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**NITROGEN OUTPUTS FROM FORESTED WATERSHEDS
IN THE CHESAPEAKE BAY DRAINAGE BASIN¹**

D R A F T

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1. INTRODUCTION

The Chesapeake Bay Watershed Model (Linker et al. 1993) is designed to simulate nutrient loads delivered to the estuary under different management scenarios. The nutrient loads are differentiated into anthropogenic loads amenable to management, and nonanthropogenic loads which are considered to be uncontrollable. The Chesapeake Bay Agreement requires a 40% reduction of controllable phosphorus and nitrogen to the tidal Bay by the year 2000. To determine the quantity of the controllable nutrient load and to evaluate the efficacy of nutrient control strategies, the entire 164,000 km² of the Chesapeake Bay basin have been simulated using the HSPF model (Hydrologic Simulation Program - Fortran). The HSPF model is a modular set of computer codes that simulate hydrology, nutrient and sediment export from pervious and impervious land uses, and the transport of these loads in rivers and reservoirs (Donigian and Huber 1991). Cropland is simulated with a detailed nonpoint-source load simulation module (AGCHEM) that includes application of fertilizer, manures, atmospheric deposition, crop uptake, soil binding, denitrification, and surface/subsurface export. Although 60% of the Chesapeake Bay basin is in forest, there is currently no module in HSPF to simulate forest nutrient outputs.

In order to select nutrient management options, it is necessary to have confidence in current estimates of contributions from different land uses and the ability of a model to provide acceptable estimates of contributions for possible future scenarios. From simulations in Phase II of the modeling activity it was known that the model was not adequately predicting nitrogen (N) for some basins (Donigian, et al. 1991). Usually N loadings from forests would be considered an uncontrolled source; however, atmospheric N deposition to forests is expected to change with implementation of the 1990 Clean Air Act Amendments.

This report focuses on the identified need of the Chesapeake Bay Program to better simulate nitrogen (N) outputs from the forested portions of the Bay drainage and a short-term desire to the U.S. Environmental Protection Agency (EPA) to be able to build off of the existing HSPF model, if possible, for implementation within one to

two years. In addition, EPA was interested in a model that would be responsive to changes in atmospheric deposition. We undertook three activities to meet EPA's needs 1) reviewed the literature on forest N pools and fluxes, 2) reviewed N data from research catchments in the Chesapeake Bay Drainage Basin, and 3) convened a workshop of scientists knowledgeable about forest N literature, data, and models. Eighteen participants attended the workshop on 9-10 February 1994 in Annapolis, Maryland (Appendix A). The workshop participants undertook the following tasks.

- Evaluate how realistic the estimated N loads were from forested watersheds using the current model.
- Evaluate the HSPF AGCHEM module structure with regard to possible modification and use for a new forest module.
- Identify available data for parameterization and verification of a new forest module.

We report on our findings and conclusions from these activities. Our recommendations are oriented towards the Chesapeake Bay Program's short-term model needs, and the recommended approach is not meant to undermine the need for process models of N cycling in forests which should be most responsive to changes in atmospheric deposition and disturbance events.

2. CURRENT MODEL APPROACH

2.1 HSPF Results for Forested Portions of the Chesapeake Basin

Currently the HSPF simulations for the Chesapeake Bay Drainage Basin predict that nitrate is the dominant form of hydrologic N output from forests (Table 1). The model predicts mean annual nitrate concentrations from forests ranging from 0.292 mg N/L in the James River Drainage to 2.28 mg N/L in the Susquehanna River Drainage. Outputs of nitrate range from 0.86 to 7.09 kg/ha/y. The model predicts a much lower and narrower range of ammonium concentrations of 0.019 (Patuxent) to

0.036 mg N/L (James) and outputs of 0.04 to 0.10 kg N/ha/y. Similarly, the model predicts low concentrations and outputs of dissolved organic nitrogen (DON) of 0.01 (Susquehanna) to 0.05 mg N/L (Potomac) and 0.13 to 0.42 kg/ha/y, respectively.

In the Susquehanna and Potomac River Drainages the HSPF simulations underestimate the output of all forms of N measured at the fall line stations on these rivers (as indicated by Model/Measurement Output values < 1 in Table 1). This would imply that there are additional sources of all forms of N in these drainages not accounted for by the model. In the James River Drainage, the HSPF simulation overpredicts the nitrate and ammonium output and underpredicts the DON output. In the Patuxent River Drainage the model and fall line measurements are in reasonably good agreement.

Verification and evaluation of the HSPF simulations of N concentrations and outputs can best be accomplished by comparing the model simulation results with empirical data collected from completely forested catchments within each of the major drainage basins in the Chesapeake Bay Basin. In Section 4 of this report, we present the empirical data on N concentrations and outputs available for forested catchments in this region and compare these data with the HSPF simulations.

3. NITROGEN INPLITS TO REGION

Annual wet deposition of nitrate in the Chesapeake Bay Drainage Basin ranges from 2 to 5 kg N/ha and annual wet deposition of ammonium ranges from 1.5 to 3 kg N/ha, for a total N wet deposition range from 3.5 to 8 kg N/ha (NAPAP 1991). The majority of the basin receives a moderate amount of wet N deposition (about 3.4 kg N/ha/yr) while a high deposition rate would be > 4.5 kg N/ha/yr. There are only a few direct estimates of dry deposition of N, and these indicate that dry deposition is approximately 40% of total N deposition (NAPAP 1991). Using this estimate of dry deposition, total annual N deposition to the Chesapeake Bay Drainage Basin ranges from 6 to 13 kg N/ha. This estimate indicates that forests in the Chesapeake Bay

Drainage Basin are at the low end of the range for "critical loads" of nitrogen (Section 5.1).

4. MEASUREMENTS OF NITROGEN CONCENTRATIONS AND OUTPUTS FROM FORESTS

4.1 Summary of Available Data

There are few data on nitrogen concentrations or outputs from forested catchments in the Chesapeake Bay Drainage Basin (Figure 1). Most of the data that do exist are from research catchments established by the U.S. Geological Survey (USGS) and the Smithsonian Environmental Research Center, or from the USGS Lower Susquehanna NAWQA project. There are also more data on nitrate than on ammonium or dissolved organic N (DON) outputs. The lack of DON data is probably because it is a rather difficult analysis to perform.

The data that we have been able to locate on annual average N concentration and output from forested catchments is compiled in Table 2. The range in nitrate concentrations is 0.014 to 0.346 mg N/L and outputs range from 0.04 to 2.4 kg N/ha/y. There is some evidence that nitrate concentrations and outputs in the Susquehanna River Drainage and the northwestern portions of the Potomac River Drainage are somewhat higher than in the Virginia portions of the Chesapeake Bay Drainage Basin. This may be the result of somewhat higher levels of atmospheric nitrate deposition in northern and western portions of the Basin, or a longer history of high N deposition rates. Nitrate concentrations from 0.5 to 1.0 mg N/L are now common in some streams of the Catskill Mountains of New York (Stoddard 1991) and streams at the Fernow Experimental Forest in West Virginia (Adams et al. 1993). However, all available data for forested catchments in the Chesapeake Bay Drainage Basin suggest that nitrate outputs are still quite low, with concentrations generally in the range of 0.08 to 0.35 mg N/L in the Pennsylvania and Maryland portions of the

Basin and in the range of 0.01 to 0.04 mg N/L in the Virginia portion of the Basin. Although we have identified data for only one forested catchment in the Coastal Plain and have no data for the Piedmont, we expect that nitrate outputs from forests in these physiographic provinces are similar to those for the highland regions.

Concentrations and outputs of ammonium from forested catchments are consistently low, much lower than for nitrate. This is because ammonium is both biologically and chemically very reactive and thus its mobility is restricted in forested catchments. Ammonium concentrations ranged from 0.016 to 0.064 mg N/L and outputs ranged from 0.07 to 0.18 kg N/ha/y in our compiled dataset (Table 2). The somewhat higher values for the Coastal Plain catchment may reflect somewhat lower geochemical retention of ammonium in sandy soils compared to the clay-rich soils of the highlands.

Concentrations of nitrate in streams draining forested catchments in this region generally exhibit seasonal variation, with somewhat higher levels during the non-growing season when forest vegetation is dormant. Stream discharge is also generally greater during the non-growing season, particularly in spring in regions that receive appreciable snowfall. The concentrations presented in Table 2 are primarily discharge-weighted concentrations; consequently, nitrate concentrations during the non-growing season in forested catchments are probably only slightly greater than the annual averages, whereas nitrate concentrations during the growing season may be considerably lower than the annual averages.

Comparisons of total inorganic N outputs (nitrate plus ammonium) and total N inputs (wet plus dry deposition) indicate that forested catchments in the Chesapeake Bay Drainage Basin retain much of the N they receive via atmospheric deposition. Total annual outputs of inorganic N (ranging from 0.1 to 2.4 kg N/ha) are considerably lower than the annual N inputs (6 to 13 kg N/ha, see section 3 of this report). Low nitrate concentrations in stream water and low nitrate outputs relative to N inputs are indicative of stages 0 or 1 of watershed N saturation, as presented by Stoddard (1994) and described in section 5.1 of this report.

Concentrations and outputs of DON are generally similar to those of nitrate, although we have fewer measures of DON (Table 2). Concentrations of DON range from 0.21 to 0.34 mg N/L and outputs range from 0.2 to 1.7 kg N/ha/y. It is generally believed that a considerable portion of the DON output is biologically refractory and will not be remineralized to ammonium and nitrate very rapidly. However, there is considerable uncertainty as to exactly what fraction of the DON is indeed refractory and what fraction will be remineralized within streams and rivers and thus contribute to the N pool available to algae in the Chesapeake Bay.

4.2 Comparison Between Measurements and HSPF Simulations

Comparison between the empirical measurements of N concentration and output from forested catchments (Table 2) and the HSPF simulation predictions (Table 1) clearly indicates that nitrate concentrations and outputs are overestimated by the model. The largest discrepancy between the model results and the empirical data is for the Susquehanna River Drainage. The model predicts forest nitrate concentrations and outputs 5-10 times larger than indicated by the measured values data. The overprediction of nitrate concentrations and outputs by the model for the other drainages is somewhat less, but is still on the order of 2-5 times the measured values. It should be noted that even the larger catchments for which there are measurements for N output (up to about 1.2 km², Young Womans Creek, Table 2) are relatively small compared to the catchments being modeled. However, in order to obtain unambiguous output concentrations and fluxes for forests, we must use data from catchments that are completely forested (or very nearly so). Large forested catchments are generally not found in this portion of the U.S., thus we must use data from smaller forested catchments. We believe that the N outputs from these small forested catchments do reasonably represent the output from forests over larger areas.

There is general agreement between the model and measured values for ammonium concentration and outputs. However, the model underpredicts the

concentrations and outputs of DON by 5-10 times, based on the measured values. Comparison between the DON in the model and the measured values must be treated with caution because the model does not really simulate all DON exported from forests. DON output in the model is calculated as a small fraction (5.3%) of the output of biochemical oxygen demand and thus only represents the fraction of DON that is associated with readily oxidized organic material. The measured values include all DON, only a small portion of which may be readily remineralized. Therefore, the model and measured values may not be in large disagreement with regard to DON. The model at present does not simulate total DON output and the available measurements do not permit an estimate of the remineralizable fraction of total DON output.

5. FOREST NITROGEN POOLS AND FLUXES RELEVANT TO HSPF

The purpose of this section is to summarize information on nitrogen cycling in forests, with particular attention to "big-science" research that has resulted in a synthesis of data from numerous temperate forest ecosystems. Two examples of this type of research were the International Biological Program (1964-1974) that provided data on 116 forest research sites around the world (Reichle 1981), and the recently completed Integrated Forest Study (Johnson and Lindberg 1992) that included 17 forest research sites (16 in North America). This summary focuses on nitrogen pools and fluxes that are important to parameterizing the proposed module to the HSPF model for simulating nitrogen exports from forest watersheds (Figure 2). Estimates for default values for HSPF state variables and fluxes have been derived for use in lieu of site specific data on forest nitrogen cycling. A simple mathematical model was developed to check the validity of estimated N pools and annual fluxes to determine if they yield predictions that are reasonable given our current understanding and empirical knowledge of forest N cycling (Appendix B).

