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Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles

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Abstract. The interactions between the biotic processes of reproduction, growth, and death and the abiotic processes which regulate temperature and water availability, and the interplay between the biotic and abiotic processes regulating N and light availabilities are important in the dynamics of forest ecosystems. We have developed a computer simulation that assembles a model ecosystem which links these biotic and abiotic interactions through equations that predict decomposition processes, actual evapotranspiration, soil water balance, nutrient uptake, growth of trees, and light penetration through the canopy. The equations and parameters are derived directly from field studies and observations of forests in eastern North America, resulting in a model that can make accurate quantitative predictions of biomass accumulation, N availability, soil humus development and net primary production.

Introduction

Interactions between demographic processes regulating plant populations, microbial processes and climatic factors regulating nitrogen availability, and climatic and geologic factors regulating water availability may explain much of the observed variation in ecosystem carbon and nitrogen storage and cycling (Figure 1). In this view, geomorphology, soil texture, and climate are constraints within which feedbacks between vegetation and light or nitrogen availabilities operate. These geologic and climatic factors constrain these feedbacks by affecting plant and microbial physiology and thereby affecting species composition. Ecosystem feedbacks therefore work within a geological framework. This concept can be found in the classic writings of Cooper (1923), Raup (1941), Billings (1941), Kittredge (1948), and Jenny (1941, 1980). Recently, several field studies have suggested that species replacement along geologic or climatic gradients causes changes in ecosystem properties (Monk, 1966; Van Cleve et al., 1983; Pastor et al., 1984; McClaugherty et al., 1985).

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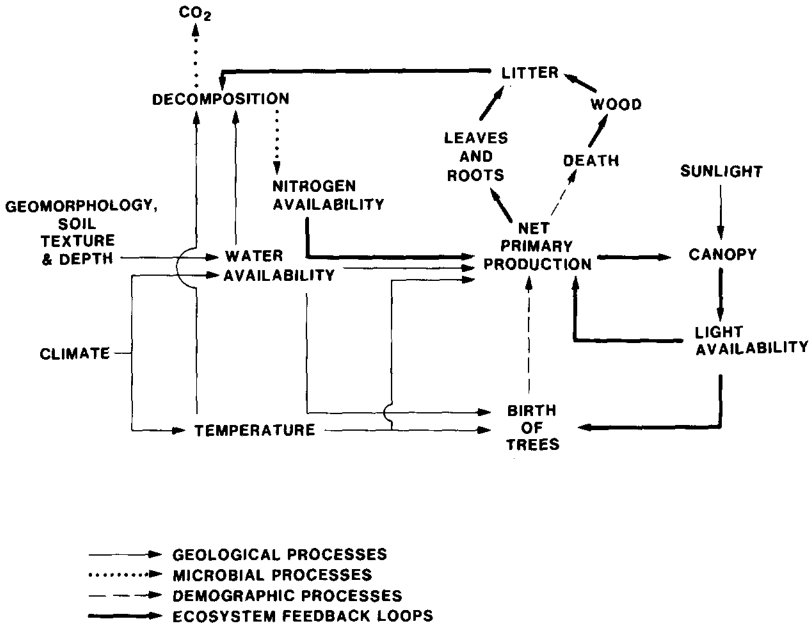


Figure 1. Hypothesized interactions between geological, microbial, and demographic processes, and ecosystem feedback loops.

We have developed a simulator that assembles model forest ecosystems according to this hypothesized configuration. The *JABOWA* class of tree population models (Botkin et al., 1972; Shugart and West, 1977) is used as a basis because they predict ecosystem dynamics through the interaction between vegetation and available resources. Aber et al. (1982) and Weinstein et al. (1982) modified these models to simulate ecosystem nutrient cycles. Mann and Post (1980) modified Shugart and West's (1977) model to include effects of soil water deficits on tree growth. Solomon et al. (1984) generalized Mann and Post's model to predict species composition of most upland forests of eastern North America from climatic and soil moisture factors. We combined some of the features of the Aber et al. (1982) and Solomon et al. (1984) models and incorporated more recent data on carbon and nitrogen dynamics during decomposition to examine the interactions between climate, soil moisture, and carbon and nitrogen cycles during stand development. We believe this is the first attempt to formulate a forest ecosystem model with explicit feedbacks between light, water, and nitrogen availabilities and their resultant effects on productivity and species composition.

Model structure

A complete description of the model is given by Pastor and Post (1985). The basic structure of the model is a set of three subroutines (*Tempe, Moist, Decomp*) which determine site conditions (degree-days, available soil water, available soil N, respectively) and a set of three demographic subroutines (*Birth, Grow, Kill*) which calculate tree growth and population dynamics (Figure 2). These two sets of subroutines are linked by a subroutine (*Gmult*) which calculates degree-day, soil moisture, and soil nitrogen growth multipliers. The amount of light available to each tree, an additional site

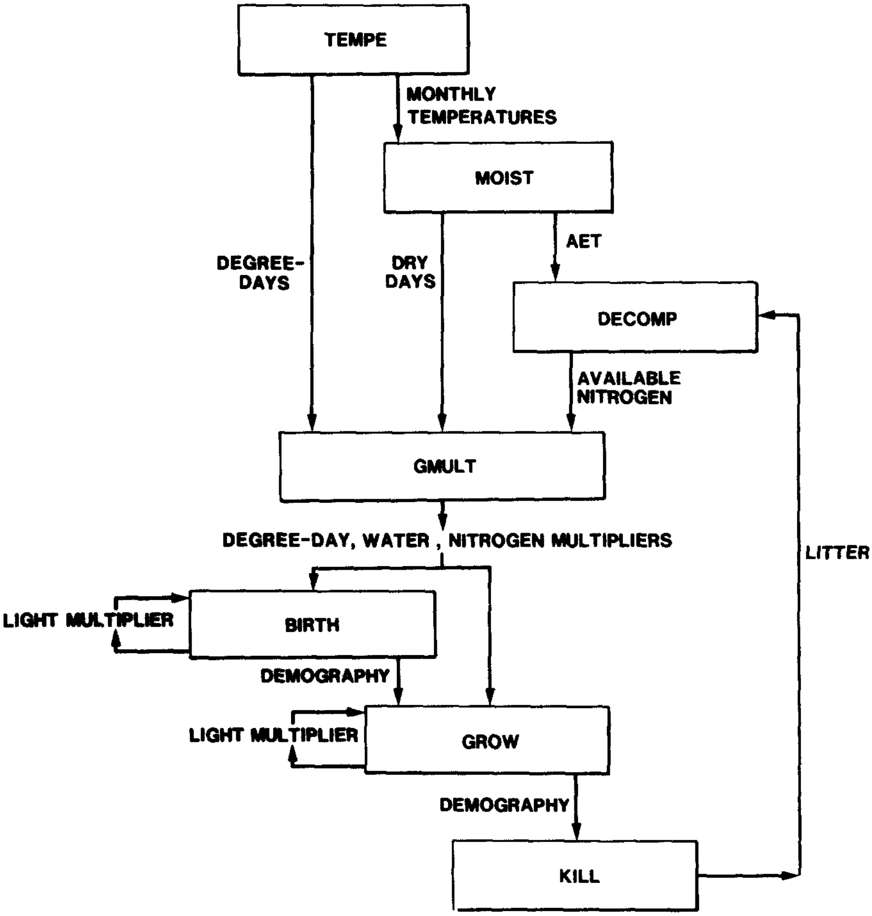


Figure 2. Model flowchart. Rectangles represent subroutines, and arrows indicate important information flows between subroutines.

