_6 \cdot F_4 \cdot Q_1 + K_9 \cdot Q_2 + K_{17} \cdot Q_5 + K_{22} \cdot F_4 \cdot Q_6$$

$$+ 0.5 \cdot K_{28} \cdot F_{10} \cdot Q_8 - K_{29} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_9$$

$$- K_{30} \cdot K_{29} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_9$$

Q_{10} = Dead roots

$$dQ_{10}/dt = K_{13} \cdot Q_3 + K_{15} \cdot Q_4 + K_{17} \cdot Q_5 + K_{24} \cdot Q_7 - K_{31} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_{10}$$

$$- K_{32} \cdot Q_{10}$$

Q_{11} = Soil particulate organic matter

$$dQ_{11}/dt = .5 \cdot K_{28} \cdot F_{10} \cdot Q_8 + K_{30} \cdot K_{29} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_{19} + K_{32} \cdot Q_{10}$$

$$- K_{33} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_{11}$$

Q_{12} = Phosphorus in pine wood

$$dQ_{12}/dt = K_{34} \cdot \frac{Q_{19}}{K_{35} + Q_{19}} \cdot Q_1 \cdot F_{11} \cdot (0.07 \cdot F_1 + 0.93 \cdot F_2)$$

$$+ (K_{36} \cdot F_3 \cdot F_2 \cdot Q_{13} - K_{37} \cdot F_{13} \cdot Q_{12})$$

$$- K_{38} \cdot \frac{Q_{12}}{Q_2 + Q_3 + Q_4 + Q_5} \cdot K_9 \cdot Q_2$$

$$- K_{39} \cdot \frac{Q_{12}}{Q_2 + Q_3 + Q_4 + Q_5} \cdot [(K_{13} \cdot Q_3) + (K_{15} \cdot Q_4)$$

$$+ (K_{17} \cdot Q_5)]$$

Q_{13} = Phosphorus in pine foliage

$$dQ_{13}/dt = K_{37} \cdot F_{13} \cdot Q_{12} - K_{36} \cdot F_3 \cdot F_{12} \cdot Q_{12} - K_{40} \cdot Q_{13} \cdot K_6 \cdot F_4 \cdot Q_1$$

Q_{14} = Phosphorus in shrubs

$$dQ_{14}/dt = K_{41} \cdot (Q_6 + Q_7) \cdot \frac{Q_{19}}{K_{42} + Q_{19}} \cdot (0.5 \cdot F_1 + 0.5 \cdot F_2)$$

$$- K_{22} \cdot F_4 \cdot Q_6 \cdot \frac{Q_{14}}{(Q_6 + Q_7)} - K_{43} \cdot \frac{Q_{14}}{(Q_6 + Q_7)} \cdot K_{24} \cdot Q_6$$

Q_{15} = Phosphorus in herbs

$$dQ_{15}/dt = K_{44} \cdot \frac{Q_{15} \cdot Q_{14}}{(K_{25} + Q_{14})} - K_{28} \cdot F_{10} \cdot Q_{15}$$

Q_{16} = Phosphorus in litter

$$dQ_{16}/dt = \left(K_{40} \cdot Q_{13} \cdot K_6 \cdot F_4 + \frac{K_{38} \cdot Q_{12} \cdot K_9 \cdot Q_2}{Q_2 + Q_3 + Q_4 + Q_5} \right.$$

$$\left. + K_{22} \cdot F_4 \cdot \frac{Q_6 \cdot Q_{14}}{Q_6 + Q_7} + 0.5 \cdot K_{28} \cdot F_{10} \cdot Q_{15} \right)$$

$$+ K_{28} \cdot \frac{Q_{16}}{Q_9} \cdot K_{17} \cdot Q_5 - K_{30} \cdot K_{29} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_{16}$$

$$- K_{49} \cdot K_{29} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_{16} - K_{46} \cdot K_{47} \cdot Q_{21}(1 - F_{14}) \cdot Q_{16}$$

Q_{17} = Phosphorus in dead roots

$$dQ_{17}/dt = K_{48} \cdot \frac{Q_{12}}{Q_2 + Q_3 + Q_4 + Q_5} \cdot [(K_{13} \cdot Q_3) + (K_{15} \cdot Q_4)] \\ + K_{43} \cdot \frac{Q_{14}}{Q_6 + Q_7} \cdot K_{24} \cdot Q_6 - K_{50} \cdot K_{31} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_{17} \\ - K_{32} \cdot Q_{17}$$

