Factors Controlling Nitrogen Cycling and Nitrogen Saturation in Northern Temperate Forest Ecosystems

John D. Aber; Jerry M. Melillo; Knute J. Nadelhoffer; John Pastor; Richard D. Boone

FACTORS CONTROLLING NITROGEN CYCLING AND NITROGEN SATURATION IN NORTHERN TEMPERATE FOREST ECOSYSTEMS[1]

JOHN D. ABER

Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, New Hampshire 03824 USA

JERRY M. MELILLO AND KNUTE J. NADELHOFFER

Ecosystem Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA

JOHN PASTOR

Natural Resources Research Institute, University of Minnesota–Duluth, Duluth, Minnesota 55812 USA

RICHARD D. BOONE

Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, New Hampshire 03824 USA

Abstract. An analysis of the factors controlling rates of nitrogen cycling in northern temperate forest ecosystems is presented based on a quantitative analysis of an extensive data set for forests in Wisconsin and Massachusetts as those data are synthesized in a computer model (VEGIE) of organic matter and nutrient dynamics. The model is of the "lumped-parameter," nutrient-flux-density type, dealing with major components of forest ecosystems rather than stems or species. It deals explicitly with the interactions among light, water, and nutrient availability in determining transient and equilibrium rates of primary production and nutrient cycling. Data are presented for parameterizing the plant component of the system at either the species or community level.

A major conclusion is that the ultimate control on equilibrium nitrogen-cycling rates resides not within the nitrogen cycle itself (for example in litter quality or net primary production [NPP] allocation patterns) but rather in ratios of resource-use efficiency by vegetation as compared with the ratios of resource availability. Litter quality and allocation patterns, along with rates of N deposition, do affect the rate at which a system approaches the equilibrium cycling rate. The model is used to explain observed variation in nitrogen-cycling rates among forest types, and to predict the timing and occurrence of "nitrogen saturation" (N availability in excess of biotic demand) as a function of nitrogen deposition rates and harvesting.

Key words: computer models; decomposition; light limitations; N mineralization; northern temperate forest; primary production; water limitations.

INTRODUCTION

Nitrogen saturation of forest ecosystems in response to pollution-derived increases in nitrogen deposition is increasingly seen as a threat to forest and freshwater resources in the industrialized regions of the northern hemisphere (Nilsson and Grennfelt 1988, Aber et al. 1989). In response, research on nitrogen cycling in temperate forests is beginning to focus more on nitrogen retention capacity and the effects of excess availability (e.g., Brown 1988, Skeffington and Wilson 1988, van Breeman and van Dijk 1988, van Dijk and Roelfs 1988, Waring 1988, Schulze 1989) and less on ways to conserve and manage what has been historically a growth-limiting resource.

We have defined nitrogen saturation as the availability of mineral N in excess of biotic demand (Aber et al. 1989). This definition implies limitations on biological activity by some other resource such as light, water, or other nutrients. Prediction of the timing and consequences of N saturation will depend, then, on the development of forest ecosystem models which deal with the availability and use of several potentially growth-limiting resources.

However, forest ecosystem models generally deal with a single nutrient (e.g., Waide and Swank 1977) or with the interactions of a single nutrient and carbon, with the implicit assumption that the nutrient dealt with is limiting production and/or decomposition (e.g., Aber et al. 1982a, Ågren 1984). Models that deal with several potentially growth-limiting resources are rare. Pastor and Post (1986), building on earlier stem-based models of forest ecosystem dynamics (Botkin et al. 1972, Shu-

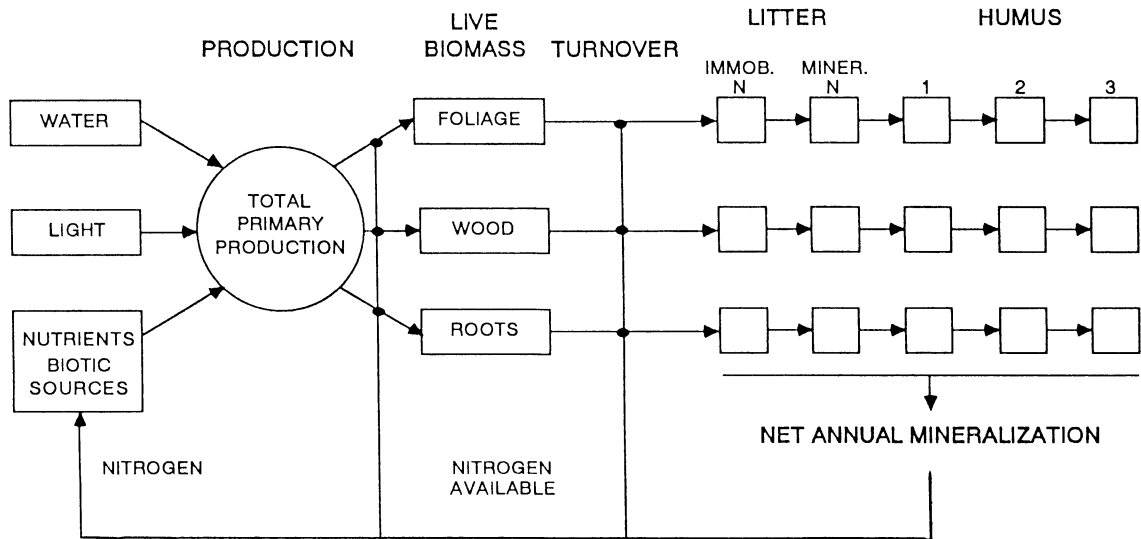PRODUCTION   LIVE BIOMASS   TURNOVER   LITTER   HUMUS

FIG. 1. Structure of the VEGIE model.

gart and West 1977, Aber et al. 1982a), have presented one of the first attempts to model explicitly the interactions of water, light, and nitrogen in controlling forest ecosystem function over periods of decades to centuries.

For more than a decade we have studied the major processes that affect N cycling in northern temperate forests, including litter decomposition (e.g., Aber and Melillo 1982, Melillo et al. 1982, McClaugherty et al. 1985, Aber et al. 1990a), mineralization from soil organic matter (Nadelhoffer et al. 1983, Pastor et al. 1984), plant uptake, allocation, and retranslocation above ground (Nadelhoffer et al. 1984, 1985, Pastor et al. 1984, Lennon et al. 1985), fine root productivity and turnover (McClaugherty et al. 1982, 1985, Aber et al. 1985, Nadelhoffer et al. 1985), interactions with water use (Fownes 1985), and trace gas fluxes (Melillo et al. 1983, Steudler et al. 1989). This research now includes experimental chronic nitrogen additions to examine factors affecting nitrogen-retention capacity and the effects of chronic, excess N availability (Aber et al. 1989).