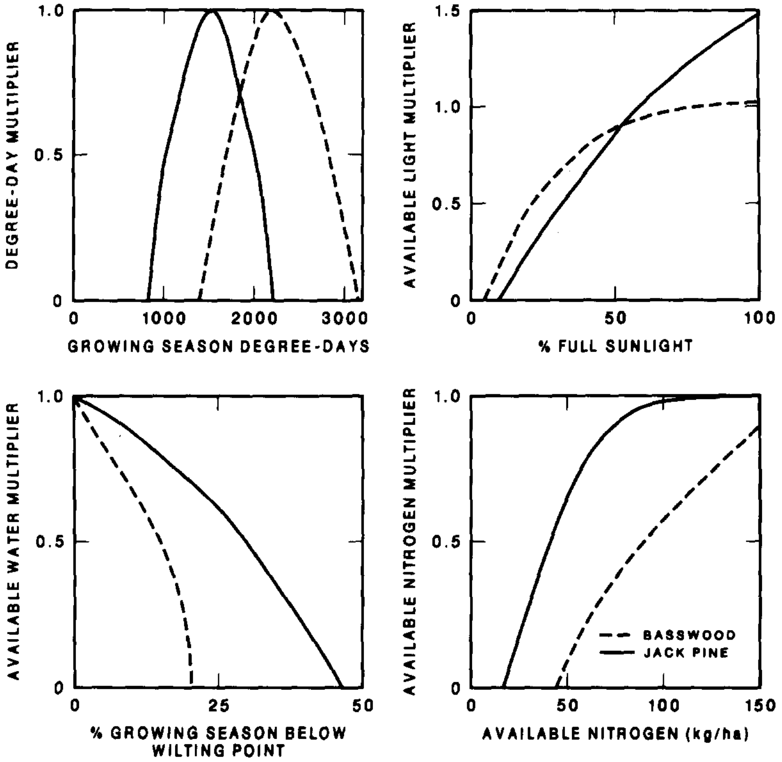


Figure 3. Growth multiplier curves for jack pine and basswood, two very different northern species.

characteristic, is a function of the forest canopy structure and is modeled in both *Birth* and *Grow*. Subroutines *Moist* and *Decomp* implement the equations modeling soil water and N availability described below. Subroutine *Tempe* calculates monthly temperatures, which vary stochastically around mean values.

Growth multipliers (Figure 3) decrease reproduction and diameter growth from optimal values. Soil moisture multipliers and soil N multipliers are calculated as described below. Degree-day multipliers are symmetrically parabolic between the minimum and maximum degree-days tolerated by each species (Botkin et al., 1972). Light extinction through the canopy is a negative exponential function of leaf biomass (Botkin et al., 1972; Aber et al., 1982) and the light multipliers for shade-tolerant and shade-intolerant species are from a model by Shugart and West (1977).

The birth of trees is calculated in a manner similar to that of Aber et al. (1982) using degree-day, soil moisture, and light multipliers to decrease species-specific reproduction rates from maximal values reported from clearcuts. Initial diameter at breast height (dbh) is stochastically chosen between 1.27 and 1.57 cm.

The growth of each tree starts with an optimal diameter increment, depending on the species, tree size, and age (Botkin et al., 1972). Unlike all previous versions of these models which decrease growth of each tree using all available multipliers, we decrease growth from optimum using only the multiplier of the resource that is most restrictive to growth.

Leaf biomass is predicted from allometric relationships between dbh, crown area, leaf weight per unit crown area (Aber et al., 1982), and foliage retention time in years (1 for deciduous trees, 2 for pines, and 3 for other conifers). The woody biomass of each tree is predicted from an allometric function of dbh (Sollins et al., 1973). The annual woody biomass production of each tree is the net increase in wood biomass after dbh is incremented.

The probability of mortality for each tree increases with age (Botkin et al., 1972) and if its diameter growth is less than a specified amount for two consecutive years (Solomon et al., 1984).

Litter is added to the soil at the end of each year and begins to decay the following year. Leaf litter production is calculated as was leaf biomass, without multiplying by foliage retention time, unless the tree is dead. Wood litter from dead trees is calculated as was woody biomass, assuming a 40% decline in density during a standing dead period (Aber et al., 1982). Fine root litter is assumed to be 30% greater than leaf litter (Aber et al., 1982).

Simulated plot size is 1/12-ha, which corresponds to the average gap size created by a dominant tree in eastern North American forests (Shugart and West, 1979).

Modeling forest-soil interactions

Evapotranspiration and water deficits

We used the method of Thornthwaite and Mather (1957) to predict evapotranspiration and water deficits because of its low data requirements and high correlations with ecosystem processes such as net primary production (Rosenzweig, 1968) and decay rates (Meentemeyer, 1978). Potential evapotranspiration (PET) is empirically related to latitude and monthly temperature (Thornthwaite and Mather, 1957). When precipitation is less than PET, the difference is partly supplied from soil water storage. Thornthwaite and Mather (1957) empirically relate the amount of water retained in the soil (W_r) to the soil's field moisture capacity (FC) and accumulated potential monthly water loss (ACCPWL). Pastor and Post (1984) summarize this relationship as:

$$W_r = \mathrm{FC} \exp((0.000461 - 1.10559/\mathrm{FC})\mathrm{ACCPWL}) \qquad (1)$$

where all variables are in centimeters of water.

For those months when PET is greater than precipitation, the actual evapotranspiration (AET) is precipitation plus the change in W_r from the previous month to the current month. For months when PET is less than precipitation, AET equals PET. Excess water is added to W_r, or if the soil is at field capacity, it is assumed to run off or drain. The amount of soil water, in cm, is tracked monthly and the proportion of the growing season in which soil water is below a specified wilting point (see below) is calculated as an index of plant moisture stress.

Effects of water on growth

Available soil moisture is an important variable in determining the growth rates of forest trees. Water stress in plants is difficult to evaluate in the field by leaf water potential or other direct methods (Zahner and Stage, 1966; Morrow and Slatyer, 1971; Sucoff, 1972; Federer and Gee, 1976; Reich and Hinckley, 1980) because of the temporal and spatial variance of water potential within a tree (Hinckley et al., 1978) or within a stand of trees. Also, the relationship between soil water tension and leaf water potential is not known with sufficient detail for most species of trees.

Mann and Post (1980) developed a general method of identifying species-specific parameters that express the relationship between soil moisture availability and tree growth for any upland tree species in eastern North America. A parameter, d_i, is defined for each species, i, as the fraction of growing season 'drought' days that species i can tolerate before all annual growth is prevented. A drought day is one in which soil moisture is below a critical soil moisture tension of -15×10^5 Pa, i.e., the soil wilting point specified above. The parameter d_i is identified in a manner similar to growing degree days (Botkin et al., 1972) by examining the range of soil moisture conditions that species i encounters in its geographical range. In eastern North America, the soil moisture conditions at the southwestern or most xeric edge of a species' range is used to determine d_i (Table 1, Figure 4). This is used to define a species-specific function, $S_{W,i}$, that relates soil moisture conditions and tree growth. At one extreme, where the number of drought days is zero, the potential growth or diameter increment is not reduced ($S_{W,i} = 1$). At the other extreme, determined by observing the soil moisture conditions at the most xeric edge of a species' range (Little, 1971, 1977), the potential growth or diameter increment is reduced to zero ($S_{W,i} = 0$). Basset (1964) found that basal area increment in southern pines is linearly related to the number of growing season days with adequate soil moisture. We therefore define $S_{W,i}$ for the diameter increment as:

$$\begin{aligned} S_{W,i} &= (1 - D/d_i)^{1/2} \qquad && D < d_i; \\ S_{W,i} &= 0 && D \geqslant d_i, \end{aligned} \tag{2}$$

where D is the fraction of drought days during the growing season.