Simple models that are used to summarize information on forest nitrogen cycling usually consist of no less than 3 or 4 state variables: organic-N in mineral soil, nitrogen in forest floor organic matter, available nitrogen in soil and forest floor layers, and total plant N (see for example, Cole and Rapp 1981, Aber et al. 1983, Nadelhoffer et al. 1985). The primary inputs to forests are atmospheric nitrogen deposition and nitrogen-fixation. The principal exports are leaching losses from soil and denitrification. Nitrogen inputs in deposition, retention of ammonium-N by soils, the release of organically bound nitrogen through mineralization, and uptake of available nitrogen by plant roots and microorganisms each play some role in determining the amount of nitrate leaching from forest soils.

5.1 Nitrogen Saturation in Forest Ecosystems

Nitrogen deficiency is a common condition in forests, and nitrogen deficient forests tend to retain and conserve nitrogen entering the ecosystem via fertilizer applications or atmospheric nitrogen deposition (Johnson 1992). However, with continuous long-term nitrogen inputs, forests may progress through several stages to a condition of "nitrogen saturation" (Aber et al. 1989, Stoddard 1994). Nitrogen saturation occurs when nitrogen sources in the ecosystem exceed nitrogen sinks, i.e., when the combined inputs from nitrogen mineralization and atmospheric deposition exceed the nitrogen uptake capacity by plants and soil microorganisms (Stoddard 1994).

Stoddard (1994) has described various stages leading up to nitrogen saturation in forested watersheds. During the early stages, streamwater nitrate concentrations exhibit seasonal patterns attributable to changing seasonal demands of trees and soil microorganisms for available soil nitrogen. Forests in these early stages are not nitrogen saturated. However, in later stages biological controls over nitrogen export are lost, nitrate concentrations become elevated in groundwater, and measured nitrogen outputs from watersheds (via nitrate leaching) exceed atmospheric nitrogen inputs. Nitrogen saturation can occur without dramatically visible changes in forest

ecosystem health (Aber et al. 1989), but excessive nitrate leaching is usually a reliable indicator of nitrogen saturation (Van Miegroet et al. 1992, Van Miegroet and Johnson 1993). Recent field experiments indicate that nitrogen saturation can be rather quickly induced in forest watersheds following increased rates of nitrogen deposition (Kahl et al. 1993).

As a minimum requirement, we would expect HSPF simulations of nitrogen outputs from forests to mimic changes in streamwater nitrate concentrations that accompany the four stages of nitrogen saturation described by Stoddard (1994). In the first stage (stage 0), streamwater nitrate concentrations are very low during the growing season (less than those measured in deposition), and may exhibit transient spring maximums that are attributable to the flushing of nitrogen stored in soils or snowpacks during the dormant season. The second stage of nitrogen saturation (stage 1) is similar to stage 0 in that demands for nitrogen by biota still exceed available supplies; consequently there is little or no nitrate leaching during the growing season. However, in stage 1 the onset of nitrogen limitation is delayed during the spring giving rise to an amplification in the seasonal pattern of stream water nitrate concentrations (i.e., concentrations during the spring are elevated and exceed concentrations typically measured in atmospheric deposition). During stage 2, there is a further reduction in nitrogen limitations to forest productivity during the growing season and nitrogen sources begin to exceed nitrogen sinks. Net nitrification is an important component of net soil nitrogen mineralization in stage 2 forests. The seasonal pattern in streamwater nitrate concentrations, which is typical of stage 0 and stage 1 forests, begins to disappear in stage 2. Stage 2 forests are characterized by elevated concentrations of nitrate in streamwater at baseflow and in groundwater. In the final stage of nitrogen saturation (stage 3), nitrogen demands by biota are exceeded at all times and biological controls on nitrogen losses from the ecosystem cease to function. Nitrogen sources (atmospheric N deposition and mineralization) exceed nitrogen sinks (biological demands) even during the growing season. At this stage, streamwater nitrate concentrations are chronically elevated above those

observed in atmospheric N deposition and hydrologic losses of nitrogen exceed nitrogen inputs to the forest.

Changes that occur along the path to nitrogen saturation illustrate that there are limits on nitrogen retention by forest ecosystems. Nilsson (1986) has attempted to define the "critical load" of nitrogen to forests (i.e., the amount of atmospheric nitrogen deposition that a forest can bear over the long-term without adverse ecological effects). The definition of critical loads for nitrogen has been difficult (Skeffington and Wilson 1988), but various estimates suggest that long-term deposition rates exceeding 5 to 20 kg N/ha per year may result in nitrogen saturation and nitrate leaching from forests (Agren and Bosatta 1988, Gundersen 1991, Hogberg et al. 1992, Stoddard 1994). The critical load is not a constant because the potential for nitrate leaching is determined by environmental factors and internal processes unique to each forest ecosystem (e.g., nitrogen uptake via tree roots and net nitrogen mineralization in soil).

5.2 Nitrogen Output Does Not Equal Nitrogen Input

Table 3 summarizes estimates of nitrogen inputs and outputs from temperate forest ecosystems based on literature data. These data must be interpreted with caution because they were derived from studies using widely varying techniques and different periods of measurement. For systems receiving more than 10 kg N/ha year, nitrogen outputs increase with nitrogen inputs (Figure 3). Grennfelt and Hultberg (1986) have published similar data indicating that nitrogen outputs increase markedly when annual inputs to forests in wet deposition exceed ≈ 10 kg N/ha. However, Figure 2 indicates that nitrogen outputs from forests are not a simple linear function of atmospheric nitrogen inputs. There is a large variation in estimated nitrogen outputs from forests where nitrogen inputs are estimated to be ≤ 10 kg N/ha per year.

The absence of a simple relationship between nitrogen input and nitrogen output is supported by results from the Integrated Forest Study where only 11% of the variation in nitrate leaching from 16 sites could be explained by a simple linear regression against atmospheric nitrogen input (Van Miegroet et al. 1992). However,

Van Miegroet et al. (1992) found that 67% of the variation in nitrate leaching across the IFS sites was explained by a combination of atmospheric nitrogen inputs, nitrogen uptake by overstory trees, and net nitrogen mineralization in the top 10 cm of mineral soil.

Nitrate leaching from forests is partly a function of the difference between nitrogen supply (atmospheric nitrogen inputs and soil nitrogen mineralization) and nitrogen demand (uptake by forest biota). Sites in the Integrated Forest Study that leached nitrate could be distinguished from those that did not on the basis of the difference between nitrogen supply and uptake of nitrogen by trees (Van Miegroet et al. 1992). Johnson (1992) also found that measurable nitrate leaching from forests occurred when annual nitrogen inputs exceeded the amount of nitrogen annually fixed in tree wood (net increment). These studies indicate that nitrate leaching should not be modeled as a function of nitrogen inputs alone, but as a function of the difference between nitrogen supplies to the ecosystem and demand for nitrogen by forest biomass.

5.3 Nitrogen in Tree Biomass

Amounts of nitrogen in aboveground (wood and leaves) and belowground (root) tree biomass are summarized for temperate deciduous and coniferous forests in Table 4. Nitrogen sequestered in belowground tree roots was estimated for forest stands during the Integrated Forest Study but not during the International Biological Program. Based on 17 sites where data on both aboveground and belowground tree nitrogen are available, the mean (\pm SD) ratio of belowground nitrogen to aboveground nitrogen in forest trees is 0.27 ± 0.13 . For sites where no estimate of belowground nitrogen in tree roots is available, the amounts of belowground tree nitrogen were predicted using this ratio. This estimation method resulted in reasonable agreement between the predicted total amounts of nitrogen in trees and reported total amounts of nitrogen in trees for sites that were part of the Integrated Forest Study (Table 4).

Temperate coniferous and deciduous forests do not differ markedly in the amount of nitrogen in aboveground tree biomass (Cole and Rapp 1981), therefore no distinction has been made here between the two forest types. For the forests summarized in Table 4, the mean (\pm SD) amount of nitrogen in aboveground tree biomass is 456 ± 199 kg/ha. The determination of nitrogen amounts in belowground root biomass is difficult and subject to large uncertainties. The mean (\pm SD) predicted amount of nitrogen in tree roots based on the data in Table 4 is 123 ± 54 kg/ha. Recent comparisons indicate that the amount of nitrogen in the fine root (less than 2 to 5 mm in diameter) biomass from North American deciduous forests is on the order of 50 to 100 kg/ha (Hendrick and Pregitzer 1993). Based on estimates presented in Table 4, the mean (\pm SD) predicted amount of nitrogen in total tree biomass in temperate forests is $579 (\pm 253)$ kg/ha.

5.4 Total Soil Nitrogen

Most of the nitrogen in forest ecosystems is sequestered as organic-N in soil. Amounts of nitrogen in the forest floor and mineral soil layers of temperate forest ecosystems are summarized in Table 5. The mean (\pm SD) amount of nitrogen in the forest floor of 41 forests was 735 ± 643 kg/ha, an amount that was on average 11% of the total nitrogen in the forest floor and mineral soil combined (6484 ± 2782 kg N/ha). The mean turnover time of forest floor nitrogen is 5.5 and 17.9 years, respectively, in temperate deciduous and temperate coniferous forests (Cole and Rapp 1981). Part of the total soil nitrogen is included in soil microbes. Holmes and Zak (1994) determined that ≈ 170 kg N/ha was tied up in soil microorganisms in temperate northern hardwood forests. This nitrogen pool was relatively constant over the growing season and did not change with seasonal changes in rates of net nitrogen mineralization.

Currently, soil nitrogen transformations and plant uptake are simulated for each of the four soil layers in the HSPF model (surface, upper soil, lower soil, and groundwater). The layers are connected by hydrologic flows. For the forest module, it has been recommended that the surface and upper soil layer be combined into a

single, biologically active soil layer which corresponds to the O + A or O + E soil horizons. The lower soil layer corresponds to soil below the A or E horizon. Nitrogen transformations in soil and plant uptake by forests will be modeled only for the upper soil layer in the HSPF forest module.

Table 6 presents data on the distribution of nitrogen between surface soil layers (O + A or O + E horizons) and lower soil layers (below A or E horizon) at low-elevation study sites in the Integrated Forest Study (Johnson and Lindberg 1992). The mean (\pm SD) amount of nitrogen in the surface soil layers of 10 forests was 2055 \pm 927 kg/ha or \approx 35% of the total soil nitrogen (5797 kg/ha) to depths \geq 45 cm. Based on detailed soils data from the Integrated Forest Study and estimates of total nitrogen in the forest floor and mineral soil from Table 5, the nitrogen content of surface forest soils is estimated to be on the order of 2200 kg/ha.

5.5 Nitrogen Fixation

Nitrogen fixation is not included as a process in the current version of HSPF, and nitrogen-fixing trees are not expected to be important in forest communities within the Chesapeake Bay drainage area. Nonsymbiotic nitrogen fixation may occur in the forest floor and in surface soils. Nonsymbiotic nitrogen-fixation in temperate forest ecosystems is estimated to range between 1 and 6 kg N/ha per year (Boring et al. 1988). In some forests, this input is comparable to inputs from atmospheric nitrogen deposition.

5.6 Denitrification

Denitrification is not expected to be important in forest watersheds contributing to Chesapeake Bay because most of these watersheds are probably at stage 0 and stage 1 of nitrogen saturation (see Section 4). Unless soil nitrate levels are elevated, losses of soil nitrate via denitrification will be negligible. Denitrification is more important as a process of nitrogen loss in forests with poorly drained soils (Zak and

Grigal 1991). Denitrification rates in well drained forest soils appear to range from 0.2 to 2.1 kg N/ha per year (Goodroad and Keeney 1984). Clearcutting can increase rates of denitrification to losses on the order of 3 to 6 kg N/ha per year (Robertson et al. 1987). HSPF is not well suited to model denitrification because this process is expected to exhibit substantial spatial heterogeneity. In many catchments only 10% of the total landscape might have soils with the potential for nitrogen losses via denitrification. Denitrification is modeled as a single flux (KDNI) from the surface soil in HSPF. Omission of this flux in HSPF simulations of nitrogen losses from forests is not expected to contribute to large errors in hydrologic nitrogen outputs.