The purposes of this paper are: (1) to derive and validate a simple, lumped-parameter (Cosby et al. 1985), nutrient-flux-density (Ågren 1984, Ågren and Bosatta 1988) model of controls on nitrogen cycling using data from the studies listed above; (2) to use this model to predict the N-cycling rates at which N saturation will occur for different soil–vegetation combinations; (3) to predict how rapidly N saturation will occur.for different combinations of soil, vegetation, and N-deposition rates (i.e., how rapidly do N-cycling rates change in response to chronically elevated N inputs); and (4) to examine the extent to which the onset of N saturation can be delayed or accelerated by interactions between N deposition, other forms of pollution (e.g., ozone), and forest harvesting.

METHODS

Model structure

General.—The model (VEGIE—Vegetation Effects on Geochemistry in Ecosystems) is a generalized, forest nutrient-cycling model designed to be strongly data-based. In this application it is driven with equations developed directly from field data from studies of temperate forests in the northeastern United States.

VEGIE deals specifically with the effects of water-, light-, and nitrogen-use efficiencies on forest productivity, transpiration, and nitrogen cycling. Like Ågren's nutrient-flux-density model (Ågren 1984, Ågren and Bosatta 1988), it simulates major functional components of forest ecosystems (e.g., foliage, stems, fine roots, litter, soil organic matter). It differs from the JABOWA/FORET family of models (Botkin et al. 1972, Shugart and West 1977, Aber et al. 1982a, Pastor and Post 1986) in that it does not deal with individual stems within the vegetation component. This means that VEGIE cannot predict or treat forest succession, but uses a constant species composition implied in the equations relating production to resource availability.

VEGIE calculates the movement of organic matter and nitrogen through the different components of a forest ecosystem (Fig. 1). In the current version the nitrogen concentration in each component is held constant. Foliage, fine roots, and wood (which includes stems, branches, and woody roots) are tracked separately through the production and decay routines. The availability of nitrogen and water, and the efficiencies with which these resources are used, determine net primary production and its allocation to foliage, wood, and fine roots according to equations developed for each species or group of species simulated. A maximum foliar biomass value sets an upper limit on total
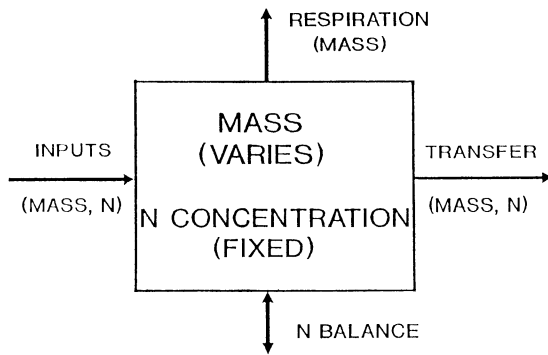
N BALANCE = NEW N CONTENT - NEW MASS·FIXED %N

Fig. 2. Organic matter and nitrogen fluxes through the decomposition stages in the model VEGIE.

primary production. Litter production is calculated as live biomass times turnover rate, which can vary with species, tissue type, and nitrogen availability. Litter decays by passing through three decay stages, each with values for respirational mass loss, transfer to the next stage, and a constant N concentration. The number of decay stages can be increased if necessary.

Organic matter decomposition and nitrogen mineralization.—Stages in the decomposition routine are separated by changes in the nitrogen dynamics of the decaying material. In the current vision each litter type is separated into an immobilization phase, a mineralization phase, and a recalcitrant soil organic matter or "humus" phase (other humus compartments, such as a clay-stabilized fraction, could be added; Fig. 1). For each compartment (Fig. 2), inputs represent either litter production or transfer from the previous stage. Losses are separated between respiration and transfer to the following stage, based on data for mass loss during each stage and the time required to complete that stage. The nitrogen concentration of each stage is the midpoint of the concentration range of material present in that stage.

The nitrogen balance (immobilization or mineralization) over each stage is determined as the net result of the transfers into and out of that stage and the requirement to maintain a constant N concentration. Nitrogen enters each stage with transferred organic matter at the nitrogen concentration of the donor stage and is transferred out at its own (generally higher) concentration. These two transfers plus the respirational loss from the stage result in a new biomass and nitrogen content. Nitrogen is then either immobilized from, or mineralized to, the available N pool to bring the N concentration in organic matter in that stage to its preset concentration. Total nitrogen availability for plant growth in a given year is the sum of the mineralization and immobilization values for all stages and tissue types in the decomposition module for that year, plus external N inputs from atmospheric deposition or fertil-

ization. It is possible to define additional stages in the nitrogen dynamics of decaying litter, and VEGIE allows the number of stages to be defined as an input variable. For example, many litter types show a brief period of N loss by leaching at the initiation of a decay study. However, this period is so brief as to have no significant effect on annual rates of N cycling within this model. Similarly, there is no mineral-stabilized humus pool analogous to the slowest turnover pool in CENTURY (Parton et al. 1988).

Net primary production and nitrogen uptake.—Net primary production (NPP) and allocation to foliage, wood, and fine roots are first calculated from a series of equations described in Nadelhoffer et al. (1985) and Aber et al. (1985). Summary regressions describing NPP of foliage and wood as a function of nitrogen availability, derived from extensive field data (see *Model parameterization,* below), are used to calculate production for these tissue types. Mean values for nitrogen concentration in each of these are then used to calculate the nitrogen required to produce them. Concentrations used for foliage are litter values, not green-foliage values. The pool of retranslocated nitrogen available for plant growth the following year is not explicitly modeled. The nitrogen remaining after these two allocations is assumed to go to fine-root growth. This allocation, divided by the nitrogen concentration in fine roots, is the calculated fine-root productivity. These relative carbon allocations and the nitrogen concentrations in each tissue type determine the nitrogen-use efficiency of biomass production. This method of calculation also ensures a mass balance for nitrogen within the productivity routine.

Total NPP may be limited by water as well as nitrogen. However, it is very difficult to combine simulations of water use, usually carried out on an hourly to daily basis (e.g., Federer and Lash 1978, Running 1984), with annual time-step simulations of nitrogen and carbon flows. In this model, limitations are expressed as a single annual time-step water-use efficiency value.