Table 1. Species tolerance and litter quality parameters

Species name	Tolerance[a]			Leaf litter quality class[b]
	Drought (d_i)	N	Shade	
Abies balsamea	0.165	1	1	10
Abies fraseri	0.025	1	2	10
Acer rubrum	0.230	1	2	2
Acer saccharinum	0.268	1	2	2
Acer saccharum	0.080	2	1	2
Aesculus octandra	0.175	3	1	5
Betula allegenesis	0.200	2	1	4
Betula lenta	0.177	2	1	4
Betula papyrifera	0.280	1	2	4
Betula populifolia	0.130	1	2	4
Carpinus caroliniana	0.300	3	1	9
Carya cordiformis	0.320	2	1	4
Carya glabra	0.200	2	1	4
Carya laciniosa	0.220	2	1	4
Carya ovata	0.200	2	1	4
Carya texana	0.478	2	1	4
Carya tomentosa	0.300	2	1	4
Castanea dentata	0.300	3	1	2
Celtis laevigata	0.085	3	1	2
Cornus florida	0.250	3	1	1
Fagus grandiflolia	0.200	2	1	8
Fraxinus americana	0.280	3	1	2
Fraxinus nigra	0.022	3	2	2
Fraxinus pennsylvania	0.114	3	2	2
Fraxinus quadrangulata	0.200	3	2	2
Juglans cinerea	0.200	2	2	9
Juglans nigra	0.300	2	2	9
Juniperus virginiana	0.397	1	2	6
Larix laricina	0.267	1	1	12
Liquidambar styraciflua	0.300	3	2	2
Liriodendron tulipifera	0.160	3	2	2
Nyssa sylvatica	0.301	3	2	2
Ostrya virginiana	0.280	2	1	9
Picea glauca	0.309	1	1	11
Picea mariana	0.270	1	1	11
Picea rubens	0.237	1	1	11
Pinus banksiana	0.411	1	2	12
Pinus echinata	0.423	1	2	12
Pinus resinosa	0.385	1	2	12
Pinus rigida	0.307	1	2	12
Pinus strobus	0.310	1	2	12
Pinus taeda	0.360	1	2	12
Pinus virginiana	0.226	1	2	12
Platanus occidentalis	0.120	2	2	5
Populus balsamifera	0.267	1	2	7
Populus grandidentata	0.267	1	2	7
Populus tremuloides	0.267	1	2	7
Prunus pensylvanica	0.060	1	2	3
Prunus serotina	0.300	3	2	3
Quercus alba	0.330	2	1	5
Quercus borealis	0.225	1	2	9
Quercus coccinea	0.286	1	1	5

Table 1. (*Continued*)

	Tolerance[a]			
Species name	Drought (d_i)	N	Shade	Leaf litter quality class[b]
Quercus ellipsoidalis	0.280	1	2	9
Quercus falcata	0.423	2	1	9
Quercus lyrata	0.031	1	2	5
Quercus macrocarpa	0.350	1	1	5
Quercus marilandica	0.422	1	2	9
Quercus muehlenbergii	0.300	2	2	9
Quercus nuttallii	0.030	1	2	9
Quercus palustris	0.013	1	2	9
Quercus prinus	0.285	1	1	9
Quercus rubra	0.225	2	1	9
Quercus shumardii	0.484	1	2	9
Quercus stellata	0.555	1	2	5
Quercus velutina	0.300	1	1	9
Quercus virginiana	0.512	1	1	5
Thuja occidentalis	0.350	1	1	6
Tilia americana	0.200	3	1	2
Tilia heterophylla	0.211	3	1	2
Tsuga canadensis	0.180	1	1	6
Ulmus alata	0.300	1	2	5
Ulmus americana	0.330	2	2	5

[a] Nitrogen tolerance: 1 – tolerant, 2 – intermediate, 3 – intolerant. Shade tolerance: 1 – tolerant, 2 – intolerant.

[b] See Table 2.

Decomposition and nutrient availability

Development of decay rate equations. A general equation is required which relates leaf litter decay rate to current climate and litter quality. Meentemeyer (1978) predicted leaf decay from actual evapotranspiration and lignin content. More recent research indicates that lignin:N ratios are better predictors of decay rates than simply lignin content (Melillo et al., 1982). We combined the approaches of Meentemeyer (1978) and Melillo et al. (1982) to develop an equation which predicts decay rate from actual evapotranspiration (AET) and lignin:N ratios. Four study sites ranging in AET from 390 mm per yr to 713 mm per yr and with materials of lignin:N ratios from 5 to 70 were chosen from the literature (Cromack, 1973; Heal et al., 1978; McClaugherty et al., 1985; Berg et al., 1985). Regressions of the form

$$\%\,\text{wt loss} = a - b(\text{lignin:N}) \tag{3}$$

were developed for each site. The slopes and intercepts of these regressions were then regressed against AET ($r^2 = 0.805$, $P < 0.05$, and $r^2 = 0.815$, $P < 0.05$, respectively). Substitution in to Eq. 3 yields our decay rate equation:

$$\begin{aligned}\%\,\text{wt loss} = {} & 0.9804 + 0.09352(\text{AET}) + [0.4956 \\ & - 0.001927(\text{AET})](\text{lignin:N}).\end{aligned} \tag{4}$$

This method is a more explicit quantification of the dependence of decay rates on the interaction between climate and litter quality than a multiple regression on these two factors. When AET is low, the decay rate does not vary much with the lignin:N ratios, but as AET increases, the lignin:N ratios account for more of the variation in decay rates. This is similar to the findings of Meentemeyer (1978).

This equation was not used to predict wood decomposition. Rather, woody litter was divided into four classes, with decay rates related to size class: (1) twigs – decay rates less than or equal to 20% per year; (2) wood from trees less than 10 cm dbh – decay rate 10% per year (Louisier and Parkinson, 1976, 1978); (3) wood from trees greater than 10 cm dbh – decay rate 3% per year (Foster and Lang, 1982); and (4) well-decayed wood – decay rate 5% per year.

Canopy openings may increase decay rates because of microclimatic changes. Modeling this is a twofold problem: (1) determining gap size and occurrence, and (2) relating decay rates to gap size. The problem is compounded by a paucity of data. Aber et al. (1982) introduced a hypothetical decay multiplier to simulate increased decay rates when leaf production falls below 2.8 Mg per ha in any given year. We generalized this decay multiplier for soils of different water holding capacity as follows: (1) closed canopy leaf production (L_c) was related to soil water availability based on data for soil texture and leaf production in old-growth forests (Pastor et al., 1984) and parameters for available soil moisture (W_s, in cm) in soils of different textures (Broadfoot and Burke, 1958):

$$L_c = 1.54 + 0.0457\, W_s. \tag{5}$$

(2) a decay multiplier (DECMLT) is then calculated by comparing this year's leaf litter, L_a, with closed canopy leaf production, L_c:

$$\text{DECMLT} = 1.0 + (-0.5 + 0.075\, W_s)(1.0 - L_a/L_c). \tag{6}$$

For soils of high water-holding capacity, DECMLT ranges from 1.0 ($L_a = L_c$) to 2.0 (no canopy) (Matson and Vitousek, 1981). For soils of low water-holding capacity, DECMLT ranges from 1.0 to 1.25.