5.7 Net Nitrogen Mineralization

Nitrogen transformation rates in forest soils can exhibit marked variations across relatively short distances (Hill and Shackleton 1989, Zak and Grigal 1991, Garten and Huston 1994). Soil nitrogen transformations are also seasonally variable with a summer maximum and a winter minimum in net nitrogen mineralization (Nadelhoffer et al. 1983, Nadelhoffer et al. 1984, Pastor et al. 1984, Hill and Shackleton 1989, Zak and Pregitzer 1990). Plant uptake, nitrogen return in leaf fall, and litter quality all potentially affect net nitrogen mineralization and nitrogen availability in forest soil, but the relative importance of each controlling factor can vary spatially and seasonally (Vitousek et al. 1982, Nadelhoffer et al. 1983, Gosz and White 1986). Although the situation is complex, recent work by Stump and Binkley (1993) supports the following three assumptions about controls on net nitrogen mineralization in forest soils: (1) net nitrogen mineralization in the forest floor is correlated with that in total soil (forest floor plus mineral soil), (2) litter chemistry controls net nitrogen mineralization rates, and (3) the lignin:nitrogen ratio controls the litter decomposition rate.

Table 7 summarizes data on annual rates of net nitrogen mineralization in forest soils. These data are from studies using widely varying methods and therefore must be interpreted with caution. Net nitrogen mineralization appears to decrease with soil depth; in hardwood stands the highest rates are found in the O + A soil horizons

(Federer 1983). Therefore, data in Table 7 are reported separately for the forest floor layer and the mineral soil. Based on data for low-elevation forests from the Integrated Forest Study, ≈ 1 to 7% of the organic nitrogen in soil is mineralized each year (Van Miegroet et al. 1992). This estimate is in agreement with earlier estimates (1.8 to 8%) of annual net nitrogen mineralization in 9 forest ecosystems in southern Wisconsin (Nadelhoffer et al. 1983). The mean (\pm SD) for net nitrogen mineralization in forest soils based on data in Table 7 is 49 ± 48 kg N/ha per year. The data are not normally distributed, but values in the upper part of the range (>100 kg N/ha per year) are not just from high elevation forest ecosystems which exhibit high rates of nitrate leaching. Based on an estimated total soil nitrogen content of 2200 kg/ha (Table 5) in the surface soil layers (O + A horizon), ≈ 2 to 7% of the organic-N in forest soil is mineralized each year. These data are in good agreement with previous estimates.

In HSPF, soil nitrogen mineralization is modeled as two processes: ammonification (KAM: conversion of organic-N to ammonium) and nitrification (KNI: conversion of ammonium to nitrate). Relative nitrification (i.e., the fractional contribution of nitrification to total nitrogen mineralization) is high in forest soils that are losing nitrogen via nitrate leaching. Otherwise, relative nitrification in forest soils is highly variable and difficult to predict. The current paradigm, which is probably oversimplified, is that nitrification rates are controlled by competition between soil microorganisms and plant roots for available soil ammonium (Riha et al. 1986, Johnson 1992, Van Miegroet and Johnson 1993). Johnson (1992) has suggested that soil nitrifiers may be better competitors for soil nitrogen than previously thought. In nitrogen deficient systems, soil heterotrophs and plant roots are more effective competitors for available ammonium than nitrifiers, but this may not be the case in forests with high nitrogen supplies. In any case, nitrification is expected to be a small fraction of total soil nitrogen mineralization in nitrogen deficient forest ecosystems. Populations of nitrifying microorganism are probably limited in nitrogen deficient soils (Montagnini et al. 1989).

Studies of various forests in Wisconsin indicate that annual rates of nitrification are positively correlated with rates of soil nitrogen mineralization (Pastor et al. 1984). Net annual nitrogen mineralization in forest soil is also inversely correlated with canopy lignin concentrations (Aber et al. 1990) and positively correlated with soil texture (% silt and clay) (Aber et al. 1991). The generality of such relationships is untested on a regional scale like the Chesapeake Bay drainage area. Robertson (1982) found that physical parameters like soil C:N ratios were poor predictors of relative nitrification rates in soil across a broad range of temperate deciduous and coniferous forests. The soil C:N ratio can only be used to broadly distinguish between forest sites that are probably "nitrogen-poor" (C:N >30) or probably "nitrogen-rich" (C:N <10). Many forest ecosystems have C:N ratios in an intermediate range (10 to 30) where either net immobilization or net mineralization can dominate soil nitrogen dynamics; therefore classification of forest nitrogen status is indeterminate (Haynes 1986, Van Miegroet et al. 1992). Relative nitrification can be adjusted in HSPF model simulations, within the limits set by estimates of net soil nitrogen mineralization, to yield realistic values of soil solution nitrate concentrations.

5.8 Nitrogen Uptake By Forest Canopies

Differences between total atmospheric nitrogen deposition to forest canopies and the nitrogen flux measured below canopies in throughfall and stemflow indicate that forest canopies take up nitrogen from deposition (Lindberg et al. 1986, Lovett and Lindberg 1993). In the Integrated Forest Study, canopy uptake of atmospheric nitrogen deposition ranged between 1 and 12 kg N/ha per year (Lovett and Lindberg 1993). Experimental studies with nitrogen-15 tracers in beech forests also indicate a foliar uptake of 3 to 10 kg N/ha per year (Brumme et al. 1992). Foliar uptake of atmospheric nitrogen deposition is not modeled in HSPF. Some of the nitrogen removal by forest canopies is apparently related to processes other than foliar uptake. At this time, it is unclear whether inorganic nitrogen deposition to forest canopies is utilized by the trees or by epiphytic organisms (algae, bacteria, and lichens) (Brumme

et al. 1992, Lovett and Lindberg 1993). The capture of nitrogen from atmospheric deposition by forests appears to be partially offset by a release of organic-N from the canopy (Lovett and Lindberg 1993). Lovett and Lindberg (1993) conclude that in most cases canopy uptake of atmospheric nitrogen deposition is small and nitrogen demands of forest trees are mainly met by uptake of soil nitrogen via roots and translocation of nitrogen from storage pools within trees.

5.9 Nitrogen Uptake By Plants

Studies of nitrogen uptake by forest biomass are summarized in Table 8. In both the Integrated Forest Study and the International Biological Program, nitrogen uptake was determined only for aboveground parts of forest biomass (i.e., nitrogen assimilated for leaf and wood production). Based on data in Table 8, the mean (\pm SD) nitrogen uptake allocated to aboveground forest biomass in temperate forest ecosystems is 58 ± 29 kg/ha per year. There are fewer studies specific to nitrogen uptake for the production of tree roots, but those studies indicate that the mean allocation of nitrogen uptake to root production (64 kg N/ha per year) is comparable to that for aboveground biomass (Table 8). Therefore, for forests in Table 8 where nitrogen uptake allocated belowground is unknown, the total nitrogen uptake is estimated as twice the nitrogen allocated aboveground. Based on this rough method of estimation, the mean (\pm SD) total nitrogen uptake by forest biomass is 116 ± 58 kg/ha per year. Although the fraction of nitrogen uptake allocated belowground is not constant across temperate forest ecosystems (Joslin and Henderson 1987), the assumption that nitrogen uptake is equally apportioned to aboveground and belowground biomass is supported by studies of 9 forest stands in Wisconsin where apparent total nitrogen uptake by vegetation ranged from 47 to 143 kg/ha per year (Nadelhoffer et al. 1985).

In HSPF, the uptake of nitrogen by plants from soil is modeled separately for available soil ammonium and available soil nitrate. It is difficult to ascertain the relative importance of ammonium and nitrate as nitrogen sources for the production of forest

biomass because plants vary widely in their utilization of different forms of inorganic soil nitrogen. Furthermore, internal processes within the trees themselves are important. Lennon et al. (1985) reported that ~70 to 75% of the total foliar nitrogen in sugar maple may be translocated to woody stems prior to autumn leaf fall: this amounted to between 54 and 80 kg N/ha per year in 7 forest stands. Similar amounts of nitrogen conservation by translocation have been reported for a chestnut oak forest in southern Illinois (Ostman and Weaver 1982). In Lennon's study the percentage of foliar nitrogen derived from translocation was inversely related to annual nitrogen mineralization. Therefore, in nitrogen deficient forest ecosystems, mobilization and translocation of nitrogen from storage pools within the tree may constitute a major source of foliar nitrogen at the beginning of the growing season. Calculations for such a forest indicate that root uptake of soil nitrogen accounts for only 25% of the nitrogen transported to spring foliage (Luxmoore et al. 1981). The findings of both Luxmoore et al. (1981) and Lennon et al. (1985) indicate that ~75% of the forest nitrogen demands for foliage production can be met by translocation of nitrogen stored within forest trees.

For forests where soil nitrification is a small fraction of total net nitrogen mineralization (i.e., forests in stage 0 of nitrogen saturation), it can be assumed that most of the total nitrogen uptake originates from the available soil ammonium pool ($\text{NH}_4\text{-S}$). Even so, the root uptake of soil ammonium may be less than that for nitrate under conditions of low soil moisture (i.e., drought) - even when plants exhibit a preference for soil ammonium (Gijlsman 1991). The contribution of soil nitrate to total nitrogen uptake is expected to progressively increase for forests at stage 1, 2, or 3 of nitrogen saturation. Studies by Nadelhoffer et al. (1984) indicate that for nine forests in southern Wisconsin (where measurable net nitrification occurred), soil nitrate supplied between 70 and 100% of the annual nitrogen uptake by forest biomass. In the absence of a better alternative, it is logical to model the fractional contribution of available soil ammonium and soil nitrate to total nitrogen uptake as a function of the stage of nitrogen saturation.

5.10 Return of Plant Nitrogen to Soil

The return of plant nitrogen to soil is modeled as a single flux (PLNTRET) in HSPF although the flux is comprised of the following three separate processes: (1) aboveground litterfall (leaf fall, woody litterfall, and reproductive parts), (2) belowground nitrogen returns (root mortality and decomposition), and (3) leaching of canopy nitrogen by precipitation.

Table 9 summarizes data on aboveground and belowground returns of plant nitrogen to soil in temperate forest ecosystems. The mean (\pm SD) return of nitrogen in aboveground litterfall is 35 ± 18 kg/ha per year. Fewer data are available on nitrogen losses from tree roots, but studies indicate a mean (\pm SD) belowground nitrogen return of 50 ± 19 kg/ha per year. When aboveground and belowground fluxes have been determined in the same study, the average ratio of belowground:aboveground nitrogen return is ≈ 1.6 . Using a factor of 1.6, the mean (\pm SD) total return of plant nitrogen to soil via litterfall and losses from roots in temperate forests was predicted to be 92 ± 46 kg/ha per year (Table 9). This estimated return was somewhat less than an estimated total nitrogen uptake by forests of 116 ± 58 kg N/ha per year (Table 8).

Estimates of nitrogen return to soil from leaching of the forest canopy by precipitation are confounded by the washoff of dry nitrogen deposition to forest canopies. Leaching losses of 4 to 10 kg N/ha per year have been reported for Walker Branch Watershed (Johnson and Van Hook 1989), Harvard Forest (Aber et al. 1983), and Hubbard Brook (Whittaker et al. 1979). In all likelihood, these estimates are too high because laboratory trials indicate that nitrogen does not readily leach from fresh foliage (Gosz et al. 1975, Potter 1991) and field studies of atmosphere-canopy interactions indicate net canopy uptake rather than release of inorganic nitrogen (Ostman and Weaver 1982, Lovett and Lindberg 1993). Leaching of plant nitrogen is negligible relative to other aboveground and belowground nitrogen fluxes to soil.

5.11 Output of Organic Nitrogen

There are very few measurements of organic N concentrations and output from forested catchments. We have identified three studies in which dissolved organic N (DON) was routinely measured in forested catchments in the Chesapeake Bay Drainage Basin. Based on these measurements, concentrations of DON in stream water range from 0.21 to 0.34 mg N/L, and annual outputs of DON range from 0.2 to 1.7 kg N/ha (Table 2). Thus, DON may be a significant portion of the total N output from forested catchments. However, it is unclear what fraction of DON output is readily remineralized and available for uptake by algae in aquatic ecosystems downstream (e.g., rivers, Chesapeake Bay). We know of no definitive studies on the remineralization rates of DON exported from forested catchments. It is possible that a considerable fraction of the DON export is relatively refractory and does not contribute to the available N pool in the Chesapeake Bay.

Even fewer measurements of concentrations and export of particulate organic N (PON) are available than for DON. Particulate organic matter losses from forested catchments are derived largely from inputs of soil organic matter and leaf litterfall to streams. Losses of PON from forested catchments are likely less than losses of DON, and a portion of the PON loss may be retained in the sediments of streams and rivers near its source. Further, as with DON, a portion of the PON loss is likely remineralized very slowly and not available for algal uptake in downstream aquatic ecosystems. Given these uncertainties, it is probably reasonable to omit PON loss from forested catchments from further consideration in this study.