Q_{18} = Phosphorus in soil particulate organic matter

$$dQ_{18}/dt = K_{50} \cdot K_{31} \cdot 3^{\frac{T_a - 20}{10}} \cdot Q_{17} + K_{32} \cdot Q_{17} + 0.5 \cdot F_{10} \cdot Q_{15} \\ - K_{51} \cdot K_{33} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_8$$

Q_{19} = Available inorganic phosphorus

$$dQ_{19}/dt = K_{52} \cdot R + K_{53} \cdot Q_{20} \cdot F_2 + K_{49} \cdot K_{29} \cdot 3^{\frac{T_a - 25}{10}} \cdot Q_{16} \\ + K_{51} \cdot K_{33} \cdot 3^{\frac{T_s - 20}{10}} \cdot Q_{18} + K_{32} \cdot Q_{17} \\ - \left[K_{34} \cdot \frac{Q_{19}}{K_{35} + Q_{19}} \cdot Q_1 \cdot F_{11} \cdot (0.07 \cdot F_1 + 0.93 \cdot F_2) \right. \\ + K_{41} \cdot (Q_6 + Q_7) \cdot \frac{Q_{19}}{K_{42} + Q_{19}} \cdot (0.5 \cdot F_1 + 0.5 \cdot F_2) \\ \left. + K_{44} \cdot Q_8 \cdot \frac{Q_{19}}{K_{45} + Q_{19}} \right] - K_{54} \cdot Q_{19} - K_{55} \cdot Q_{19} \\ \cdot [K_{47} \cdot Q_{21}(1 - F_{14})]^2 - K_{56} \cdot K_{57} \cdot 4.5 \cdot Q_{19} \cdot Q_{21}$$

Q_{20} = Unavailable inorganic phosphorus

$$dQ_{20}/dt = K_{54} \cdot Q_{19} - K_{53} \cdot Q_{20} \cdot F_2 - K_{58} \cdot Q_{20} \cdot [K_{47} - Q_{21} \\ \cdot (1 - F_{14})]^2$$

Q_{21} = Soil water in upper layer

$$dQ_{21}/dt = [R - (K_{59} \cdot R \cdot Q_1 + Q_6)] - K_{60} \cdot S \cdot e^{-F_5} \cdot e^{-F_8} \cdot e^{-F_{15}} \\ \cdot (1 - F_{14}) - K_{61} \cdot Q_1 \cdot F_1 \cdot V - K_{62} \cdot \frac{S \cdot e^{-F_5}}{1 + (K_{19} \cdot Q_6)} \cdot Q_6 \cdot F_1 \\ - K_{63} \cdot \frac{S \cdot e^{-F_5} \cdot e^{-F_8}}{1 + (K_{26} \cdot Q_{28})} \cdot Q_8 \cdot F_1 - K_{47} \cdot Q_{21} \cdot (1 - F_{14}) \\ - F_{16} \cdot F_{17} \cdot Q_{21}$$

Q_{22} = Soil water in lower layer

$$dQ_{22}/dt = F_{16} \cdot F_{17} \cdot Q_{21} - K_{64} \cdot Q_1 \cdot F_2 \cdot V - K_{65} \cdot \frac{S \cdot e^{-F_6}}{1 + (K_{19} \cdot Q_6)} \cdot Q_6 \cdot F_2 \\ - K_{57} \cdot 4.5 \cdot Q_{21}$$

TABLE A-2.

Initial conditions of state variables used in equations listed in Table A-1.