Predicting nitrogen immobilization and changes in lignin during litter decay. Litter lignin:N ratios change during decay because of N immobilization (Aber and Melillo 1982a) and because lignin concentrations increase as less recalcitrant compounds decay first and microorganisms produce lignin-like decay products (Berg et al., 1985). The percent of N in decaying material at time t is highly related to the percent of organic matter (OM) remaining at time t (Aber and Milillo, 1980):

$$\text{OM} = c + d(\text{N}). \tag{7}$$

In addition to the 48 examples already reported by Aber and Melillo (1980),

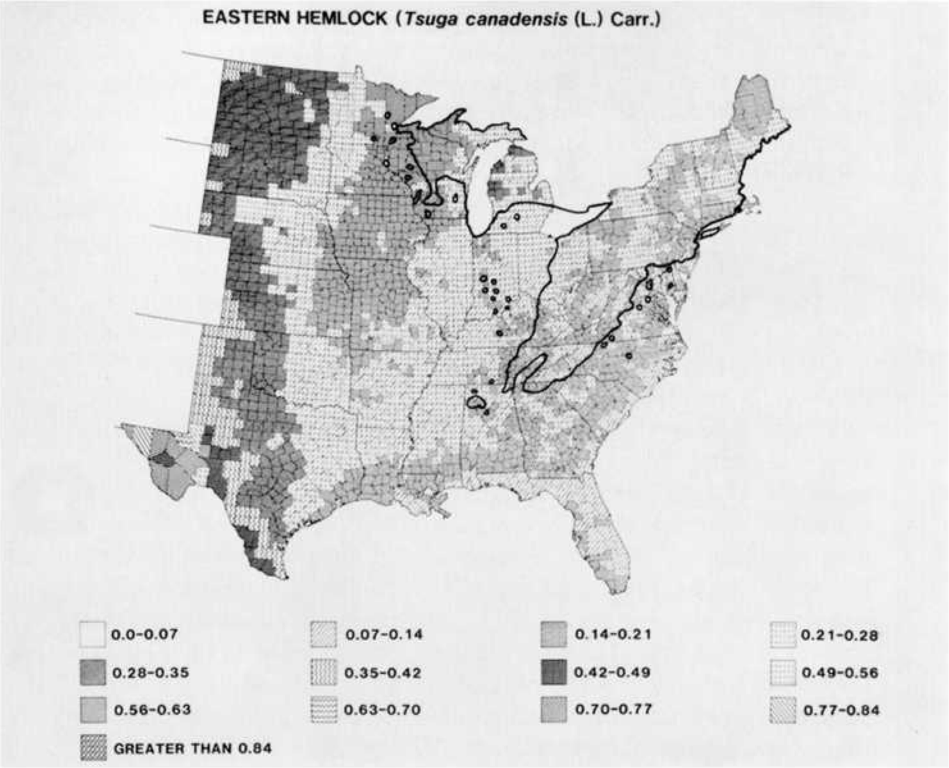


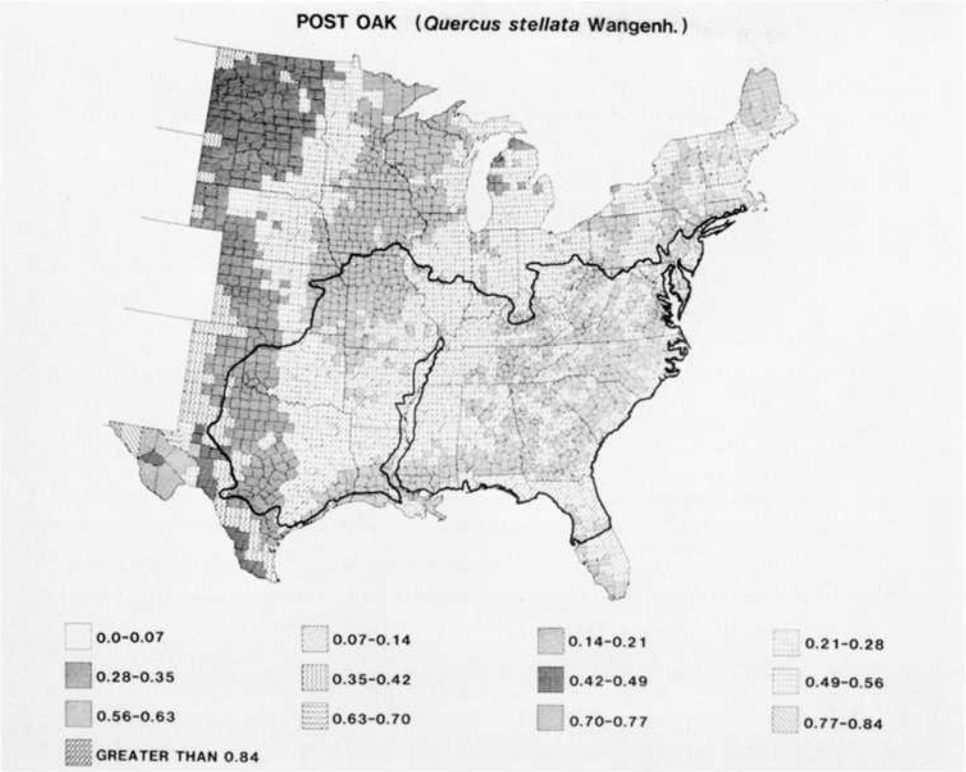
Figure 4. Overlap map of two species ranges on a drought map of eastern North America used to parameterize soil moisture multipliers. Legend values indicate fraction of the growing season below wilting point.

34 cases were found in the literature where this relationship was highly significant (r generally greater than 0.90). From these regressions, the amount of N immobilized per unit litter weight loss and the N concentration at which the material begins to mineralize N, known as the critical N concentration, were calculated for all examples found (cf. Aber and Melillo 1982a).

Berg et al. (1985) found that lignin concentrations (L) in decaying litter are also negatively correlated with the fraction of organic matter remaining:

$$L = e - f(OM). \tag{8}$$

Using data from McClaugherty et al. (1985) we found that the intercept (e) of Eq. 8 is highly related to the amount of N immobilized per unit weight loss ($r = 0.821$, $P < 0.05$), and the slope, f, is highly correlated with e ($r = -0.802$, $P < 0.05$). We can therefore predict the lignin decay parameters from litterbag studies which measured only changes in organic matter and nitrogen content during decomposition.



After assembling data from the literature on the above parameters and initial lignin and N concentrations, we classified leaf litter into 12 categories in order of increasing decay rate, based on differences in initial lignin:N ratios and N immobilization rates (Table 2). The means were calculated where data were available from several studies. These leaf litter categories delineate major genera. There are a few major genera (*Carya*, *Liriodendron*, *Nyssa*) for which no data on N immobilization are available and a number of minor genera for which any data are sketchy. Each of these was assigned to 1 of the 12 leaf litter categories, based on any available data or taxonomic relationship (Table 1). Similar data were obtained for fine root, twig, and woody litter (Table 2). Simulations of the decay and nutrient dynamics of these litter types is a weak area which needs to be improved as more data becomes available. As in the model of Aber et al. (1982), each yearly cohort of these litter categories is followed as long as it immobilizes N. Throughfall N (16% ± SE 2% of litter N, based on data from Cole and Rapp 1981) partially satisfies immobilization requirements (McClaugherty et al., 1985); the remainder is drawn from N mineralization (below).

Predicting nitrogen mineralization. In both the model of Aber et al. (1982) and the present model, when a leaf litter cohort reaches its critical N concentration, it begins to mineralize N and is transferred to humus. When woody litter reaches its critical N concentration, it is transferred to well-decayed wood; the decayed wood continues to immobilize N until a second critical percent N is reached, whereupon it is then transferred to humus. In the model of Aber et al. (1982) N is released from humus at a fixed 9.5% per year. In the present model, N is mineralized from humus as a function of the N:C ratio of the litter forming the humus (Pastor et al., 1984):

$$N_m = H\{-0.000379(N{:}C)/[-0.02984 + (N{:}C)]\}, \tag{9}$$

where N_m is the N mineralization rate ($Mg\,N\,ha^{-1}\,yr^{-1}$), H is the humus weight ($Mg\,ha^{-1}$), and N:C is the weighted averaged N:C ratio of the litter. The N mineralization rate (N_m) is multiplied by DECMLT (Eq. 6) to simulate effects of canopy openings on N mineralization.