An approximation of water availability on an annual basis is the total soil storage capacity of "available" water, that which can be extracted by plants, plus precipitation during the growing season. Assuming complete recharge of this storage capacity by precipitation outside of the growing season, and using a mean growing-season precipitation value for all years, this availability is a constant which differs between sites but not between years. In reality, both water-use efficiency and total water availability vary from year to year due to variation in weather patterns. These variations around mean values would result in minor adjustments in the patterns reported here, but would not affect the conclusions concerning rates of change or equilibrium values of nitrogen mineralization.

Water limitations occur when total NPP calculated from nitrogen availability divided by water-use effi-

ciency is greater than water availability. When this occurs, NPP is divided by the ratio of water demand to water availability, but relative allocation between tissues does not change. Nitrogen concentrations also remain the same.

Light limitations are expressed as an absolute upper limit to foliage biomass for a given species or species mix. If water or nitrogen are limiting, this maximum will not be reached. If NPP calculated from nitrogen and water availability will result in foliage biomass above the maximum, NPP of all tissues is reduced proportionally until foliage is brought down to this limit. NPP is also reduced if the increase in foliar biomass from one year to the next is above a value related to foliar turnover rate, and roughly equivalent to relative growth rate. This factor is important only in the first few years after a major biomass removal.

VEGIE contains code and data to include limitations on NPP by nutrients other than nitrogen. Nutrient demands determined following NPP calculations as limited by nitrogen and water are compared with availability of these additional nutrients determined by mineralization and the net effect of all abiotic processes (weathering, cation exchange, deposition, and leaching). Discussion of this part of the model is beyond the scope of this paper.

Litter production rates are determined by the biomass in each tissue type and the turnover rate of that biomass. Foliage, wood, and fine roots have different turnover rates. Foliage turns over annually for deciduous species. Turnover rates for evergreen foliage, wood, and fine roots can be specified either as a constant, or as a function of N availability. Litter produced by each tissue type carries with it to the first litter-decay stage the same percentage of nitrogen used to calculate nitrogen requirements (measured concentration in fresh litter).

Model parameterization

Decomposition.—We have parameterized VEGIE for the three sets of species, grouped by genera, found on our study sites: oaks (mainly *Quercus alba, Q. borealis,* and *Q. velutina*), maples (*Acer saccharum, A. rubrum*) and pines (*Pinus strobus, P. resinosa*). We have been unable to detect significant differences in function between species within the oak and maple genera (Aber et al. 1990*a,* and data presented in the present paper). Differences between the two species of pine are suggested by the data, but the number of pine systems studied is too small to allow a distinction between these two species.

Long-term decay data are available for foliage for all major species listed above (McClaugherty et al. 1985, Melillo et al. 1989, Aber et al. 1990*a*). In a previous paper (Aber et al. 1990*a*) we discussed several statistical methods for summarizing and expressing mass loss and nitrogen dynamics for these long-term data.
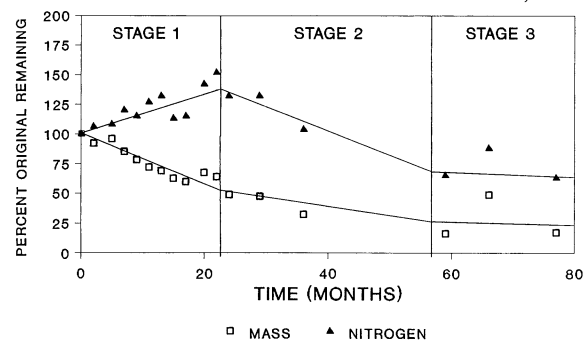

FIG. 3. Changes in total mass and nitrogen content for red oak foliage litter decaying at the Harvard Forest, Petersham, Massachusetts. The three decay stages in the version of the model VEGIE discussed here are separated according to mass loss and nitrogen dynamics as shown.

To parameterize the decay routine in VEGIE we need to know only the nitrogen concentration of fresh litter, the fraction of original mass remaining and its nitrogen concentration at the end of each stage, and the residence time within the stage.

The first stage (Fig. 3) is defined by the period of net nitrogen immobilization (net increase in the total amount of nitrogen in the material). The second stage is the period of net N mineralization up to the point where litter-mass loss rate shows a significant slowing. The third stage contains recalcitrant soil organic matter.

For each stage, values are defined for KRESP and KTRANS, the rate at which biomass is lost by respiration and by transfer to the next stage, respectively (Fig. 2). These are calculated as the mass loss and the mass remaining at the end of each stage, divided by the time required to reach the end of that stage, expressed as the k parameter in the exponential decay equation. N concentration for each stage is the mean of the values at the beginning and end of the stage (see Aber et al. [1990*a*] for further explanation; see Table 1 for listing of parameters for foliage and root litter).

The decomposition and nitrogen dynamics of the third stage of foliage and root decay, as defined in the model, are poorly understood. In earlier papers we have hypothesized that "humus" produced by the decay of these two tissues will be relatively similar in terms of decay rate (Melillo et al. 1989), but different in N content and mineralization rate (Aber et al. 1990*a*). This material is conceptually similar to the "slow" decay fraction of the CENTURY model (Parton et al. 1988), the initial secondary product of decomposition, which has a residence time of ≈ 25 yr. We have assigned a KRESP of 0.05 to the third stage for all foliar and root litter types. The percentage of N assigned is the mean of the concentration at the end of stage 2 and 4%, an approximate maximum soil-organic-matter N concentration. This means that "humus" produced from tissues with different initial N concentrations will

TABLE 1. Input parameters for decomposition routines by species group. KTRANS is the exponential decay equation parameter which determines the amount of biomass transferred to the next stage in a given year. KRESP determines the amount of biomass lost to respiration in a year. %N is the constant nitrogen concentration of material in that stage. See text (*Methods: Model parameterization: Decomposition*) for derivation.