5.12 Effects of Forest Disturbance

We cannot forecast the type or extent of forest disturbance that may impact nitrogen losses from watersheds in the Chesapeake Bay drainage. However, we can outline the theoretical framework for forest controls on nitrogen losses and thereby contribute to defining various scenarios for model simulations with the forest module of HSPF. Devegetation by clearcutting, fire, or hurricane affects evapotranspiration, hydrologic fluxes, and soil temperatures in ways that generally increase nitrogen

export from forest ecosystems. In undisturbed forest watersheds, the annual amount of soil nitrogen mineralized, or assimilated by vegetation, or returned from vegetation to the soil far exceeds annual ecosystem nitrogen losses (Swank 1986). By comparison, many studies demonstrate that forest disturbance can measurably increase ecosystem losses of nitrate-nitrogen (Likens et al. 1969; Likens et al. 1970; Vitousek and Melillo 1979; Swank 1984; Swank 1986).

Vitousek and Melillo (1979) reviewed studies on the effect of various disturbances (mostly clearcutting) on nitrate export from forests. The amount of nitrate leaching in response to forest disturbance is highly variable, and nitrogen losses from disturbed forests may be minimal if low nitrogen availability exists prior to disturbance (Vitousek et al. 1982). However, analysis of available data (Table 1 in Vitousek and Melillo 1979) indicates statistically significant increases in streamwater nitrate concentrations and nitrogen exports following forest disturbance. In Vitousek and Melillo's review, the range of nitrate-N concentrations in drainage water from 23 disturbed forests was 0.01 to 25 mg/L as compared to 0.001 to 1.7 mg/L in controls. A nonparametric Wilcoxon signed-rank test indicates that the latter difference is statistically significant ($Z = -4.03$; $p \leq 0.001$). Vitousek and Melillo's summary of data from 11 studies also indicates that nitrogen exports range between 0.6 to 124 kg nitrate-N/ha per year from disturbed forests versus exports of 0.03 to 4.5 kg nitrate-N/ha per year from control forests. Nitrogen losses as a result of disturbance are highly variable because processes like nitrogen uptake by regrowth vegetation, nitrogen immobilization, lags in nitrification, and a lack of water can act independently or in combination prevent hydrologic losses of nitrate from disturbed forests (Vitousek et al. 1979; Vitousek and Melillo 1979; Vitousek et al. 1982). Disturbances that increase soil nitrogen mineralization or reduce or eliminate plant uptake of soil nitrogen increase the likelihood of nitrogen export from forest ecosystems. Matson and Vitousek (1981) found that forest soils in clear-cut areas had higher potential nitrification rates than those in uncut forests, and warmer soil temperatures (caused by the removal of vegetation) play a role in stimulating rates of soil nitrogen mineralization and nitrification. Disturbances that reduce plant uptake (like clearcutting or defoliation

by herbivorous insects) remove biological controls on the forest nitrogen cycle. Studies at Coweeta, North Carolina, demonstrate that partial defoliation of forests by herbivorous insects is followed by increased stream export of nitrate nitrogen (Swank 1986). Consequently, increased nitrogen exports from forests following gypsy moth infestations is expected. Disturbances that decrease the uptake of soil nitrogen by vegetation can, in effect, induce a temporary condition of nitrogen saturation where inputs from atmospheric deposition and soil nitrogen mineralization exceed forest demands (Vitousek and Melillo 1979; Vitousek et al. 1979). Soil nitrogen mineralized in excess of forest demands is then at risk of loss to streamwater or groundwater. Although forest disturbance by be temporary, elevated streamwater nitrate concentrations may persist for many years after disturbance (Swank 1984).

6. RECOMMENDATIONS

6.1 Proposed Structure for a Forest Nitrogen Module

A workshop on 9-10 February 1994 (see Appendix A) concluded that the current AGCHEM module for N cycling and loss from agricultural systems in HSPF can be modified to allow simulation of N fluxes within and outputs from forested ecosystems (Figure 2). The major modifications to the AGCHEM module are:

- Subdivision of the ORG-N compartment into four soil organic N compartments, two consisting of particulate organic N pools (labile = LORG-N-P, refractory = RORG-N-P) and two soluble organic N pools (LORG-N-S, RORG-N-S) resulting from leaching of the particulate pools, and
- Addition of a flux (PLNTRET) from the plant N compartment (PLNT-N) to the soil labile organic N compartment (LORG-N-P).

The PLNTRET flux consists of both aboveground and belowground return of N to the soil. Although the modified AGCHEM module for forests is a gross simplification of the complex cycling of N in forested ecosystems, we believe that it will allow a reasonable simulation of current N exports from forests to drainage waters in the Chesapeake Bay Drainage Basin given the data available to parameterize it and current state of knowledge.

The functional formulation of the fluxes in the modified AGCHEM module for forests are somewhat different from the agricultural version (Table 10). Because plant and microbial uptake of inorganic N from forest soils is extremely efficient but can be saturated at high N concentrations, a saturation kinetics formulation of these N uptake fluxes (KPLNI, KPLAM, KIMNI, KIMAM) is preferred. The maximum plant uptake rate (U_{max}) should be a function of season (uptake is limited to the growing season) and overall growth rate of forest vegetation (function of forest maturity, insect attack, etc.).

Most of the total uptake of N by plants is returned to the soil each year. Although a portion of this plant N return (PLNTRET) occurs over the entire year (particularly the belowground portion), it can be approximated by an annual pulse to the labile soil organic N pool in October. Mineralization (KAM) and nitrification (KNI) can be approximated as first-order rates as in the agricultural AGCHEM module. Denitrification in well-drained forest soils is generally very low and can be set to zero for most of the upland forests to be considered. Ammonium partitioning and organic N leaching fluxes can be approximated with partitioning functions based on total compartment sizes. Although partitioning fractions are suggested in Table 10, these are just estimates based on best professional judgement and should be used only for initial simulations. Conversion of labile organic N to refractory organic N is a slow process that can be approximated with first-order kinetics.

6.2 Parameterization/verification of Modified AGCHEM for Forested Systems

For many of the compartment sizes and fluxes of the modified AGCHEM module for forests there are only very approximate and widely ranging estimates for

parameterization (see Section 5). Storage of N in forest vegetation (PLNT-N) is probably on the order of 400-800 kg N/ha (Section 5.3). Annual total plant uptake is probably 80-120 kg/ha (Section 5.9), and the return of plant N to the soil is about 80-90% of total plant uptake (Section 5.10). Maximum plant uptake rates (U_{max}) and return could be up to twice these values. Measurements of microbial N immobilization, total mineralization, and total nitrification rates are unavailable. Denitrification rate (KDNI) is also unknown but is probably small and can be set to 0.

For the purposes of simulating N loss from forest catchments to surface waters, the most important compartments to parameterize correctly in the modified AGCHEM module are the pools of soluble nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), and organic N (LORGN-S, RORGN-P). Fortunately, it is these compartments for which there is at least some data in the form of discharge-weighted mean annual concentrations in streams draining forested catchments (Table 2). Thus, the process of parameterizing the modified AGCHEM module for forests in the Chesapeake should be directed toward achieving realistic concentrations of stream nitrate, ammonium, and DON.

The best datasets for performing this parameterization of the forest module are those from Stony Creek (USGS dataset, Lower Susquehanna River NAWQA Project, Lemoyne, PA) and from the USGS acid deposition research program catchments in the Upper Potomac River Basin in Maryland and Virginia (Table 2). The primary features in the dataset to be simulated correctly are the seasonal variation and annual flux of N species in stream water. However, while this parameterization process will allow simulation of current N outputs from forests in the Chesapeake Bay Drainage Basin, it will be of limited value for predicting long-term N outputs because we as yet do not understand the controls of N loss from forests and their relationship to N deposition, forest maturation, and disturbance. More mechanistic, predictive models of N cycling and output from forests are currently being developed at the University of Virginia and the University of New Hampshire under funding from EPA. However, these models are not yet available.

6.3 Short-term Approach

EPA has a short-term need to better simulate N outputs from the forested portions of the Chesapeake Bay drainage and to have a model more responsive to changes in atmospheric deposition. To meet this need we recommend that a forest N module be developed for HSPF as discussed in Section 6.1 and parameterized using values from the literature (Section 5) and monitoring data (Section 6.2).

No model can be optimum for all applications (see Section 6.4), and this new module should be used with caution until it is tested adequately. The proposed forest module for HSPF should not be considered as a substitute for more process oriented models of nutrient cycling in forests. EPA is funding two groups to develop such models (John Aber at the University of New Hampshire and Bernard Cosby at the University of Virginia). The proposed module is also not appropriate for modeling buffer strips or riparian zones where processes may be important that we have not focused on for upland forests or that our recommended data are adequate to parameterize the proposed forest module. Disturbance events in forests such as clear cutting and defoliation of trees by insects like the gypsy moth are known to create nutrient pulses in receiving streams; however, we are not certain that the proposed module would be able to simulate N outputs from such activities and would need to be tested on appropriate data.

6.4 Future Directions

HSPF is a model that contains a high degree of specificity for instream processes but a low degree of specificity for terrestrial landscape processes. Hydrologic models often tradeoff temporal and spatial specificity and/or amount of detail between different processes being simulated. HSPF can be run with short time steps and routing to capture hydrologic patterns of stream flow and concentration that are driven by precipitation events. Data needs and computing time for HSPF are extensive. HSPF is a continuous simulative program and requires continuous data to drive the simulations--rainfall is required with evapotranspiration, temperature, and solar intensity desirable. However, often the possible detail of short time steps is not

utilized for management decisions where seasonal or annual averages are adequate. HSPF models terrestrial landscape processes very coarsely as it uses large subbasins (63 model segments with an average area of 260,300 ha for the Chesapeake) and ignores spatial pattern of landcover on the subbasin. The implementation of spatially explicit nonpoint-source watershed models (Moore et al. 1993, Engel et al. 1993, Levine et al. 1993) is advancing rapidly with the development of Geographic Information Systems and more powerful computers. A spatially distributed model may best serve the Chesapeake Bay Program for its long-term needs of watershed management.

The current implementation of HSPF for the Chesapeake Bay drainage is to evaluate management options with regard to the mandated 40% reduction of controllable phosphorus and nitrogen to the tidal Bay by the year 2000 (Chesapeake Bay Agreement). These reductions will have to come primarily from improved management of landuse, e.g., best management practices for agriculture and silviculture, installation of buffer strips, and reclamation or installation of wetlands and riparian zones. Landscape ecology research has shown that the position of pattern of land use on a watershed is important for modeling nonpoint-source pollutants (Peterjohn and Correll 1984, Osborne and Wiley 1988, Hunsaker et al. 1992, Weller et al. 1993). Thus for the long-term the Chesapeake Bay Program should consider a spatially explicit modeling approach. At least two such modeling activities are ongoing in the Chesapeake Bay drainage (CEES 1993, Weller 1993). The Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies (CEES), has a new research initiative linking upland terrestrial landscapes to freshwater ecosystem processes and, ultimately, to the Chesapeake Bay ecosystem (CEES 1993). This landscape initiative seeks 1) to describe in detail the structure of representative landscapes within the Chesapeake Bay watershed, 2) to investigate the current functioning of those landscapes in order to develop a predictive understanding of landscape-level ecological processes, and 3) to extrapolate those processes to the larger scales of river drainages and the Bay watershed under various scenarios of human-induced stress. Initial activities are focusing on characterization of

upland stream water quality in relation to land use and atmospheric deposition of pollutants, and modeling studies to link hydrologic processes to vegetative cover and nutrient export within central Appalachian watersheds. The Maryland International Institute for Ecological Economics at Cheapeake Biological Laboratory is designing a regional landscape simulation model that will present the effects of different management and climate scenarios on ecosystems in the Patuxent River watershed (CEES 1993). The Patuxent Landscape MODEL (PLM) estimates the changes in the watershed that result from management decisions that impact land use and agricultural practices. An objective is to provide a tool to estimate the nutrient and sediment loading that would stem from various land use patterns and practices on the watershed.