The annual amount of N mineralized (N_m) is subtracted from the total humus N pool. The microbial immobilization requirements (above) are subtracted from N_m, and the remainder is assumed to be the N availability to the plant. Carbon is assumed to be released from the humus C pool in the same proportion as N_m is released from the humus N pool.

Modeling the effects of soil nitrogen on tree growth

Mitchell and Chandler (1939) introduced the concept of N tolerance and proposed three types of response to N availability. Nitrogen intolerant species cannot survive under low N availability but grow rapidly under high N availability. Nitrogen-tolerant species survive under low N availability but do not grow as rapidly under high N availability as N-intolerant species. Species of intermediate N tolerance fall between these two extremes. Species were classified as to N tolerance (Table 1) according to studies of Mitchell and Chandler (1939), Aber et al. (1979), and Pastor et al. (1982), according to taxonomic affiliation with a studied species or according to relative growth on nutrient-poor sites (Fowells, 1965).

This concept of N tolerance was formalized mathematically by Aber et al. (1979). Nitrogen growth multiplier equations corresponding to these three tolerances reduce growth from optimum to the extent that N limits growth. We used Aber et al. equations but rescaled the multipliers so that each response curve equals 1.0 at the N availability where their growth correspondingly asymptotes.

Exploring and validating the model for northern temperate forests

According to the relationships outlined in Figure 1, primary production, biomass, nitrogen cycling, and species composition can be predicted from the climate and the water-holding capacity of the soil. Ecosystem properties

Table 2. Decomposition parameters used in subroutine *DECOMP*

Tissue type	Class	Species	Initial % N	Grams of N immobilized per gram of weight loss	Critical % N	Initial % lignin	Lignin parameters[a]		Ash-free correction[b]	References[c]
							a	b		
Leaves	1	Dogwood	0.81	0.0015	1.3	3.9	52.17	0.336	0.90	3, 11
	2	Maple, ash, Basswood	1.05	0.005	1.6	12.1	52.19	0.4	0.9	5, 10, 11, 12, 14, 15
	3	Cherry	1.2	0.0149	2.9	19.3	77.87	0.508	0.92	11
	4	Birch	0.88	0.0092	2.0	15.8	66.93	0.435	0.92	4, 5, 11, 12, 14
	5	White oaks	0.83	0.0033	1.3	18.7	51.94	0.315	0.93	2, 3, 9, 14, 16
	6	Hemlock	0.83	0.0065	1.5	20.6	68.39	0.475	0.96	2, 10, 14
	7	Aspen	0.83	0.0095	1.7	21.4	70.59	0.46	0.94	2, 7, 10, 14, 15
	8	Beech	0.9	0.0367	4.8	24.1	19.67	0.790	0.91	5, 11
	9	Red oaks	0.86	0.0089	1.8	24.8	61.05	0.359	0.95	2, 10, 14, 16
	10	Fir	0.7	0.0052	1.5	28.0	59.26	0.383	0.97	4, 7, 12, 17
	11	Spruce	0.46	0.0215	0.72	21.6	90.52	0.594	0.97	6, 13
	12	Pine	0.45	0.0042	0.82	28.3	56.46	0.327	0.96	2, 4, 10, 12, 14, 16
Roots	13	All	0.93	0.0108	1.5	25.3	70.00	0.456	0.98	9
Fresh wood	14, 15	All	0.3	0.0	0.5	17.3	48.31	0.299	0.99	1, 2
Twigs	16	All	0.3	0.0113	0.9	17.3	48.31	0.299	0.96	8, 10
Well-decayed wood	17	All	0.5	0.0113	2.0	42.3	90.61	0.299	0.99	1, 2

[a] % lignin = a − b (% weight remaining).

[b] Ash-free weight = ash-free correction multiplied by dry weight.

[c] References:

1. Aber and Mellillo (1982b)
2. Berg et al. (1985)
3. Cromack (1973)
4. Daubenmire and Prusso (1963)
5. Gosz et al. (1973)
6. Hayes (1965)
7. Lousier and Parkinson (1976, 1978)
8. MacLean and Wein (1978)
9. McClaugherty et al. (1984)
10. McClaugherty et al. (1985)
11. Melillo et al. (1982)
12. Melin (1930)
13. Moore (1984)
14. Pastor et al. (1984)
15. Pastor and Bockheim (1984)
16. Sharpe et al. (1980)
17. Vogt et al. (1983)

should change predictably along soil texture, climate, and successional gradients. We now examine these consequences of our model for northern forests by simulating such gradients and testing model predictions against measurements, when available. Validation for southern forests is currently underway. In all simulations the model begins with no trees on site and monthly temperatures and precipitation, soil field moisture capacity and wilting points, and initial soil organic matter and nitrogen contents specified. Unless otherwise noted, all results are means of 20 runs in which temperature, precipitation, initial dbh, and the probability of mortality vary stochastically.

Biomass, productivity, and nitrogen availability of old-growth stands in relation to soil texture

Pastor et al. (1984) and McClaugherty et al. (1985) found increases in aboveground biomass, net primary production, N mineralization, and leaf litter N in old-growth stands along a soil texture gradient from sand to silty clay loam in central Wisconsin. They hypothesize that changes in litter quality because of species replacement along the soil texture gradient cause differences in N availability, which in turn controls net primary productivity. We simulated this soil texture gradient by running the model for four soil textures and using central Wisconsin climate, an average initial soil organic matter of 74 $\mathrm{Mg\,ha^{-1}}$, and an initial N content of 2.23 $\mathrm{Mg\,ha^{-1}}$. The four soil textures correspond to (1) sand (field moisture capacity (FC) = 15 cm, wilting point (DRY) = 5 cm); (2) sandy loam (FC = 22.9, DRY = 10.4); (3) silt loam (FC = 35.0, DRY = 18.3); and (4) silty clay loam (FC = 38.3, DRY = 20.0). Some of the data used to model decomposition (Table 2) came from Pastor et al. (1984) and McClaugherty et al. (1985). These runs therefore test the internal consistency of the hypothesis set forth in these two papers and the consistency of the model with some of the data used to parameterize it. They are not validations in a strict sense.