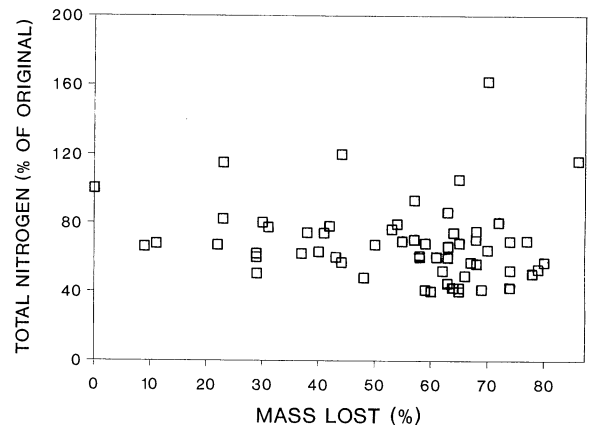|		KTRANS	KRESP	%N
Maple				
Leaf	Stage 1	1.38	.720	1.11
	Stage 2	.227	.480	2.10
	Stage 3	.000	.050	3.05
Root	Stage 1	.998	.260	1.75
	Stage 2	.054	.158	2.73
	Stage 3	.000	.050	3.37
Oak				
Leaf	Stage 1	.376	.266	1.48
	Stage 2	.109	.211	2.40
	Stage 3	.000	.050	3.38
Root	Stage 1	.720	.264	1.55
	Stage 2	.072	.180	2.77
	Stage 3	.000	.050	3.38
Pine				
Needle	Stage 1	.421	.262	0.66
	Stage 2	.095	.197	1.32
	Stage 3	.000	.050	2.66
Root	Stage 1	.528	.277	1.41
	Stage 2	.088	.199	2.82
	Stage 3	.000	.050	3.97
All species				
Wood	Stage 1	.020	.050	0.75
	Stage 2	.000	.050	0.26

FIG. 4. Changes in total nitrogen content in decaying birch wood at the Harvard Forest, Petersham, Massachusetts. There was a 25% decline in total N content between live wood (the initial—or 0% mass lost—data point), and the mean of the woody litter samples. We attribute this to loss of N during the transition from live to dead wood. Total N content remains constant during the decay process following stem death.

maintain those differences all the way through to the production of recalcitrant organic matter.

Relatively little is known about the decay of woody litter, particularly in the northern temperate forests of the eastern United States. One study carried out on decomposing branches and stems in two of our sites showed no significant change in total nitrogen content (i.e., no net immobilization or mineralization) for up to 80% of mass loss (Fig. 4). We use a two-stage decay structure for woody litter, which maintains a constant total nitrogen content through 80% of mass loss (stage 1), with mass loss occurring at 5% per year (Table 1). The second stage continues the 5% mass-loss rate but has a percentage of nitrogen representing the mean of the end of stage 1 and 4%.

Primary production. —Foliage and wood production on our study sites (Pastor et al. 1984, Aber et al. 1985, Lennon et al. 1985, Nadelhoffer et al. 1985) show significant linear relationships with N availability at two levels: the species group and the community. Slopes and intercepts are significantly different between species groups (Table 2; note that sugar maple leaf production, which was statistically constant across a range of N-mineralization values of 36 to 120 kg·ha^{-1}·yr^{-1}, has zero slope). In addition, due to the differential relative importance of oaks and pines along the N-avail-

ability gradient, both foliage and wood production can be represented by single linear equations across the entire gradient (Fig. 5A and B). Calculated fine-root production shows an even tighter relationship with N uptake at both the species-group and community levels (Fig. 5C).

Total NPP, including calculated fine-root production (Fig. 6A) is very tightly coupled with N uptake. This is not due solely to the use of the N-budgeting process to estimate root production. Differences in production allocation patterns and/or nitrogen concentrations in foliage, wood, and roots could produce very different total NPP values for different species groups at a given N-uptake rate. However, allocation patterns are also tightly coupled with N uptake (Fig. 6B). These results suggest community-level constraints on NPP and N-use efficiency (also closely linked to N uptake: Fig. 6C, cf. Vitousek 1982) within which the different species operate.

With these data, modeling of production can be done at either the species-group or community scale. VEGIE could be used to predict the effects of chronic N additions on a given species group, or on the entire community. Using the community-level values assumes that shifts in species abundance occur in close temporal connection with changes in N availability. This assumption is not reasonable for the relatively short time scales considered in this paper. Therefore, only the species-group data (Table 2) are used here.

Fine-root turnover is a quadratic function of nitrogen availability, and is the same for all three species groups (Aber et al. 1985; Table 2). Turnover rate for wood is 2.5%/yr for all three species groups (calculated from Whittaker et al. [1974] data on relationship between NPP and standing biomass for mature forests),

TABLE 2. Parameters for production, allocation, turnover rate, water-use efficiency, and maximum foliar biomass for each species group.

		Linear regression*				TRN (%/yr)	N concentration (% litterfall dry mass)
	P_1	P_2	R^2	n	P		
Species group							
Maple							
Leaf	3.62	.0	⋯	10	⋯	100	.82
Wood	2.04	.0266	.62	10	.003	2.5	.25
Root							1.12
		Water-use efficiency = 330 kg/cm					
		Maximum foliage biomass = 3620 kg/ha					
Oak							
Leaf	−.409	42.8	.78	8	.002	100	.86
Wood	.969	44.4	.62	8	.012	2.5	.25
Root							1.21
		Water-use efficiency = 420 kg/cm					
		Maximum foliage biomass = 5000 kg/ha					
Pine							
Leaf	1.88	27.2	.66	5	.092	50	.69
Wood	−.706	73.6	.81	5	.033	2.5	.25
Root							1.10
		Water-use efficiency = 510 kg/cm					
		Maximum foliage biomass = 7000 kg/ha					
All species							
Root	See text for production calculations						
	Turnover = $(0.811 - 1.72X + 19.5X^2)$ 100, where X is N availability in kg·ha⁻¹·yr⁻¹.						

Whole community production parameters

	P_1	P_2	R^2	n	P
Leaf	2.53	14.3	.30	23	.001
Wood	1.34	38.3	.68	23	.000

* P_1 and P_2 are coefficients for a linear equation $Y = P_1 + P_2X$, where Y is annual NPP in Mg·ha⁻¹·yr⁻¹ and X is N availability in kg·ha⁻¹·yr⁻¹. TRN is turnover of live biomass. See text (*Methods: Model parameterization: Decomposition*) for derivation and sources of data.

and foliage turnover time is 1.0 yr for deciduous species and 2.0 yr for pines, and does not vary with N availability.

Water-use efficiency values for oak and maple are taken from an intensive study of transpiration in several of our deciduous forest sites with different soil types and species mixtures (Fownes et al. 1985). Total net primary productivity measured in these forests divided by evapotranspiration for the growing season yields water-use efficiency for oak and maple. The number for pines is assumed to be higher than for the broadleaved species (Larcher 1975), but no measured value is available from our study. Maximum foliage-biomass values used are equivalent to the highest measured values found in any of our stands.