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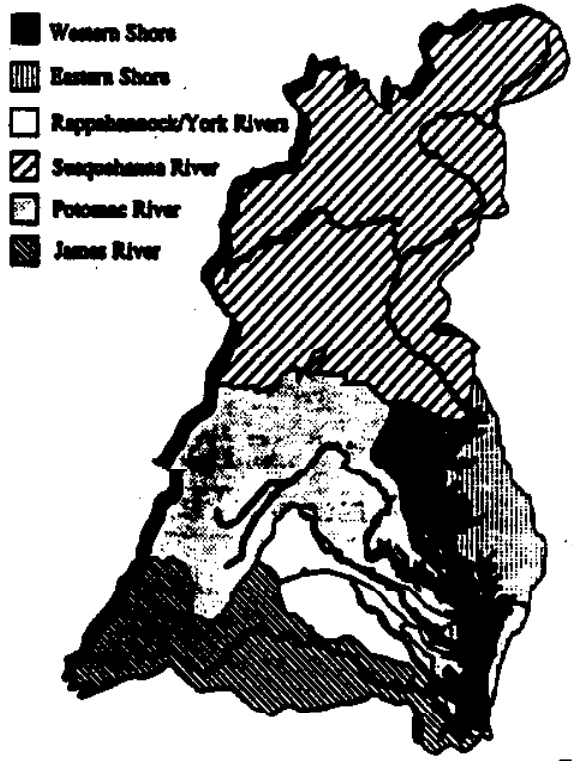


Figure 1

Modified AGCHEM Module for Forest N Transformations

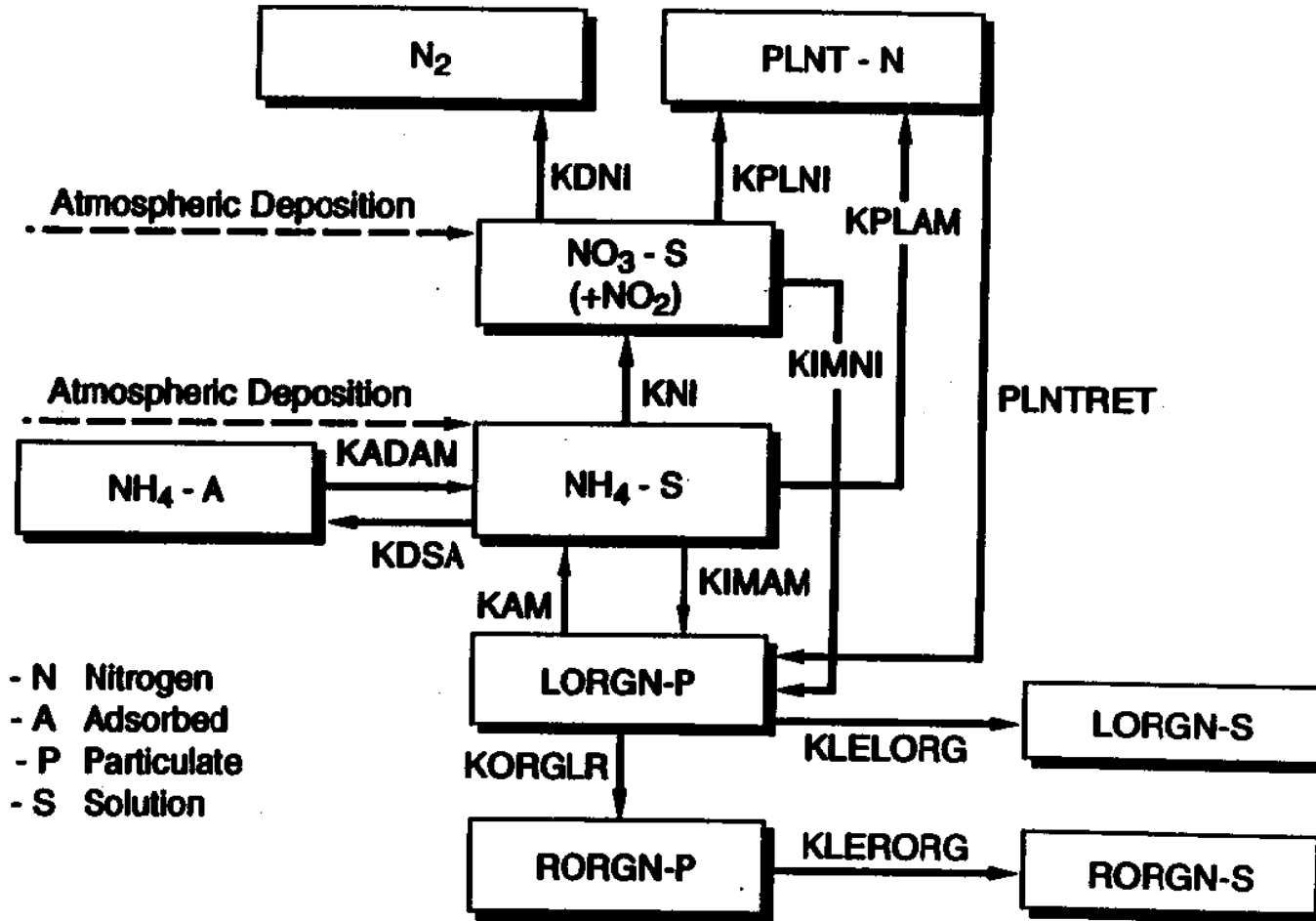


Figure 2

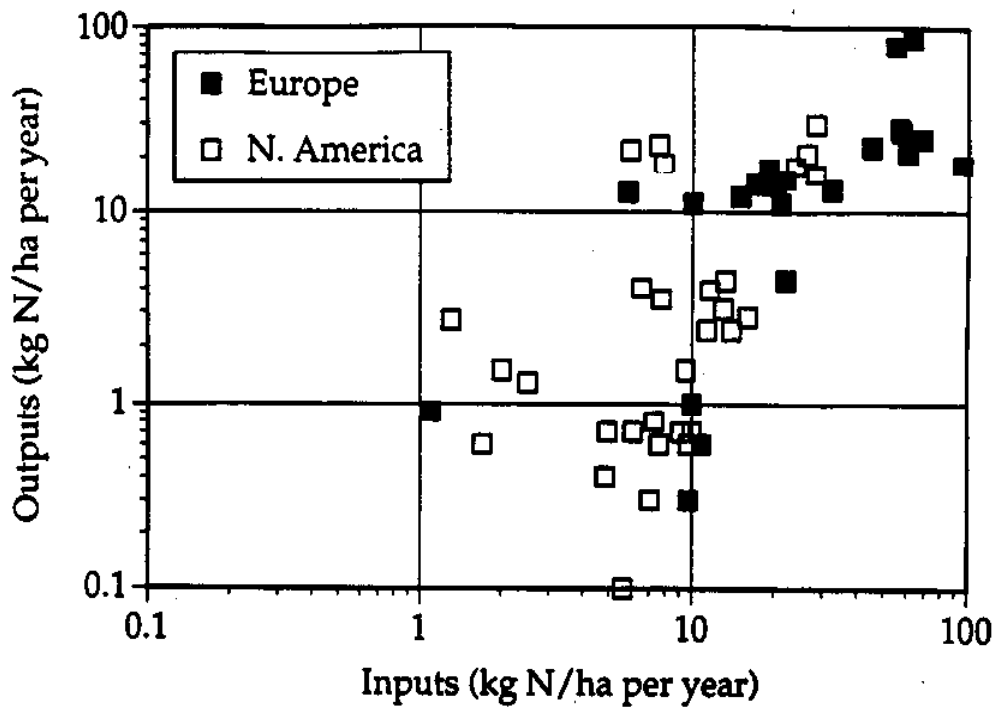


Figure 3. Relationship between atmospheric nitrogen inputs and nitrogen outputs (nitrate leaching) in temperate forest ecosystems (see Table 5.2 for data and references).