The measured biomass, production, N availability, and leaf litter N of six stands 200 ± 25 years old (Pastor et al., 1984; McClaugherty et al., 1985) were generally within the 95% confidence intervals of model runs (Figure 5). The model predicts sugar maple (*Acer saccharum*)-basswood (*Tilia americana*)-oak (*Quercus borealis*, *Q. alba*) stands on silty clay loam, oak-maple-pine (*Pinus strobus*) stands in silt loam and sandy loam, and pine-oak-maple stands on sand. This corresponds to changes in vegetation composition along the textural gradient on Blackhawk Island (Pastor et al., 1982) as well as elsewhere in central Wisconsin (Curtis, 1959; Peet and Loucks, 1977) except that the proportion of oak in the simulations was less than observed in the field, perhaps because the effects of fire on maintaining oak forests was not simulated. It is significant that the model chose northern and excluded southern species in the simulations by predicting correctly the growing season degree days for central Wisconsin, which are too few for southern species. This is in contrast to many other *JABOWA* or *FORET*

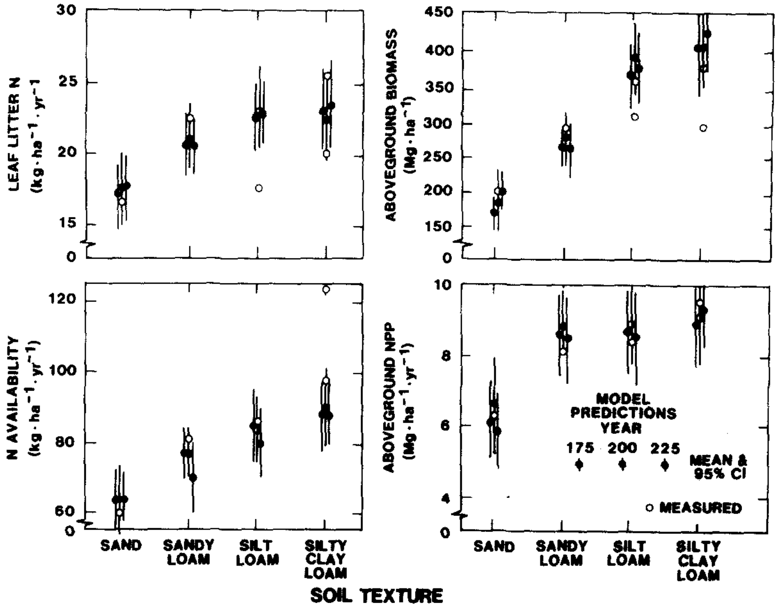


Figure 5. Aboveground biomass, aboveground net primary production (NPP), available N, and leaf litter N along a soil moisture gradient, as predicted by the model and as measured by Pastor et al. (1984) and McClaugherty et al. (1985).

type models in which a species list for a given site is user specified (Shugart, 1984). Both measured and simulated increases in N availability and litter N return with increases in soil silt plus clay content were due to the increased abundance of high-quality litter as oak replaces pine but in turn is replaced by maple along the textural gradient.

Controls over tree growth during succession and gap recovery

In the model, the growth of each tree is controlled by one of four variables (light, degree-days, water, and N), whichever is most restricting. Thus, not all species or trees are necessarily limited by the same resource, and the resource that is most limiting to each tree may change during succession. To examine this, we kept track of what proportion of the total simulated tree population in one plot in any one year was limited by light, water, N, or degree-days on a sand and a silty clay loam in central Wisconsin (Figure 6). The trees were classified into three height classes: 0–10 m, 10–20 m, and 20–30 m. During the first 15 years of stand development on silty clay loam, growth was limited by degree-days and N. After establishment of a 10–20 m canopy in year 50, light was most restricting to growth in the 0–10 m height class. Light was less restrictive in the 10–20 and 20–30 m height classes, where N and temperature were most growth limiting. During the first 30 years of white pine-oak-maple stand development on sand, N was the factor most limiting to the growth of seedlings and young trees. After 50 years,

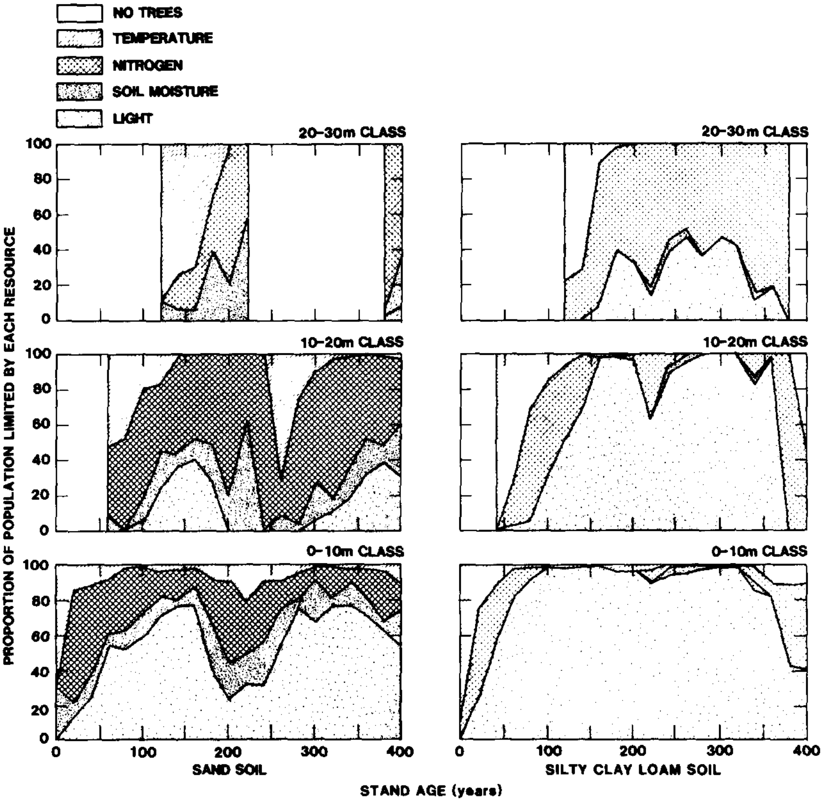


Figure 6. Proportion of tree population limited by each resource for two model runs simulating a forest stand on a droughty sand soil and on a mesic silty clay loam soil. The trees were divided into three size classes to show differences in responses of trees of different heights.

light availability assumed the major role in limiting growth of the 0–10 m class. However, soil N and water availability played a significant role in growth limitation of this class compared to the simulation run with the more mesic silty clay loam. These results indicate not only that soil moisture limitation increases with lower water holding capacity, but also that low water availability alters the composition of tree species, which in turn affects N availability.

The interplay between light availability and N dynamics is demonstrated by events following the mortality of some large trees in both the sand and the silty clay loam simulations. During years 180–200 on sand N became sharply more limiting in the lower canopy classes, and light limitations were reduced substantially. Several large aspens in the 20–30 m height class died at this time, creating a gap. This increased light availability to the smaller trees and returned a large amount of wood to the soil, which subsequently immobilized much available N (available N dropped from 77 to 56 kg ha^{-1}). Between years 200 and 250, as the nitrogen was released from the wood and the canopy closed, N became less limiting (approximately 70 kg ha^{-1} available N), and light once again became the resource most limiting to small trees. A similar, though less dramatic, pattern occurs on the silty clay loam. At year 200 a large sugar maple died and temporarily released the lower canopy from light limitation but these trees were then N limited. Available N dropped from 101 kg ha^{-1} yr^{-1} in year 200 to 75 kg ha^{-1} yr^{-1} in year 220. Without the additional limitation of low soil moisture, the gap rapidly closed. However, in year 360 several large sugar maples died, with the remaining upper canopy maple dying by year 380. The immediate effect of these events was a drastic reduction in light limitation and an increase in proportion of trees which were N limited.

Recovery of net primary production during succession in relation to soil texture

During succession, net primary production is thought to increase to a maximum, then decline and oscillate around a lower steady-state level (Peet 1981). The peak in net primary production is thought to occur when the stand is composed of mature early successional trees in the overstory and late successional trees in the understory (Loucks, 1970, Pastor and Bockheim, 1984). If soil moisture partly determines which late successional species eventually occupy a site, it may then also affect the recovery of net primary production and the N cycle. In Michigan, aspen (*Populus grandidentata*, *P. tremuloides*) is succeeded by pine and oak on Rubicon sand and net primary production is maximum immediately before the aspen dies (Cooper, 1981). On finer-textured soils, aspen stands last longer, are more productive, and are succeeded by northern hardwoods (Graham et al., 1961). In order to examine the effects of soil moisture and succession on net primary production and N availability, we simulated aspen succession on Rubicon sand (U.S. Soil Conservation Service, 1980) and on a silty clay loam, given the climate of the northeastern Lower Peninsula of Michigan (U.S. Department of Commerce, 1968, 1982).