State Variable	Amount (g/m ²)
Q ₁ : Pine foliage, C	390.
Q ₂ : Pine stems and branches, C	7450.
Q ₃ : Coarse pine roots, C	1000.
Q ₄ : Fine pine roots in mineral soil, C	340.
Q ₅ : Fine pine roots in litter layer, C	100.
Q ₆ : Shrubs, C	60.
Q ₇ : Shrub roots, C	590.
Q ₈ : Herbs, C	7.
Q ₉ : Litter, C	1700.
Q ₁₀ : Dead roots, C	350.
Q ₁₁ : Soil particulate organic matter, C	6560.
Q ₁₂ : Phosphorus in pine wood	2.
Q ₁₃ : Phosphorus in pine foliage	0.29
Q ₁₄ : Phosphorus in shrubs	1.
Q ₁₅ : Phosphorus in herbs	0.01
Q ₁₆ : Phosphorus in litter	1.
Q ₁₇ : Phosphorus in dead roots	6.97 E-2
Q ₁₈ : Phosphorus in soil particulate organic matter	1.1
Q ₁₉ : Available inorganic phosphorus	0.1
Q ₂₀ : Unavailable inorganic phosphorus	30.
Q ₂₁ : Soil water in upper layer	46. mm
Q ₂₂ : Soil water in lower layer	100. mm

TABLE A-3.

Functions used in equations listed in Table A-1. Y = Time of year (0. = Jan; 1. = 31 Dec). When the value of a state variable (or time) falls between the values given below, the value of the function is calculated by linear extrapolation from the next highest to the next lowest.

$$F_1 = \begin{cases} 1. & \text{if } Q_{21} \geq 21. \\ 0.1 & \text{if } Q_{21} = 20. \\ 0. & \text{if } Q_{21} = 0. \end{cases}$$

F_1 decreases the photosynthesis rate when water in the top soil horizon becomes limiting. Interpretation of the soil moisture curve for this horizon suggests that limitation may begin at 33% of saturation. We assumed that photosynthesis would be an order of magnitude lower at 31% of saturation and would decrease linearly as soil moisture approached zero.

$$F_2 = \begin{cases} 1. & \text{if } Q_{22} \geq 65. \\ 0.01 & \text{if } Q_{22} = 61. \\ 0. & \text{if } Q_{22} = 0. \end{cases}$$

F_2 decreases the photosynthesis rate when water in the lower soil horizon becomes limiting. Interpretation of the soil moisture curve for this horizon suggests that limitation may begin at 23% of saturation. We assumed that photosynthesis would be two orders of magnitude lower at 21% of saturation and would decrease linearly as soil moisture approached zero. The same function limits the rate at which unavailable P becomes available with decreases in soil moisture.

$$F_3 = \begin{cases} 1. & \text{if } 0.3 \leq Y \leq 0.8 \\ 0.4 & \text{if } 0. \leq Y \leq 0.2, Y = 1.0 \end{cases}$$

F_3 affects the relative rate of translocation of carbon from foliage to wood and from wood to roots; this function is shown in Figure 1a. We assumed that this function would increase with foliage biomass and remain constant through the summer because of continued needle growth during this time (Hendry and Gholz 1986). During the times when F_3 remains constant, translocation is proportional to foliage biomass.

$$F_4 = \begin{cases} 1.4 & \text{if } 0.8 \leq Y \leq 0.95 \\ 0.66 & \text{if } 0.55 \leq Y \leq 0.7 \\ 0.63 & \text{if } Y = 0., Y = 1. \\ 0.42 & \text{if } 0.1 \leq Y \leq 0.45 \\ 0.26 & \text{if } 0.05 \leq Y \leq 0.2 \end{cases}$$

F_4 affects the relative rate of litterfall in both pines and shrubs. The function follows observed phenology (Gholz 1985b). Actual litterfall rates also depend on foliage biomass.

$$F_5 = \begin{cases} 1. & \text{if } Q_1 \geq 300. \\ 0. & \text{if } Q_1 = 0. \end{cases}$$

F_5 is a scalar that determines the shading effect of pine foliage on photosynthesis in shrubs. We assumed that maximum shade (37% of incident sunlight) is reached when carbon in pine foliage is 300 g/m².

$$F_6 = \begin{cases} 0.4 & \text{if } 0 \leq Y \leq 0.12, 0.75 \leq Y \leq 1 \\ 0.3 & \text{if } Y = 0.25, Y = 0.58 \\ 0.1 & \text{if } 0.33 \leq Y \leq 0.5 \end{cases}$$

F_6 affects the relative rate of translocation of carbon from aboveground to belowground shrub biomass. We assumed that this rate decreases in mid-summer.

$$F_7 = \begin{cases} 1. & \text{if } K_{21} \cdot F_6 \cdot Q_6 \leq 500. \\ \frac{500.}{K_{31} \cdot F_3 \cdot Q_6} & \text{if } K_{21} \cdot F_6 \cdot Q_6 > 500. \end{cases}$$