RESULTS AND DISCUSSION

VEGIE can be used in the nitrogen saturation context to propose answers to several questions: (1) What is the maximum amount of nitrogen that can be retained and cycled within a forest ecosystem, and what determines those limits? (2) How rapidly will N-cycling rates

increase as a result of increased N deposition to the system? (3) How will the trajectory toward nitrogen saturation be altered by interactions with other pollutants, or with forest management?

Validation: equilibrium rates of nitrogen mineralization

In VEGIE, production, allocation, water use, and decomposition rates are all defined as functions of nitrogen availability, nitrogen- and water-use efficiencies, and other input parameters. Predicted nitrogen mineralization is a direct consequence of the way in which these processes interact and are parameterized. It is not constrained or defined as an input, and can conceivably take on any value. Comparing model predictions of equilibrium N-mineralization rates for given stand and soil combinations with measured rates can then be both a validation exercise for the model, and an examination of the factors that determine the equilibrium rate.

Predicting equilibrium N cycling for any stand in the absence of light and water limitation produces a nearly trivial, but interesting, result: there is none. N-cycling
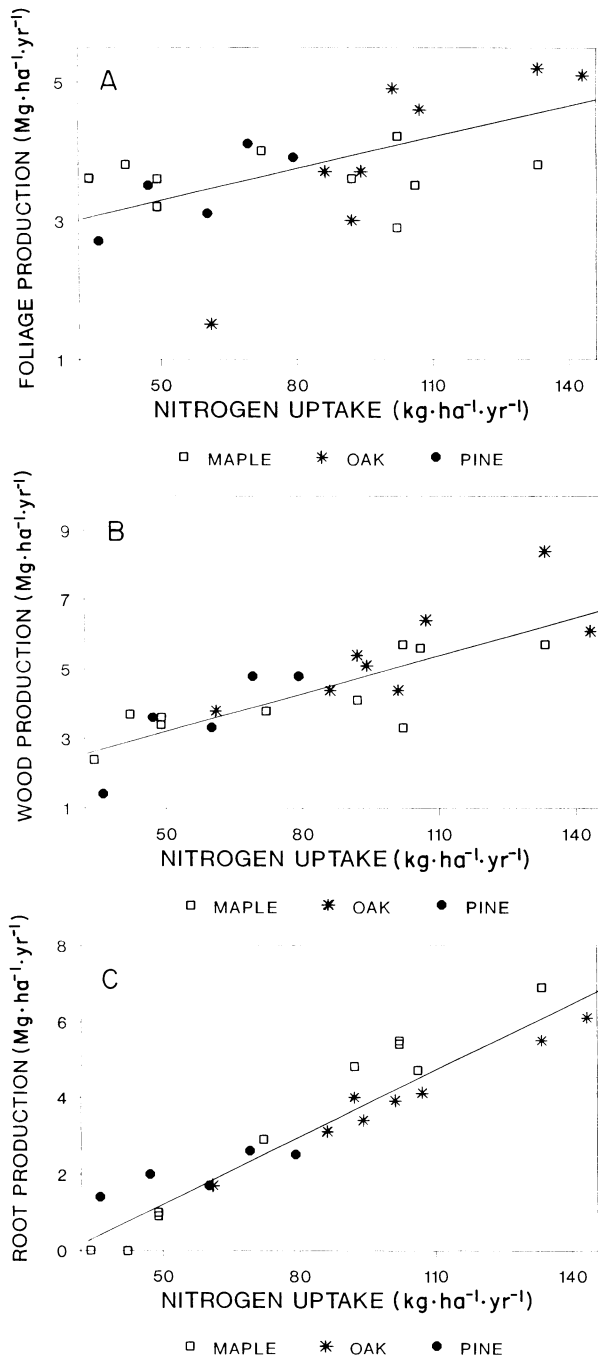
FIG. 5. Net primary production as a function of nitrogen uptake. (A) Foliage production (measured), (B) wood production (measured), and (C) fine-root production (calculated by N-budgeting method). Lines represent linear regression of data combined for all species groups. See Table 2 for coefficients and statistics for species-group regressions.

rates continue to increase indefinitely as long as nitrogen inputs in precipitation are non-zero. It might be argued that this occurs because no variation in the nitrogen concentrations in different biomass fractions are allowed in this version of the model. However, the

feedbacks commonly described (e.g., lower N availability reducing litter quality and hence mineralization rate) would be positive, moving the system away from an equilibrium mineralization rate, not toward one. In addition, we have seen little variation in leaf litter quality across large gradients in N mineralization in our sites (e.g., Pastor et al. 1984, Aber et al. 1990b) in marked contrast to results from fertilizer trials (e.g., Turner 1977).

The second argument against a continuous increase in mineralization rate is that at some point nitrogen will start to leak from the system until inputs equal outputs and internal cycling rates stabilize. However, significant nitrogen leaching implies availability in excess of biotic demand, which in turn implies important limitations on production by some other resource.

The implication of this result is that equilibrium nitrogen-cycling rates are not determined within the cycle itself; not by litter quality, production allocation, or turnover. Rather, equilibrium N-mineralization rates represent the level of N availability at which some other resource becomes limiting to total N uptake and primary production.

Adding water as a second limiting resource causes different species groups to equilibrate at different maximum nitrogen-mineralization rates given the same water availability (Fig. 7A). These rates are a direct function of the relative water- and nitrogen-use efficiencies of each species and the total water available.

The prediction that pine-dominated ecosystems will cycle as much or more nitrogen than oaks or maples at all levels of water availability contradicts a wealth of field data showing higher N-cycling rates for maples and oaks (Gosz 1981, Melillo 1981, Pastor et al. 1984, Nadelhoffer et al. 1985). However, adding the maximum foliar biomass limitation alters predicted equilibrium N-cycling rates considerably, and brings them into line with field-measured values (Fig. 7B). The pattern of predicted N-mineralization rates as a function of water availability is similar to the measured pattern for a series of mature stands in Wisconsin (Fig. 8), while a set of disturbed and restored stands have mineralization rates below the equilibrium values, as expected. Measured patterns of species distribution in a series of mature sites shows that pines dominate on the drier sites, oaks on moderate sites, and maples on the more mesic sites (Aber et al. 1982b, Pastor et al. 1982). It is interesting that this model, which ignores succession and competition between individuals, produces the same result as a more complex model that simulates populations dynamics in the context of N, water, and light limitations (Pastor and Post 1986).