On sand, net primary production peaks at 50–60 years, then declines slightly when the aspen is succeeded by pine and oak (Figure 7). This is in good agreement with the data of Cooper (1981). In contrast, production is higher on silty clay loam, the peak is more pronounced and sustained for a longer period, and aspen is succeeded by sugar maple and other northern hardwoods. The differences between the litter quality of these associated species on the two soils (Table 2) were responsible for the differences in simulated N mineralization (Figure 7). Although N availability continues to increase after aspen is succeeded by sugar maple on silty clay loam, production is not as high as when mature aspen coexists with a shade tolerant sugar maple understory, maximizing use of both available N and light. On

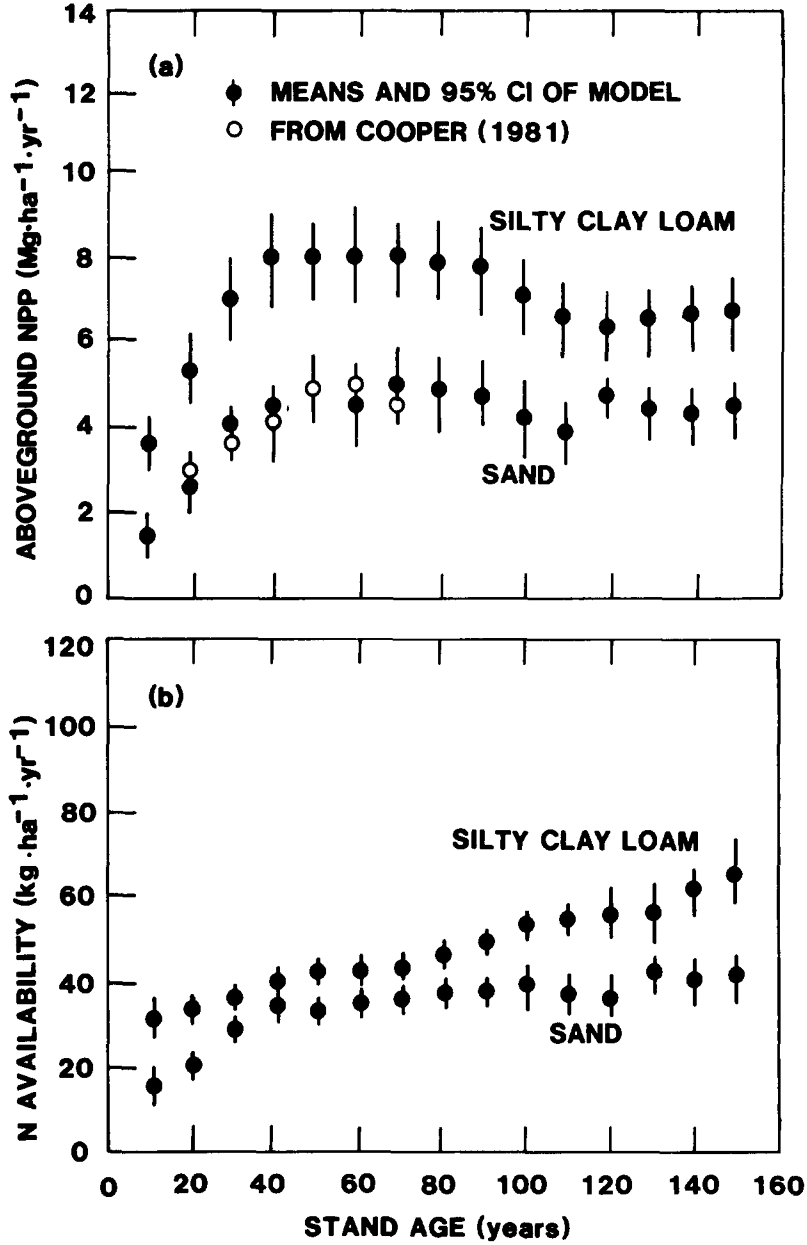


Figure 7. (a) Aboveground net primary production (NPP) during development of aspen succession on two soils, as predicted by the model and as measured by Cooper (1981). (b) Simualted nitrogen availability during aspen succession on two soils.

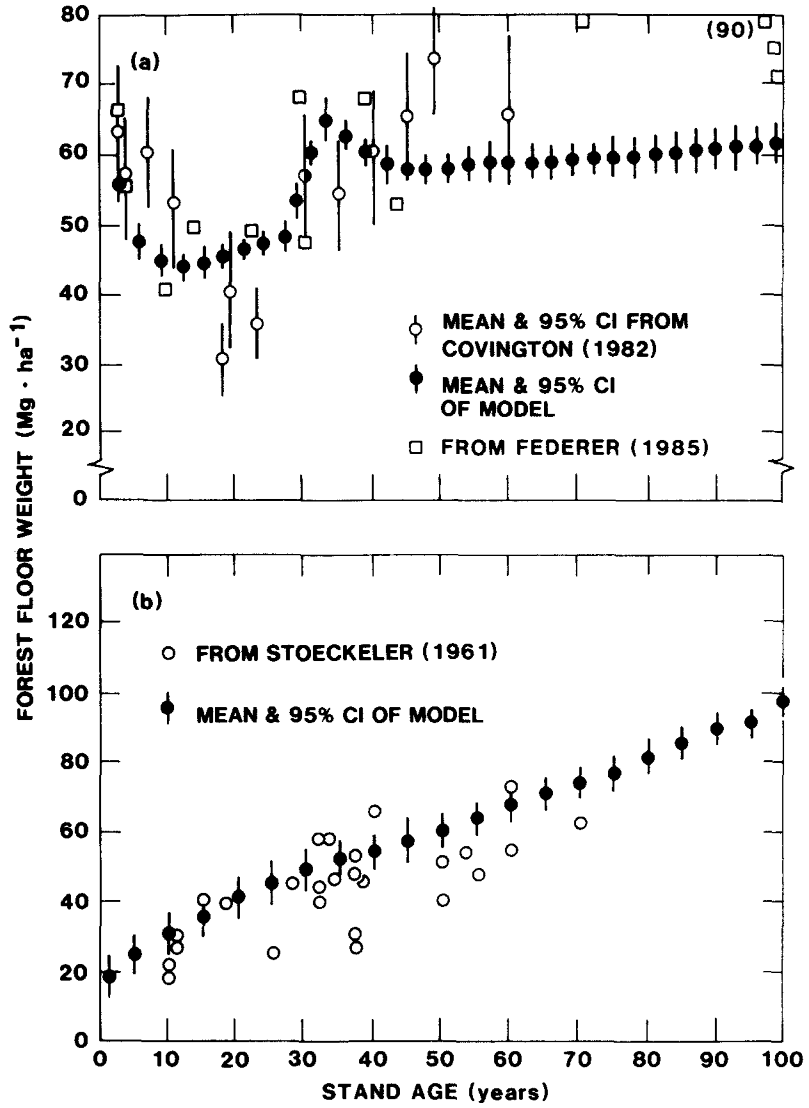


Figure 8. (a) Changes in forest floor weight in pin cherry-northern hardwood succession after clearcutting, as predicted by the model and as measured by Covington (1981) and Federer (1985). (b) Changes in forest floor weight during aspen-hardwood succession after fire, as predicted by the model and as measured by Stoeckeler (1961).

sand, the coexistence of aspen with shade-intolerant pine and oak with low-quality litter results in lower N availability, low net primary production with less decline as pine and oak succeed aspen.