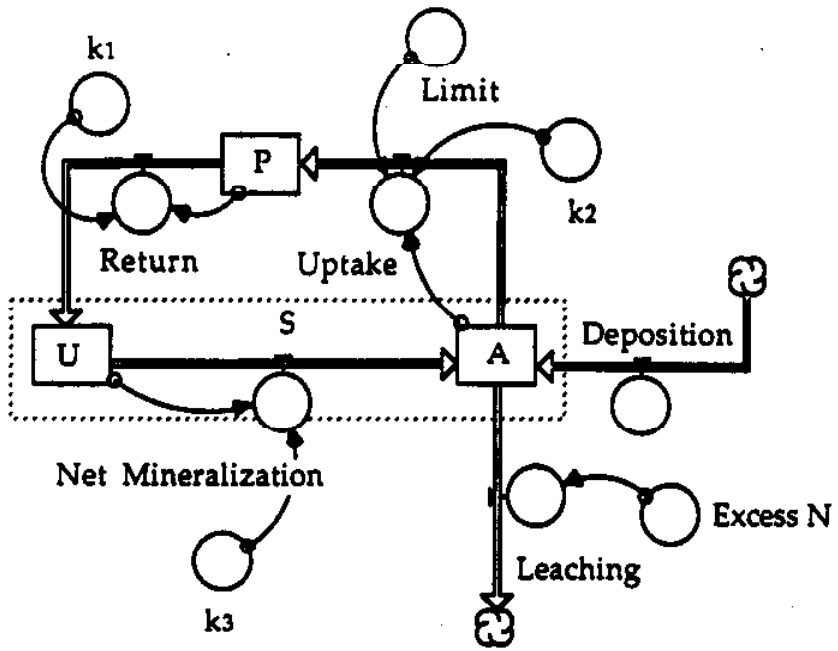


Figure B1

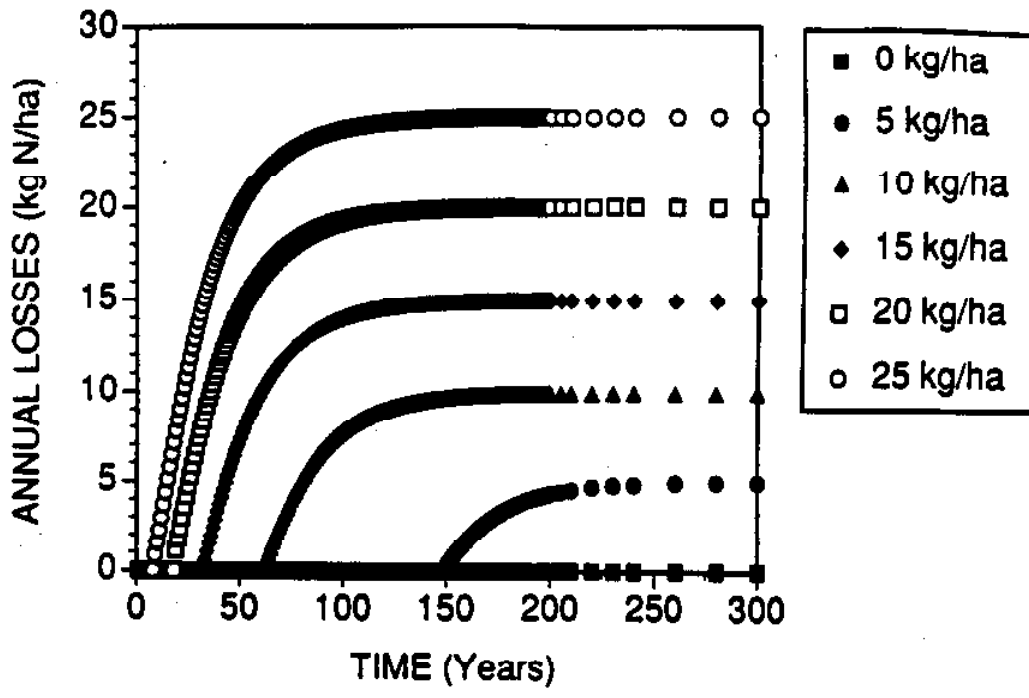


Figure B2

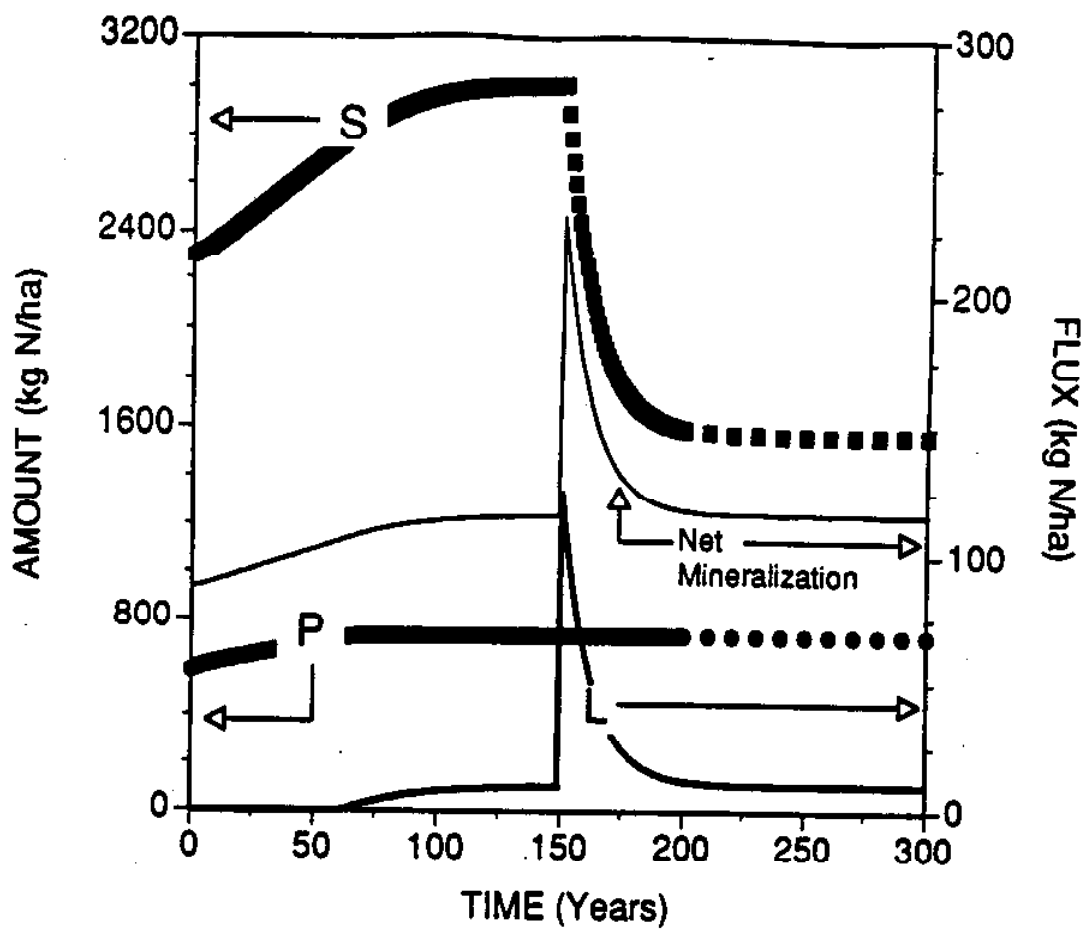


Figure B3

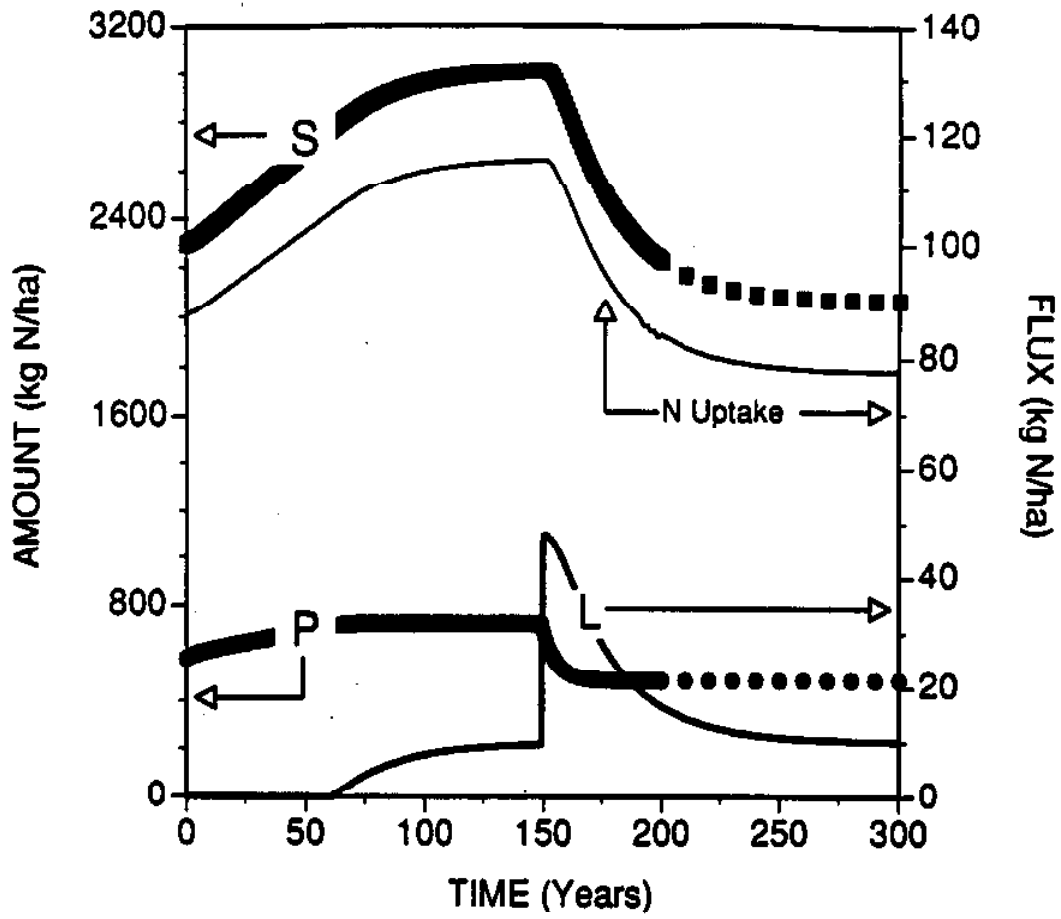


Figure B4

Table 1. Model estimates of subsurface forest nitrogen concentrations and outputs, and comparison between model and measured outputs (provided by B.R. Bicknell, AQUA TERRA Consultants, Jan. 1994). Model concentrations and outputs are means of values from all segments.

Drainage basin	Model Concentrations ($\mu\text{g N/L}$)			Model Outputs (kg N/ha/y)			Model/Meas. Outputs**		
	NO_3	NH_4	Org N*	NO_3	NH_4	Org N	NO_3	NH_4	Org N
Susquehanna	2283	32	12-24	7.09	0.10	0.35	0.78	0.68	0.52
Potomac (AFL)	1257	21	23-46	3.55	0.06	0.37	0.77	0.78	0.65
Rappahannock (AFL)	372	21	15-30	0.93	0.06	0.16	-	-	-
James (AFL)	292	36	21-42	0.86	0.10	0.42	1.18	1.21	0.84
Patuxent (AFL)	712	19	21-42	1.22	0.04	0.21	1.0	1.01	1.12
Potomac (BFL)	973	21	21-42	2.57	0.04	0.24	-	-	-
Western Shore MD (BFL)	973	21	21-42	2.57	0.05	0.16	-	-	-
Rappahannock (BFL)	398	21	15-30	1.22	0.07	0.13	-	-	-
James (BFL)	1000	36	26-53	2.94	0.10	0.28	-	-	-
Eastern Shore (MD, VA)	1053	21	21-42	2.51	0.04	0.16	-	-	-

*Lower value is groundwater concentration, upper value is interflow concentration.

**1984-1986 mean

Table 2. Nitrate concentrations and fluxes from forested catchments in the Chesapeake Bay Drainage Basin. All concentrations are discharge-weighted (unless denoted by *) and expressed as $\mu\text{g N/L}$. All fluxes are expressed as kg N/ha/y .

Catchment	Physiographic province	Catchment area (ha)	Mean Conc. ($\mu\text{g N/L}$)			Mean Flux (kg N/ha/y)			Period	Ref.**
			NH_4	NO_3	DON	NH_4	NO_3	DON		
Susquehanna River Drainage:										
Stony Ck. (PA)	Valley and Ridge	5670	36	82	340	0.18	0.40	1.72	85-86	L. Reed
Young Womans Ck. (PA)	Appal. Plateaus	11970	16	310	214	0.07	1.44	1.00	85-89	L. Reed
Leading Ridge (PA)	Valley and Ridge	122	-	16	-	-	-	-	76-87	J. Lynch
Patuxent River Drainage:										
Rhode R. Trib (MD)	Coastal Plain	63	64	116	210	0.11	0.20	0.2	81-84	D. Weller
Potomac River Drainage:										
Hauver Br. (MD)	Blue Ridge	550	-	346	-	-	2.1	-	82-92	K. Rice
Bear Br. (MD)	Blue Ridge	98	-	330	-	-	2.4	-	91-92	K. Rice
Fishing Ck. Tr. (MD)	Blue Ridge	104	-	111	-	-	0.6	-	88-92	K. Rice
Mill R. (VA)	Valley and Ridge	303	-	20	-	-	0.07	-	83-92	A. O'Brien
Shelter R. (VA)	Valley and Ridge	36	-	14	-	-	0.04	-	83-92	A. O'Brien
Rappahannock River Basin:										
S. F. Brokenback R. (VA)	Blue Ridge	-	-	41	-	-	0.13	-	83-91	A. O'Brien
<hr/>										
344 Western VA streams	Valley and Ridge, Blue Ridge	-	-	14 (80% < 100)*	-	-	-	-	spr. 87	R. Webb

**L. Reed, USGS-WRD, Lemoyne, PA; J. Lynch, School of Forest Resources, Pennsylvania State Univ., University Park, PA; D. Weller, Smithsonian Environmental Research Center, Edgewater, MD; K. Rice, USGS-WRD, Charlottesville, VA; A. O'Brien, USGS-WRD, Reston, VA; R. Webb, Dept. of Environmental Sciences, Univ. of Virginia, Charlottesville, VA.

Table 3. Estimates of nitrogen inputs and outputs from temperate forest ecosystems. References are as follows: (1) Cole and Rapp (1981), (2) Johnson (1992), (3) Lovett and Lindberg (1993), (4) Agren and Bosatta (1988), (5) Gundersen (1991), (6) Kelly and Meagher (1986), (7) Likens et al. (1977)

Forest type	Location	kg N/ha per year		Reference
		Inputs	Outputs	
Coniferous	USSR	1.1	0.9	(1)
	WA (USA)	1.3	2.7	(2)
	WA (USA)	1.7	0.6	(1)
	OR (USA)	2.0	1.5	(2)
	WA (USA)	2.5	1.3	(2)
	WA (USA)	4.8	0.4	(2)
	WA (USA)	4.9	0.7	(3)
	NC (USA)	5.9	21.6	(2)
	FL (USA)	6.1	0.7	(3)
	NC (USA)	7.3	0.8	(3)
	ME (USA)	7.6	0.6	(3)
	GA (USA)	9.1	0.7	(3)
	Sweden	9.7	0.3	(4)
	TN (USA)	9.7	0.6	(2)
	Denmark	10.0	1.0	(5)
	Sweden	10.0	11.0	(5)
	TN (USA)	10.0	0.7	(3)
	Norway	10.8	0.6	(2)
	NC (USA)	14.0	2.4	(2)
	Denmark	15.0	12.0	(5)
	Sweden	16.0	0.0	(5)
	NY (USA)	16.0	2.8	(2)
	England	17.0	14.0	(5)
	Denmark	19.0	17.0	(5)
	Germany	20.0	0.0	(5)
	Germany	20.0	14.0	(5)
	Germany	21.0	11.0	(5)
	Germany	21.8	14.9	(1)
	NC (USA)	26.0	20.5	(2)
	NC (USA)	28.0	16.0	(3)
	NC (USA)	28.0	29.3	(3)
	Germany	32.0	13.0	(5)
	Germany	57.0	27.0	(5)
Germany	60.0	21.0	(5)	
Netherlands	68.0	25.0	(5)	
Netherlands	95.0	18.0	(5)	

Table 3 (continued)