F_7 prevents the rate of translocation of carbon from aboveground to belowground shrub biomass from exceeding an upper threshold. This function was included to control the behavior of shrub biomass in simulations evaluating management practices not discussed in this paper.

$$F_8 = \begin{cases} 1. & \text{if } Q_6 \geq 200. \\ 0. & \text{if } Q_6 = 0. \end{cases}$$

F_8 is a scalar that determines the shading effect of understory biomass on photosynthesis in herbs. We assumed that the maximum effect of this component (37%) is reached when carbon in aboveground shrub biomass is 200 g/m².

$$F_9 = \begin{cases} 1. & \text{if } Q_9 = 0. \\ 0. & \text{if } Q_9 \geq 2000. \end{cases}$$

F_9 is a scalar that decreases herb photosynthesis as litter accumulates. This function was included to reflect the decrease in germination success observed in a growing stand and has no significant effect on the simulations discussed in this paper.

$$F_{10} = \begin{cases} 1. & \text{if } 0.13 \geq Y \geq 0.96 \\ 0. & \text{if } 0.13 < Y < 0.96 \end{cases}$$

F_{10} simulates frost-induced mortality in herbs between mid-December and mid-February.

$$F_{11} = \begin{cases} 0.5 & \text{if } Y = 0.2 \\ 0.3 & \text{if } 0.3 \leq Y \leq 1. \end{cases}$$

F_{11} affects the relative rate of P uptake by pine trees and is shown in Figure 1c. We assumed that this would increase in spring. Uptake is also affected by concentration of available phosphorus, foliage biomass, and soil moisture.

$$F_{12} = \begin{cases} 3. & \text{if } Y = 0.75 \\ 2. & \text{if } Y = 0.7, 0.8 \\ 1. & \text{if } Y = 0., 1. \\ 0.2 & \text{if } Y = 0.65 \end{cases}$$

F_{12} affects the relative rate of P translocation in pine trees from foliage into wood; the pattern is shown in Figure 1c. We assumed that this rate would peak in the fall before abscission of the 2-yr-old needles.

$$F_{13} = \begin{cases} 10. & \text{if } Y = 0.3 \\ 5. & \text{if } Y = 0.2 \\ 1. & \text{if } 0.4 \leq Y \leq 1. \end{cases}$$

F_{13} affects the relative rate of P translocation in pine trees from roots and wood to foliage; the pattern is shown in Figure 1c. We assumed that this rate would increase in spring, peaking slightly later than the rate of uptake. Simulated P translocation is also affected by the concentration of P in the wood.

$$F_{14} = \begin{cases} 1. & \text{if } Q_{21} \geq 64 \\ 0. & \text{if } Q_{21} < 64. \end{cases}$$

F_{14} allows evaporation and runoff to occur when water in the upper soil horizon reaches saturation.

$$F_{15} = \begin{cases} 1. & \text{if } Q_8 \geq 300. \\ 0. & \text{if } Q_8 = 0. \end{cases}$$

F_{15} is a scalar that determines the shading effect of herbs on the rate of evaporation from the forest floor. We assumed that maximum shade is reached when C in herb biomass equals 300 g/m².

$$F_{16} = \begin{cases} 0. & \text{if } Q_{21} \leq 21. \\ 6. & \text{if } Q_{21} = 24. \\ 20. & \text{if } Q_{21} = 27. \\ 80. & \text{if } Q_{21} = 30. \\ 170. & \text{if } Q_{21} = 33. \\ 450. & \text{if } Q_{21} = 37. \\ 1000. & \text{if } Q_{21} \geq 41. \end{cases}$$

F_{16} reflects the rate of percolation from the upper soil horizon to the lower soil horizon and is based on hydraulic conductivity data.

$$F_{17} = \begin{cases} 1. & \text{if } Q_{22} \geq 288. \\ 0. & \text{if } Q_{22} \leq 288. \end{cases}$$

F_{17} stops percolation from the upper soil horizon to the lower soil horizon when saturation of the lower horizon is reached.

TABLE A-4.

Values of constants used in equations listed in Table A-1.