Changes in soil organic matter during succession

After clearcutting, forest floor weight declines by 20–50%, then slowly recovers in pin cherry (*Prunus pensylvanica*)-hardwoods successional seres in New Hampshire (Covington, 1981; Federer, 1984). We simulated clearcutting after 70 years of stand development, given the New Hampshire climate and a loam of 0.5 m depth with an initial humus weight of 65 Mg ha^{-1} and an initial N content of 1.3 Mg ha^{-1} (Likens et al., 1977; Aber et al., 1982b). Pin cherry was the only early successional species allowed.

The simulated changes in forest floor weight agreed better with Federer's data than with Covington's (Figure 8). Both Federer's data and the present simulations as well as those of Aber et al. (1982) show a rapid initial decline of about 20% in forest floor weight followed by little change until year 20, then a slow increase as slash becomes incorporated into the forest floor and soil organic matter.

During aspen succession on sand in northern Minnesota, forest floor weight increases steadily after clearcutting and fire (Stoeckeler, 1961). We simulated such a stand development, given the climate of north-central Minnesota and initial forest floor weights and N contents of 20 Mg ha^{-1} and 0.32 Mg ha^{-1} (Stoeckeler, 1961). The model simulations agree well with Stoeckeler's data (Figure 8).

It is difficult to determine whether these two patterns result from differences in species or initial levels of soil organic matter. To examine this, we simulated both pin cherry and aspen succession in New Hampshire on a 0.5 m-thick loam soil with initial organic matter contents of 25, 50, 75, and 100 Mg ha^{-1} and an initial C:N ratio of 25. For both species, soil organic matter declines initially, then rises as productivity recovers (Figure 9). The initial decline is greater when initial organic matter is high and negligible when initial organic matter is low, and less under aspen succession than under pin cherry. Aspen maintained higher levels of soil organic matter than pin cherry, but soil organic matter levels converged at 60–90 Mg per ha after 120 years with residual variation attributable to initial levels and successional species. In addition, under aspen succession, with high initial soil organic matter, the soil organic matter rises to a peak about years 90–100, then declines back to about 100 Mg ha^{-1}. This peak occurs 40–50 years after the peak in net primary production in these simulations when the amount of woody litter from aspen mortality about years 70–80 is transferred to soil organic matter. In all simulations, aspen succession returns 1.5 to 2 times more woody litter than does pin cherry succession by virtue of its longer life and sustained high rate of productivity. Leaf and root litter return are similar in both simulated series. Therefore, differences in patterns of soil organic matter are related to differences in initial organic matter levels and differences between successional species, especially in the amounts of woody litter produced.

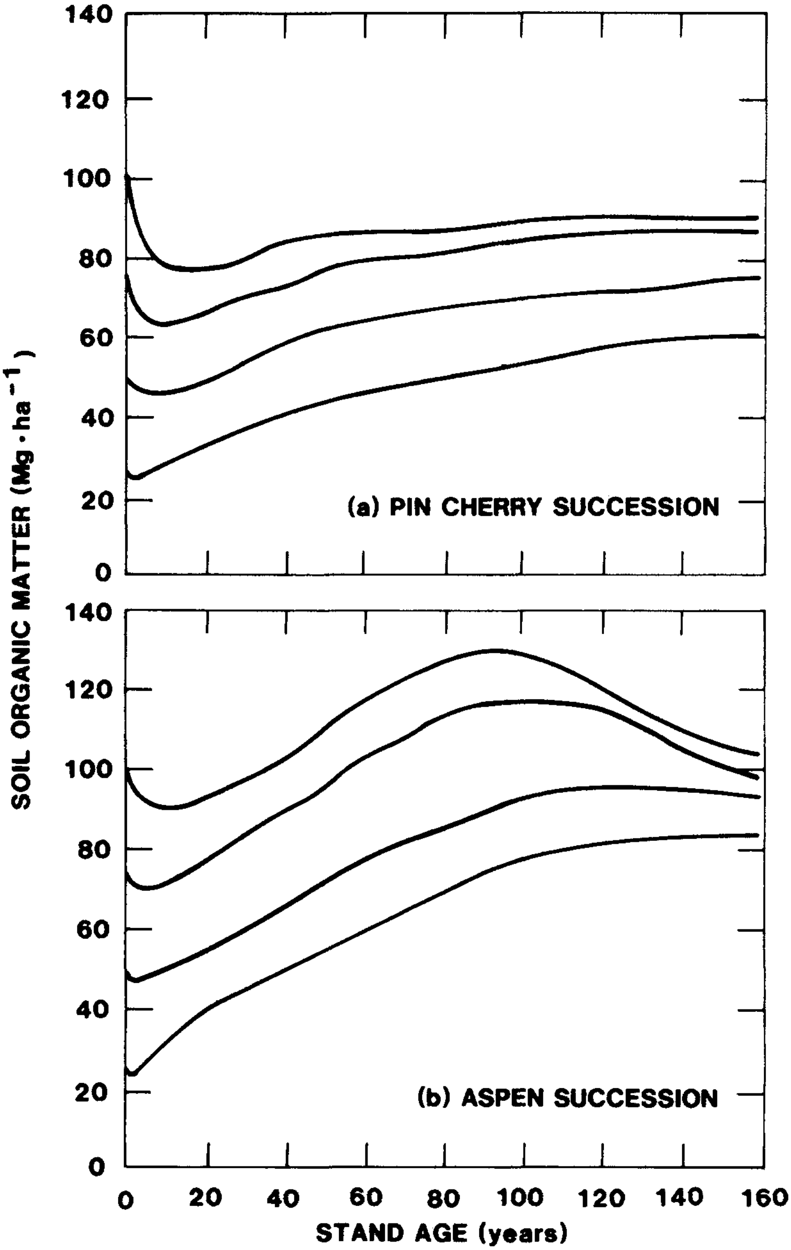


Figure 9. Effects of early successional species on changes in soil organic matter during stand development.

Discussion

Ecosystem carbon and nitrogen cycles are reciprocally linked because the type of carbon compounds in litter, a species characteristic, controls N availability which in turn controls the rate of biomass accumulation. Canopy biomass in turn determines light availability for recruitment. Within a climatic region, local variation in linked carbon and nitrogen cycles and light availability is due to differential species responses to soil water availability. This is apparent in the simulations of forest stands with different soil textures in Wisconsin and in northern Michigan. Although this conclusion has been inferred from field studies in this region (Peet and Loucks, 1977; Pastor et al., 1984; McClaugherty et al., 1985), this is the first model demonstrating the internal consistency in this logic. Local variation in seed sources of major species and past disturbances influencing initial conditions can also influence carbon and nitrogen cycles for long periods, as shown in the soil organic matter simulations.

The ability of our model to predict a variety of ecosystem responses from only a few specifications on climate, soil moisture characteristics, and initial conditions has implications for landscape and global ecology. On a landscape scale, our model suggests that variation in ecosystem properties can be partly explained by considering differential species responses to gradients of soil water availability and their resultant effect on linked carbon and nitrogen cycles, thus uniting classical Gleasonian ecology (eg., Curtis, 1959) with more recent process level ecosystem studies. On a global scale, the wide variety of carbon dynamics within a climatic zone depending on soil water availability and successional sere may add uncertainty to predictions of global carbon models. The effect of climatic change or human disturbance on productivity over large regions (Houghton et al., 1983; Solomon et al., 1984) may be tempered by local variations in soil water availability and linked carbon and nitrogen cycles. Geologic and climatic factors determining soil water availability and historical factors determining seed sources should be considered when extrapolating from site specific ecosystem studies to larger landscape and global scales.

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