Forest type	Location	kg N/ha per year		Reference
		Inputs	Outputs	
Deciduous	WI (USA)	5.6	0.1	(2)
	England	5.8	12.6	(1)
	NH (USA)	6.5	4.0	(2)
	NC (USA)	7.0	0.3	(2)
	Ontario	7.5	23.0	(2)
	TN (USA)	7.7	3.5	(1)
	Ontario	7.8	18.2	(2)
	NY (USA)	9.5	1.5	(2)
	TN (USA)	11.3	2.4	(6)
	TN (USA)	11.6	3.9	(6)
	TN (USA)	13.0	3.1	(2)
	TN (USA)	13.2	4.4	(6)
	Germany	21.8	4.4	(1)
	NH (USA)	23.6	17.4	(7)
	Holland	44.6	22.5	(2)
	Holland	54.5	78.5	(2)
Holland	56.2	28.1	(2)	
Holland	62.8	87.6	(2)	

Table 4. Amounts of nitrogen aboveground (leaves and wood) and belowground (root) in temperate forest ecosystems. The estimated belowground nitrogen [EBG] was calculated as 27% of the aboveground nitrogen. References are as follows: (1) Johnson and Lindberg (1992), (2) Cole and Rapp (1981), (3) Gundersen (1991), (4) McLaugherty et al. (1982), (5) Nadelhoffer et al. (1985), (6) Johnson and Van Hook (1989), (7) Mitchell et al. (1975), (8) Hendrick and Pregitzer (1993)

Forest type	Stand type	Location	[AG] Above ground kg N/ha	[BG] Below ground kg N/ha	Total [AG + BG] kg N/ha	Ref.	[EBG] Estimated below ground kg N/ha	Estimated total [AG + EBG] kg N/ha
Coniferous	Pine	TN (USA)	192	.	.	(1)	52	244
	Pine	NC (USA)	205	29	234	(1)	55	260
	Pine	TN (USA)	215	.	.	(2)	58	273
	Pine	NC (USA)	224	.	.	(2)	60	284
	Fir	WA (USA)	227	.	.	(2)	61	288
	Spruce	USSR	282	.	.	(2)	76	358
	Spruce	NC (USA)	291	95	386	(1)	79	370
	Fir	WA (USA)	316	.	.	(2)	85	401
	Fir	WA (USA)	339	43	382	(1)	92	431
	Pine	FL (USA)	340	122	462	(1)	92	432
	Spruce	Denmark	400	.	.	(3)	108	508
	Spruce	NC (USA)	414	110	524	(1)	112	526
	Pine	NC (USA)	431	422	853	(1)	116	547
	Spruce-Fir	NY (USA)	440	188	628	(1)	119	559
	Spruce	Germany	449	.	.	(2)	121	570
	Spruce	Denmark	450	.	.	(3)	122	572
	Spruce	ME (USA)	466	95	561	(1)	126	592
	Fir	OR (USA)	566	.	.	(2)	153	719
	Pine	GA (USA)	569	78	647	(1)	154	723
	Fir	Japan	573	.	.	(2)	155	728
	Hemlock	Japan	582	.	.	(2)	157	739
	Spruce	Germany	628	.	.	(2)	170	798
	Spruce	Sweden	720	.	.	(2)	194	914
	Hemlock	OR (USA)	721	.	.	(2)	195	916
	Spruce	Germany	729	.	.	(2)	197	926
	Fir	WA (USA)	845	228	1073	(1)	228	1073
	Pine	MA (USA)	.	42	.	(4)	.	.

Table 4 (continued)

Forest type	Stand type	Location	[AG] Above ground kg N/ha	[BG] Below ground kg N/ha	Total [AG + BG] kg N/ha	Ref.	[EBG] Estimated below ground kg N/ha	Estimated total [AG + EBG] kg N/ha
	Pine	WI (USA)	-	44	-	(5)	-	-
	Spruce	WI (USA)	-	46	-	(5)	-	-
	Pine	WI (USA)	-	50	-	(5)	-	-
	Pine	WI (USA)	-	59	-	(5)	-	-
Deciduous	Hardwood	TN (USA)	234	104	338	(6)	63	297
	Alder	WA (USA)	240	-	-	(2)	65	305
	Poplar	TN (USA)	267	104	371	(2)	72	339
	Oak-Birch	England	278	-	-	(2)	75	353
	Poplar	TN (USA)	304	-	-	(2)	82	386
	Oak-Birch	NH (USA)	367	-	-	(2)	99	466
	Oak	Belgium	368	-	-	(2)	99	467
	Oak-Hickory	TN (USA)	369	-	-	(2)	100	469
	Beech	TN (USA)	377	185	562	(1)	102	479
	Beech	Germany	404	-	-	(2)	109	513
	Beech	Germany	407	-	-	(2)	110	517
	Oak-Hickory	NC (USA)	408	151	558	(7)	110	518
	Oak	TN (USA)	431	104	535	(6)	116	547
	Hardwood	NY (USA)	474	66	540	(1)	128	602
	Hardwood	Ontario	528	52	580	(1)	143	671
	Beech	Germany	581	-	-	(2)	157	738
	Hardwood	NC (USA)	591	434	853	(1)	160	751
	Oak	Belgium	728	-	-	(2)	197	925
	Alder	WA (USA)	917	167	1084	(1)	248	1165
	Beech	Sweden	1071	-	-	(2)	289	1360
	Oak	WI (USA)	-	32	-	(5)	-	-
	Oak	WI (USA)	-	36	-	(5)	-	-
	Oak	WI (USA)	-	39	-	(5)	-	-
	Birch	WI (USA)	-	42	-	(5)	-	-
	Oak	MO (USA)	-	48	-	(8)	-	-

Table 4 (continued)

Forest type	Stand type	Location	[AG] Above ground kg N/ha	[BG] Below ground kg N/ha	Total [AG + BG] kg N/ha	Ref.	[EBG] Estimated below ground kg N/ha	Estimated total [AG + EBG] kg N/ha
	Maple	WI (USA)	-	50	-	(5)	-	-
	Hardwood	MA (USA)	-	65	-	(4)	-	-
	Maple	MI (USA)	-	85	-	(8)	-	-
	Maple	MI (USA)	-	85	-	(8)	-	-
	Poplar	TN (USA)	-	96	-	(8)	-	-
		Mean	456	106	588		123	579
		SD	199	96	232		54	253
		n	46	34	19		46	46

Table 5. Amounts of nitrogen in the forest floor and mineral soil, and estimates of total soil nitrogen in temperate forest ecosystems. Soil depth is variable but usually >50 cm. References are as follows: (1) Cole and Rapp (1981), (2) Johnson and Lindberg (1992), (3) Aber et al. (1983), (4) Gundersen (1991), (5) Mitchell et al. (1975), (6) Johnson and Van Hook (1989)

Forest type	Stand type	Location	[FF] Forest floor kg N/ha	Percent of total soil N	[MS] Mineral soil kg N/ha	Total soil [FF + MS] kg N/ha	Ref.	
Coniferous	Fir	WA (USA)	223	8%	2476	2699	(1)	
	Spruce	Sweden	245	3%	6900	7145	(1)	
	Pine	TN (USA)	277	5%	5257	5534	(2)	
	Pine	NC (USA)	282	10%	2498	2780	(2)	
	Pine	FL (USA)	286	9%	2850	3136	(2)	
	Pine	TN (USA)	290	7%	4100	4390	(1)	
	Pine	GA (USA)	310	2%	12589	12899	(2)	
	Fir	WA (USA)	379	7%	5080	5459	(2)	
	Fir	OR (USA)	445	9%	4560	5005	(1)	
	Pine	NC (USA)	450	21%	1678	2128	(2)	
	Hemlock	OR (USA)	474	12%	3490	3964	(1)	
	Hemlock	Japan	507	16%	2732	3239	(1)	
	Fir	WA (USA)	575	7%	7620	8195	(2)	
	Pine	MA (USA)	755	15%	4290	5045	(3)	
	Spruce	Denmark	800	24%	2500	3300	(4)	
	Spruce	Germany	960	12%	7100	8060	(1)	
	Spruce	ME (USA)	1123	27%	3058	4181	(2)	
	Spruce	Denmark	1300	30%	3000	4300	(4)	
	Spruce	Germany	1430	18%	6650	8080	(1)	
	Spruce	NC (USA)	1916	26%	5357	7273	(2)	
	Spruce	NC (USA)	2165	19%	9042	11207	(2)	
	Spruce	Germany	2260	24%	7060	9320	(1)	
	Spruce-Fir	NY (USA)	2642	21%	9821	12463	(2)	
	Deciduous	Oak	Belgium	44	1%	4480	4524	(1)
		Poplar	TN (USA)	78	1%	7650	7728	(1)
		Beech	Sweden	86	1%	7800	7886	(1)
Oak-Hickory		NC (USA)	137	3%	3968	4105	(5)	
Poplar		TN (USA)	187	2%	7300	7487	(1)	
Beech		TN (USA)	232	2%	9053	9285	(2)	
Hardwood		NC (USA)	245	6%	4077	4322	(2)	
Mixed		TN (USA)	290	7%	4100	4390	(6)	
Oak		TN (USA)	298	6%	4700	4998	(1)	
Oak-Hickory		TN (USA)	334	7%	4500	4834	(1)	
Beech		Germany	810	10%	7340	8150	(1)	
Beech		Germany	815	11%	6332	7147	(1)	
Hardwood		MA (USA)	846	15%	4785	5631	(3)	
Alder		WA (USA)	887	14%	5450	6337	(1)	
Hardwood		Ontario	927	8%	9980	10907	(2)	
Beech		Germany	1050	10%	9452	10502	(1)	
Hardwood		NY (USA)	1152	13%	7985	9137	(2)	
Alder		WA (USA)	1629	19%	7050	8679	(2)	
		Mean		735	11%	5749	6484	
		SD		643	8%	2513	2782	
	n		41	41	41	41		

Table 6. Distribution of soil nitrogen in low-elevation forests from the Integrated Forest Study. Surface soil includes O + A or O + E horizons. Data are from Johnson and Lindberg (1992). Total soil nitrogen includes forest floor and mineral soil layers.

Forest type	Location	Elevation (m)	Surface soil kg N/ha	Soil below A or E horizon kg N/ha	Total soil kg N/ha	Depth of total soil cm
Coniferous	NC (USA)	725	1039	1722	2498	91
	WA (USA)	220	2355	3020	5080	45
	NC (USA)	213	1279	849	1678	80
	GA (USA)	145	4131	8768	12589	80+
	TN (USA)	114	2701	2827	5257	57
	TN (USA)	114	2012	4030	5769	83
	ME (USA)	65	1330	1728	3058	52
Deciduous	NC (USA)	725	1555	2757	4077	89
	NY (USA)	530	2576	6561	7985	58
	Ontario	350	1572	9335	9980	57
	Mean		2055	4160	5797	
	SD		927	3012	3457	
	n		10	10	10	

Table 7. Annual net nitrogen mineralization rates in temperate forest ecosystems. References are as follows: (1) Aber et al. (1983), (2) Gundersen (1991), (3) Hill and Shackleton (1989), (4) McClaugherty et al. (1985), (5) Nadelhoffer et al. (1983), (6) Nadelhoffer et al. (1985), (7) Pastor et al. (1984), (8) Strader et al. (1989), (9) Stump and Binkley (1993), (10) Lennon et al. (1985), (11) Updegraff et al. (1990), (12) Zak et al. (1989)

Forest type	Stand type	Location	Soil depth cm	[MS] Net mineralization in mineral soil kg N/ha per yr	[FF] Net mineralization in forest floor kg N/ha per yr	Total net mineralization [MS + FF] kg N/ha per yr	Ref.
Coniferous	Pine	MA (USA)	-	53	31	84	(1)
	Spruce	Denmark	-	-	-	26	(2)
	Spruce	Denmark	-	-	-	97	(2)
	Hemlock	Ontario	8	1.2	-	-	(3)
	Hemlock	Ontario	8	5.5	-	-	(3)
	Pine	Ontario	8	17.9	-	-	(3)
	Pine	Ontario	8	28.8	-	-	(3)
	Hemlock	WI (USA)	15	0.0	29.0	29.0	(4)
	Pine	WI (USA)	15	9.4	42.6	52.0	(4)
	Pine	WI (USA)	10	32.4	-	-	(5)
	Pine	WI (USA)	10	50.1	-	-	(5)
	Pine	WI (USA)	10	79.7	-	-	(5)
	Spruce	WI (USA)	10	47.3	-	-	(5)
	Pine	WI (USA)	20	39	-	-	(6)
	Mixed Pine	WI (USA)	20	61	-	-	(6)
	Pine	WI (USA)	20	81	-	-	(6)
	Spruce	WI (USA)	20	58	-	-	(6)
	Pine	WI (USA)	4	-	-	26	(7)
	Pine	WI (USA)	4	-	-	39	(7)
	Hemlock	WI (USA)	4	-	-	29	(7)
	Spruce-fir	NC (USA)	10	-	-	144	(8)
	Spruce-fir	NC (USA)	10	-	-	180	(8)
	Spruce-fir	NC (USA)	10	-	-	31	(8)
	Spruce-fir	NC (USA)	10	-	-	69	(8)
	Spruce-fir	NC (USA)	10	-	-	145	(8)
	Spruce-fir	NC (USA)	10	-	-	169	(8)