This validation exercise suggests that the control over equilibrium nitrogen mineralization resides not within the N cycle itself, but in the species-specific ratios of water to nitrogen-use efficiency values, in the upper limits to production set by tolerance for low light levels, and in foliar retention time, as expressed in the max-
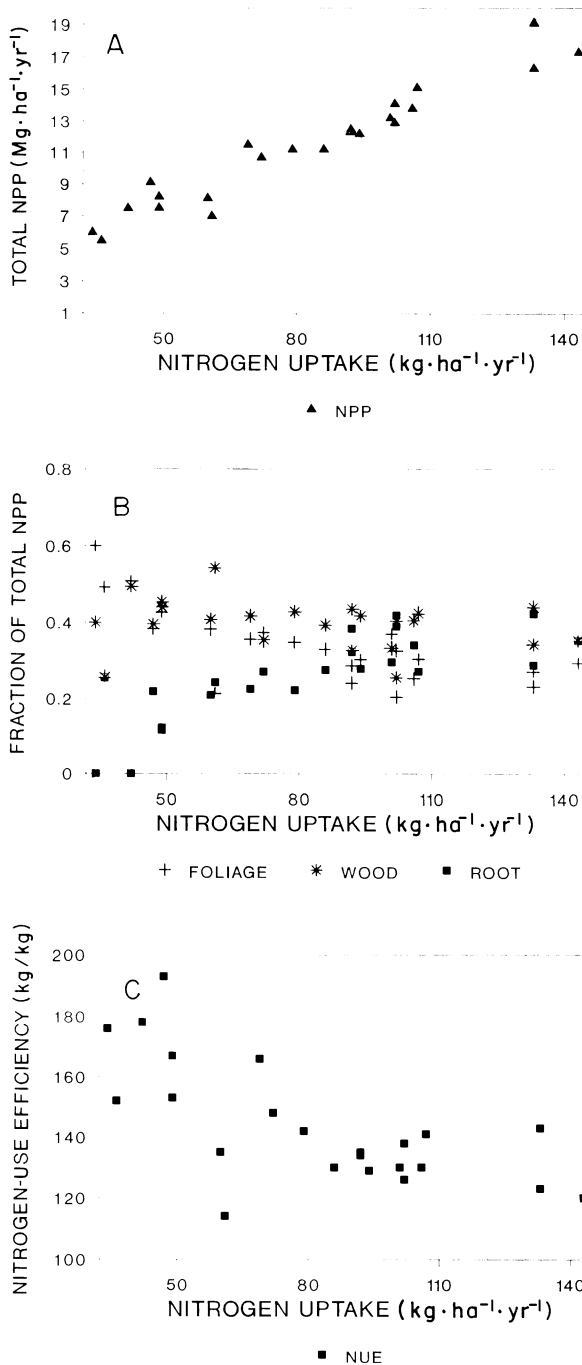
FIG. 6. Combined field data on (A) total net primary production, (B) production allocation, and (C) nitrogen-use efficiency as a function of total annual nitrogen uptake.
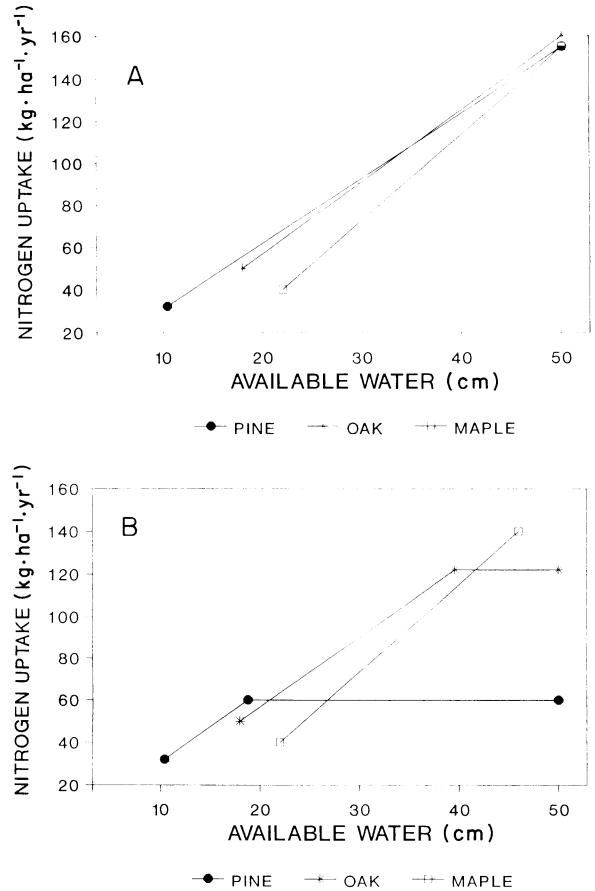

FIG. 7. Predicted equilibrium nitrogen-cycling rate for the three species groups as a function of available water: (A) without the limitation imposed by the maximum foliage values, and (B) with the maximum foliage values in place.

imum foliar biomass value. Differences in turnover rates of biomass and litter pools affect how quickly this equilibrium is achieved, but not the equilibrium value itself. Pines thus cycle less nitrogen on mesic sites because longer needle-retention time causes the maxi-

mum foliar biomass to be attained at relatively low rates of N uptake. On a given site, oaks will cycle more N than maples because of their higher water-use efficiency, which is only partially offset by maples' lower nitrogen-use efficiency at high N availability. No plateau is reached for sugar maple because of the constant foliage production value used in the production routine for this species.