Constant	Value	Units	Constant	Value	Units
K_1	3.46 E-2	m ² /MJ	K_{11}	1.2E-4	m ² · gC ⁻¹ · yr ⁻¹
K_2	0.6	gC ⁻¹	K_{12}	0.227	yr ⁻¹
K_3	1.75 E-4	gP/gC	K_{13}	0.014	yr ⁻¹
K_4	4.4	yr ⁻¹	K_{14}	2.4E-3	m ² · gC ⁻¹ yr ⁻¹
K_5	8.26	yr ⁻¹	K_{15}	0.25	yr ⁻¹
K_6	1.22	yr ⁻¹	K_{16}	0.36	m ² · gC · yr ⁻¹
K_7	0.51		K_{17}	0.34	yr ⁻¹
K_8	0.13	yr ⁻¹	K_{18}	2.1E-2	m ² /MJ
K_9	6.73E-3	yr ⁻¹	K_{19}	0.1	gC ⁻¹
K_{10}	0.33	yr ⁻¹	K_{20}	0.012	m ² · gC ⁻¹ · yr ⁻¹

Constant	Value	Units	Constant	Value	Units
K_{21}	10.5	yr^{-1}	K_{34}	1.5E-3	$\text{gP} \cdot \text{gC}/\text{yr}$
K_{22}	0.76	yr^{-1}	K_{35}	1.E-2	gP/m^2
K_{23}	0.24	yr^{-1}	K_{36}	0.214	yr^{-1}
K_{24}	0.175	yr^{-1}	K_{37}	0.04	yr^{-1}
K_{25}	7.7E-2	m^2/MJ	K_{38}	0.20	
K_{26}	0.8	gC^{-1}	K_{39}	1.2	
K_{27}	0.12	$\text{m}^2 \cdot \text{gC}^{-1} \cdot \text{yr}^{-1}$	K_{40}	0.46	gC^{-1}
K_{28}	6.	yr^{-1}	K_{41}	2.E-4	$\text{gP} \cdot \text{gC}^{-1} \cdot \text{yr}^{-1}$
K_{29}	0.208	yr^{-1}	K_{42}	1.2E-4	gP/m^2
K_{30}	0.0227		K_{43}	0.1	$\text{gC}^{-1} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$
K_{31}	0.151	yr^{-1}	K_{44}	1.96-3	yr^{-1}
K_{32}	2.55	yr^{-1}	K_{45}	3.E-2	yr^{-1}
K_{33}	0.027	yr^{-1}	K_{46}	1.2E-5	$\text{gP}/\text{gH}_2\text{O}$

Constant	Value	Units
K_{47}	0.4	yr^{-1}
K_{48}	1.2	
K_{49}	2.	gP/gC
K_{50}	2.	gP/gC
K_{51}	2.	gP/gC
K_{52}	1.5E-5	$\text{gP}/\text{gH}_2\text{O}$
K_{53}	0.051	gP/gC
K_{54}	14.	yr^{-1}
K_{55}	5.E-6	$\text{m}^4 \cdot \text{yr}/(\text{gH}_2\text{O})^2$
K_{56}	5.E-4	$\text{m}^2/\text{gH}_2\text{O}$
K_{57}	0.05	yr^{-1}
K_{58}	1.1E-9	$\text{m}^4 \cdot \text{yr}/(\text{gH}_2\text{O})^2$
K_{59}	4.E-4	m^2/gC
K_{60}	0.01	m^2/MJ
K_{61}	0.24	$\text{gH}_2\text{O} \cdot \text{yr}^{-1} \cdot \text{gC}^{-1} \cdot \text{kPa}^{-1}$
K_{62}	4.4E-4	$\text{gH}_2\text{O} \cdot \text{m}^2 \cdot \text{yr}^{-1} \cdot \text{MJ}^{-1} \cdot \text{gC}^{-1}$
K_{63}	7.18E-5	$\text{gH}_2\text{O} \cdot \text{m}^2 \cdot \text{yr}^{-1} \cdot \text{MJ}^{-1} \cdot \text{gC}^{-1}$
K_{64}	6.5	$\text{gH}_2\text{O} \cdot \text{yr}^{-1} \cdot \text{gC}^{-1} \cdot \text{kPa}^{-1}$
K_{65}	3.5E-4	$\text{gH}_2\text{O} \cdot \text{yr}^{-1} \cdot \text{MJ}^{-1} \cdot \text{gC}^{-1}$

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