An interesting implication for nitrogen-deposition control policy is that the equilibrium nitrogen-cycling rate for any site can be estimated directly by a calculation based on water availability, and the water- and nitrogen-use efficiencies and maximum foliar biomass attainable by the species group occupying the site. No modeling need be involved. This equilibrium rate is also the *maximum* rate of nitrogen uptake that can be sustained on a given site. If total mineral-N availability is higher than this value as a result of increased N deposition, then N saturation has occurred and N-leaching losses would be expected. A comparison of measured N-cycling rates with the calculated equilib-
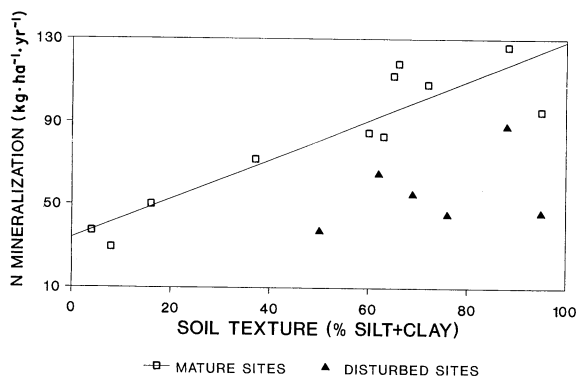
FIG. 8. Measured nitrogen mineralization rates for several stands in Wisconsin in relation to soil texture. □ = mature stands, △ = disturbed and restored stands. Regression line has been fit to mature site data ($y = 33.5 + 0.952x$, $n = 11$, $R^2 = 0.82$, $P < .001$).

rium values indicates how close to N saturation a stand is.

Rates of change in N cycling

VEGIE predicts that cycling rates will increase very slowly under current ambient rates of nitrogen input in precipitation for forests not heavily impacted by pollution-derived N deposition (Fig. 9). Increases on the order of $1-2$ kg·ha^{-1}·yr^{-1} in a decade might be expected with a precipitation, N input of 10 kg·ha^{-1}·yr^{-1}. This results from the large mass of nitrogen in the soil system and its generally slow turnover rate. Thus, systems in which moderate- to long-term N cycling has been reduced by removal of nitrogen (e.g., due to fire or forest harvesting) can be expected—in the absence of elevated N-deposition rates, commercial fertilization, or a large input from nitrogen fixing species—to return to the equilibrium mineralization rate very slowly. If nutrient removals are frequent or substantial, such as in commercially managed or fire-dominated systems, the equilibrium value may be irrelevant. This may explain the general limitations by nitrogen on production in managed, northern temperate forests.

In areas heavily affected by industrial pollution, N deposition may be many times higher than background (e.g., Lovett et al. 1982, van Breeman and van Dijk 1988). This will result in a much-faster approach to the equilibrium N-cycling rate, and to N saturation (Fig. 9). Perhaps even more importantly, increased N deposition reduces the amount of N from mineralization that is required to saturate biotic demand (availability is the sum of mineralization and inputs). Increased N deposition then will speed the approach to saturation by both increasing the mineralization rate and reducing the mineralization rate at which saturation will occur. However, even under high N-deposition rates the approach to saturation will be gradual,

and may be evidenced by slowly increasing rates of nitrate leaching.

Reductions in the N-mineralization rate can also occur rapidly when low-demanding species are planted on sites with high nitrogen availability (Fig. 9: pine-conversion run). In the current version of VEGIE, 90% of the available nitrogen not taken up in a given year is assumed to be lost from the system in that same year. When demand is well below availability, large losses can occur and mineralization can decline quickly (cf. Nadelhoffer et al. 1983). This decline is not due to slow decay of low-quality litter, but rather to the lower uptake potential of pines (see Fig. 7b).

Predicting time to N saturation

VEGIE can be used to predict the time to N saturation for any combination of species and site for which the modest set of input parameters required can be specified. For sugar maple growing on a site with an initial N-mineralization rate of 65 kg·ha^{-1}·yr^{-1}, the time to N saturation can vary from 0 to well over 250 yr, depending on the availability of water on the site and the rate of N-deposition (Fig. 10). In general, the time to saturation is shorter for stands with low water availability and high N-deposition rates.

While we have not yet parameterized VEGIE for high-elevation spruce–fir forests, it is clear from this analysis that the time to saturation would be very short in this forest type due to high N-deposition rates (Lovett et al. 1982, Scherbatskoy and Bliss 1984) and low N-cycling capacity (long needle retention, low NPP; Gosz 1981, Sprugel 1984). That N saturation has occurred in some portions of the spruce–fir zone is suggested by increased nitrification rates in heavy N-deposition areas (McNulty et al. 1990), elevated needle-nitrogen content (Lang et al. 1982), and increased nitrate leaching from the root zone (Johnson et al. 1990) in selected sites.
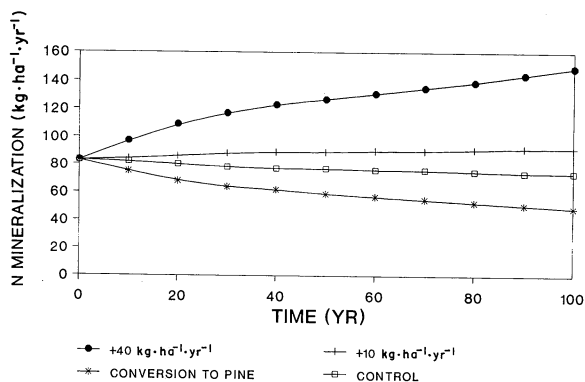

FIG. 9. Rates of change in net annual N mineralization in relation to N deposition and plant demand. All simulations begin with a maple stand with an N-mineralization rate of 82 kg·ha^{-1}·yr^{-1}. The conversion to pine is to a plant community with total N-uptake potential of 45 kg·ha^{-1}·yr^{-1}.
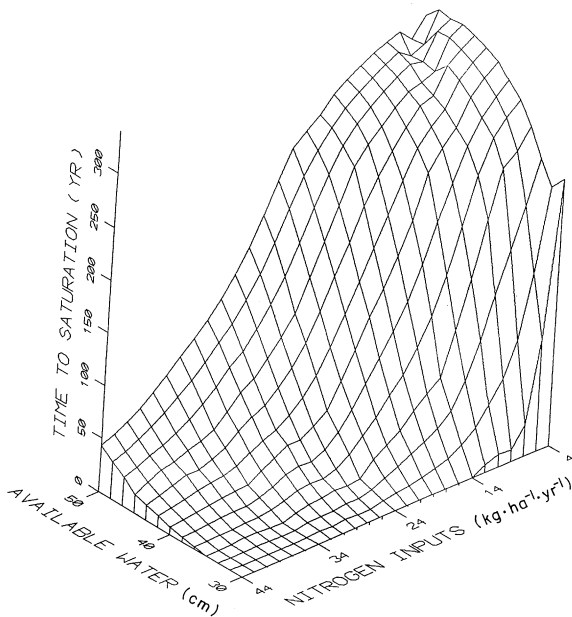
FIG. 10. The time to N saturation as a function of available water and N deposition rate for a maple stand with an initial N-mineralization rate of 65 kg·ha^{-1}·yr^{-1}.

Harvesting effects

Harvesting can represent a significant drain on the nitrogen capital of forest ecosystems (Boyle and Ek 1973, Kimmins 1977, Hornbeck and Kropelin 1979), which will be reflected in reduced N-mineralization rates (Aber et al. 1982a). However, this effect is limited to the amount of nitrogen sequestered in harvested biomass over the management rotation. Using a 50-yr rotation length, winter whole-tree harvesting, and N deposition of 20 kg·ha^{-1}·yr^{-1} in the maple forest type (Fig. 11), VEGIE predicts that harvesting would mainly change the timing of the occurrence of saturation rather than eliminate it.

Each simulated rotation follows a similar trend for N mineralization. N mineralization increases substantially in the first two years following cutting, then declines through time as the pulse of nitrogen represented by the cohorts of slash and litter produced by the cutting pass through the decay stages present in the model.

Superimposed on this cyclic pattern is a longer term trend of increasing mineralization rates due to N deposition (Fig. 11). In each rotation, the 2nd-yr peak in net N mineralization is somewhat higher. In the first rotation N saturation does not occur. In the second N availability is in excess of biotic demand for 5 yr. The period of N saturation increases with each rotation until saturation occurs throughout the entire final 50-yr period. This occurs because the 1000 kg/ha of N added by deposition over each 50-yr rotation more than offsets the 322 kg/ha removed in the harvest. The timing and extent of N saturation predicted for the

second rotation in this simulation mimics results of the clear-cutting experiments carried out in the northern hardwood forest type in New England (Likens et al. 1970, Martin and Pierce 1980). With increased N deposition in this region, the next round of harvesting on these same sites could yield even higher concentrations of nitrate in stream water, and larger total N losses. In this simulation, harvesting actually decreased the time until the first episode of nitrogen loss from the system (Fig. 11).

The potential to use forest harvesting as a means to delay N saturation may also be severely limited by the concurrent removal of nutrient cations which have been found to reach critically low levels in forest soil saffected by acid deposition (Schulze 1989). A version of VEGIE that deals with pools and availability of cations is being developed.

Interactions with ozone and other pollutants

VEGIE does not deal with the effects of ozone exposure in a mechanistic way, but rather through impacts on relative resource-use efficiencies. Ozone reduces net photosynthesis as a linear function of cumulative dose (concentration × hours; Reich and Amundson 1985). This translates into reduced NPP per unit of water used. Reduced water-use efficiency will lead to N saturation at a lower level of N mineralization (Fig. 12). This suggests that forests exposed to both elevated ozone concentrations and increased N deposition will reach saturation faster than those experiencing increased N deposition alone. In contrast, extreme rates of heavy-metals deposition may reduce the decomposition rate of soil organic matter (Tyler 1976, Ebregt and Boldewijin 1977, but see also Friedland et al. 1986). This would reduce N-mineralization rates and delay the onset of saturation.
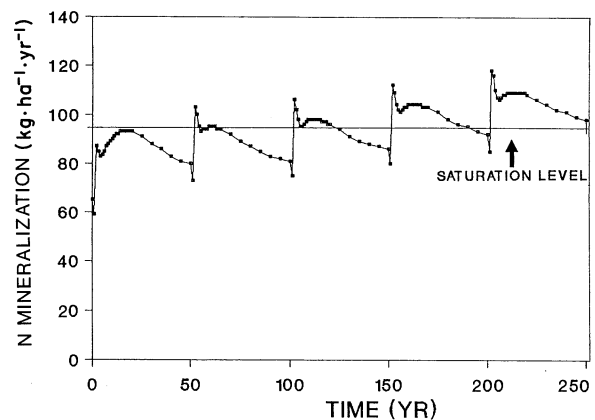

FIG. 11. The effects of sequential harvests on the pattern of N mineralization. This run is for maple with an initial N-mineralization rate of 65 kg·ha^{-1}·yr^{-1} and N deposition of 20 kg·ha^{-1}·yr^{-1}.
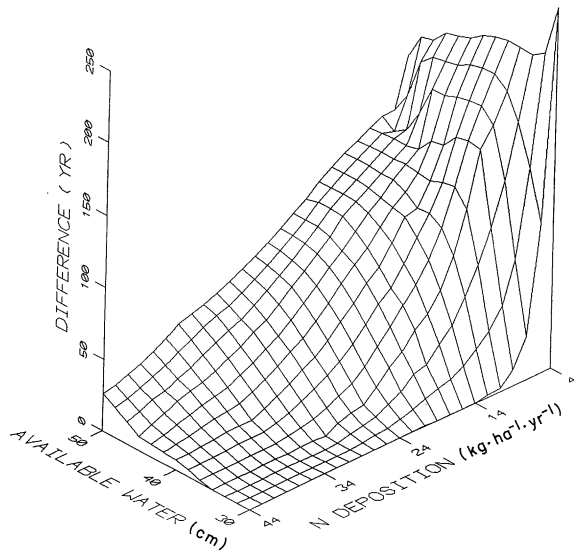
FIG. 12. The change in the time to saturation for the same initial conditions as Fig. 10, but with a 10% reduction in water-use efficiency used as a surrogate for a 10% reduction in net photosynthesis due to ozone. Note that the large difference values at low N-deposition rates mean that N saturation will occur within 50 yr, rather than within 300 yr.

Relationship of results to critical loads assessment

Several predictions from the VEGIE model are relevant to the current effort to establish critical loads for nitrogen deposition (Nilsson and Grennfelt 1988). First, all forests will reach N saturation at some point in the absence of nitrogen removal, as long as N inputs are non-zero. Increased N deposition shortens the time to saturation, reduces the N-mineralization rate required to induce saturation, and increases the nitrogen-leaching losses to be expected after saturation has occurred. This suggests that critical loads must be set within a specific temporal framework, and with reference to expected management practices. Second, the removal of nitrogen *either* as harvested biomass or through leaching implies a loss of nutrient cations as well. Either process may have significant negative effects in terms of nutrient cation availability, soil pH, and aluminum mobility, particularly for systems in which acid deposition is reducing soil cation pools. Third, interactions with other forms of pollution may increase or decrease the time required to reach saturation for a given system. Fourth, alterations in the species composition in a forest ecosystem from higher to lower N-use efficiency, when such species are available, may delay the onset of N saturation by increasing the N-cycling potential of the system.

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