Table 7 (continued)

Forest type	Stand type	Location	Soil depth cm	[MS] Net mineralization in mineral soil kg N/ha per yr	[FF] Net mineralization in forest floor kg N/ha per yr	Total net mineralization [MS + FF] kg N/ha per yr	Ref.
	Spruce-fir	NC (USA)	10	-	-	34	(8)
	Spruce-fir	NC (USA)	10	-	-	100	(8)
	Spruce-fir	NC (USA)	10	-	-	85	(8)
	Spruce-fir	NC (USA)	10	-	-	146	(8)
	Spruce-fir	NC (USA)	10	-	-	68	(8)
	Spruce-fir	NC (USA)	10	-	-	90	(8)
	Spruce-fir	NC (USA)	10	-	-	138	(8)
	Spruce-fir	NC (USA)	10	-	-	58	(8)
	Spruce-fir	NC (USA)	10	-	-	48	(8)
	Spruce-fir	VA (USA)	10	-	-	26	(8)
	Spruce-fir	VA (USA)	10	-	-	100	(8)
	Spruce-fir	VA (USA)	10	-	-	128	(8)
	Spruce-fir	VA (USA)	10	-	-	85	(8)
	Pine	CO (USA)	15	0.5	1.5	2.0	(9)
	Pine	CO (USA)	15	-0.5	1.5	1.0	(9)
	Pine	CO (USA)	15	2.0	4.0	6.0	(9)
	Pine	CO (USA)	15	0.5	1.0	1.5	(9)
	Pine	CO (USA)	15	2.0	2.0	4.0	(9)
	Pine	CO (USA)	15	1.5	1.5	3.0	(9)
	Pine	CO (USA)	15	0.8	0.7	1.5	(9)
	Pine	CO (USA)	15	-5.0	0.5	-4.5	(9)
	Pine	CO (USA)	15	-1.5	1.0	-0.5	(9)
	Pine	CO (USA)	15	0.0	2.0	2.0	(9)
	Spruce-fir	CO (USA)	15	3.0	6.0	9.0	(9)
	Spruce-fir	CO (USA)	15	2.0	2.1	4.1	(9)
	Spruce-fir	CO (USA)	15	0.5	3.5	4.0	(9)
	Spruce-fir	CO (USA)	15	1.5	4.5	6.0	(9)
	Spruce-fir	CO (USA)	15	3.0	9.0	12.0	(9)
	Spruce-fir	CO (USA)	15	2.1	6.9	9.0	(9)

Table 7 (continued)

Forest type	Stand type	Location	Soil depth cm	[MS] Net mineralization in mineral soil kg N/ha per yr	[FF] Net mineralization in forest floor kg N/ha per yr	Total net mineralization [MS + FF] kg N/ha per yr	Ref.
	Spruce-fir	CO (USA)	15	2.5	2.0	4.5	(9)
	Spruce-fir	CO (USA)	15	0.5	0.2	0.7	(9)
	Spruce-fir	CO (USA)	15	2.0	9.0	11.0	(9)
	Spruce-fir	CO (USA)	15	0.0	2.0	2.0	(9)
Deciduous	Hardwoods	MA (USA)	-	54	41	95	(1)
	Maple	Ontario	8	74.2	-	-	(3)
	Maple	Ontario	8	113.5	-	-	(3)
	Maple	WI (USA)	30	26	-	-	(10)
	Maple	WI (USA)	30	34	-	-	(10)
	Maple	WI (USA)	30	41	-	-	(10)
	Maple	WI (USA)	30	41	-	-	(10)
	Maple	WI (USA)	30	64	-	-	(10)
	Maple	WI (USA)	30	84	-	-	(10)
	Maple	WI (USA)	30	94	-	-	(10)
	Aspen	WI (USA)	15	25.4	22.6	48.0	(4)
	Maple	WI (USA)	15	37.5	87.5	125.0	(4)
	Oak	WI (USA)	15	9.2	74.8	84.0	(4)
	Oak	WI (USA)	10	111.3	-	-	(5)
	Oak	WI (USA)	10	91.0	-	-	(5)
	Oak	WI (USA)	10	100.0	-	-	(5)
	Birch	WI (USA)	10	51.4	-	-	(5)
	Maple	WI (USA)	10	62.1	-	-	(5)
	Oak	WI (USA)	20	135	-	-	(6)
	Oak	WI (USA)	20	125	-	-	(6)
	Oak	WI (USA)	20	99	-	-	(6)
	Birch	WI (USA)	20	84	-	-	(6)
	Maple	WI (USA)	20	94	-	-	(6)
	Oak	WI (USA)	4	-	-	53	(7)

Table 7 (continued)

Forest type	Stand type	Location	Soil depth cm	[MS] Net mineralization in mineral soil kg N/ha per yr	[FF] Net mineralization in forest floor kg N/ha per yr	Total net mineralization [MS + FF] kg N/ha per yr	Ref.
	Oak	WI (USA)	4	-	-	60	(7)
	Oak	WI (USA)	4	-	-	67	(7)
	Maple	WI (USA)	4	-	-	78	(7)
	Maple	WI (USA)	4	-	-	84	(7)
	Aspen	CO (USA)	15	12	13	25	(9)
	Aspen	CO (USA)	15	5	7	12	(9)
	Aspen	CO (USA)	15	12	14	26	(9)
	Aspen	CO (USA)	15	8	12	20	(9)
	Aspen	CO (USA)	15	3	4	7	(9)
	Aspen	CO (USA)	15	5	6	11	(9)
	Aspen	CO (USA)	15	25	5	30	(9)
	Aspen	CO (USA)	15	21	5	26	(9)
	Aspen	CO (USA)	15	20	30	50	(9)
	Aspen	CO (USA)	15	22	5	27	(9)
	Hybrid Poplar	MI (USA)	30	-	-	56	(11)
	Maple-Basswood	MI (USA)	10	111.8	-	-	(12)
	Maple-Oak	MI (USA)	10	94.1	-	-	(12)
	Maple-Oak	MI (USA)	10	100.1	-	-	(12)
	Oak	MI (USA)	10	86.1	-	-	(12)
	Oak	MI (USA)	10	85.3	-	-	(12)
	Oak	MI (USA)	10	84.4	-	-	(12)
	Oak	MI (USA)	10	88.9	-	-	(12)
	Oak	MI (USA)	10	89.8	-	-	(12)
	Oak-Maple	MI (USA)	10	96.2	-	-	(12)
		Mean		41.6	13.3	49.1	
		SD		40.5	20.0	47.8	
		n		77	37	67	

Table 8. Aboveground, belowground, and total nitrogen uptake by tree biomass in temperate forests. Predicted total uptake was estimated as twice the nitrogen allocated aboveground (see text). References are as follows: (1) Nadelhoffer et al. (1985), (2) McClaugherty et al. (1982), (3) Johnson and Lindberg (1992), (4) Cole and Rapp (1981), (5) Nadelhoffer et al. (1983), (6) Grundersen (1991), (7) Aber et al. (1983), (8) Joslin and Henderson (1987), (9) Hendrick and Pregitzer (1993), (10) Johnson and Van Hook (1989), (11) Huff et al. (1978), (12) Mitchell et al. (1975)

Class	Dominant Genus	Site	kg N/ha per year			Ref.	Predicted Total uptake [A x 2]
			[A] Uptake allocated aboveground	[B] Uptake allocated belowground	Total uptake [A + B]		
Coniferous	Pine	WI (USA)	27	20	47	(1)	54
	Spruce	WI (USA)	44	22	66	(1)	88
	Pine	WI (USA)	38	41	79	(1)	76
	Pine	MA (USA)	-	44	-	(2)	-
	Pine	MA (USA)	-	122	-	(2)	-
	Hardwood	MA (USA)	-	-	184	(2)	-
	Spruce	NC (USA)	3	-	-	(3)	7
	Spruce	NC (USA)	9	-	-	(3)	18
	Fir	WA (USA)	9	-	-	(3)	19
	Fir	WA (USA)	10	-	-	(3)	21
	Pine	TN (USA)	17	-	-	(3)	35
	Fir	OR (USA)	24	-	-	(4)	47
	Pine	FL (USA)	24	-	-	(3)	48
	Pine	NC (USA)	26	-	-	(3)	51
	Hemlock	Japan	28	-	-	(4)	55
	Fir	WA (USA)	34	-	-	(4)	67
	Spruce	USSR	34	-	-	(4)	69
	Fir	WA (USA)	36	-	-	(4)	72
	Spruce-Fir	NY (USA)	37	-	-	(3)	74
	Pine	NC (USA)	37	-	-	(3)	74
	Pine	WI (USA)	40	-	-	(5)	81
	Spruce	Denmark	42	-	-	(6)	84
	Fir	Japan	44	-	-	(4)	87
	Pine	TN (USA)	49	-	-	(4)	97
	Pine	NC (USA)	50	-	-	(4)	100
	Spruce	Germany	53	-	-	(4)	107
	Fir	WI (USA)	55	-	-	(5)	110
	Spruce	Germany	56	-	-	(4)	111
	Pine	WI (USA)	58	-	-	(5)	116
	Hemlock	OR (USA)	59	-	-	(4)	117
	Spruce	Germany	63	-	-	(4)	126
	Pine	WI (USA)	78	-	-	(5)	155
Spruce	Sweden	88	-	-	(4)	176	
Pine	MA (USA)	89	-	-	(7)	178	
Spruce	Denmark	99	-	-	(6)	198	
Deciduous	Oak	MO (USA)	-	22	-	(8)	-
	Pine	WI (USA)	33	36	69	(1)	66
	Birch	WI (USA)	49	43	92	(1)	98
	Maple	WI (USA)	55	47	102	(1)	110
	Oak	WI (USA)	60	47	107	(1)	120
	Oak	WI (USA)	71	62	133	(1)	142
	Hardwood	MA (USA)	-	73	-	(2)	-

Table 8 (continued)

Class	Dominant Genus	Site	kg N/ha per year			Ref.	Predicted Total uptake [A x 2]
			[A] Uptake allocated aboveground	[B] Uptake allocated belowground	Total uptake [A + B]		
	Poplar	TN (USA)	-	76	-	(9)	-
	Oak	WI (USA)	64	79	143	(1)	128
	Maple	MI (USA)	-	87	-	(9)	-
	Maple	MI (USA)	-	88	-	(9)	-
	Hardwood	NY (USA)	33	-	-	(3)	67
	Hardwood	NC (USA)	34	-	-	(3)	68
	Hardwood	Ontario	35	-	-	(3)	70
	Beech	TN (USA)	36	-	-	(3)	73
	Oak-Hickory	NC (USA)	43	-	-	(4)	86
	Poplar	TN (USA)	48	-	-	(4)	96
	Mixed	TN (USA)	52	-	-	(10)	104
	Poplar	TN (USA)	58	-	-	(4)	116
	Birch	WI (USA)	59	-	-	(5)	119
	Oak	TN (USA)	62	-	-	(10)	124
	Oak	TN (USA)	69	-	-	(4)	138
	Oak-Hickory	TN (USA)	69	-	-	(4)	138
	Maple	WI (USA)	70	-	-	(5)	140
	Maple-Birch	NH (USA)	74	-	-	(4)	149
	Beech	Germany	76	-	-	(4)	151
	Beech	Sweden	78	-	-	(4)	157
	Oak-Birch	England	79	-	-	(4)	158
	Alder	WA (USA)	79	-	-	(3)	158
	Oak	Belgium	80	-	-	(4)	160
	Oak	Belgium	86	-	-	(4)	173
	Beech	Germany	88	-	-	(4)	175
	Beech	Germany	91	-	-	(4)	183
	Oak-Hickory	NC (USA)	92	-	-	(11)	185
	Oak	WI (USA)	99	-	-	(5)	198
	Hardwood	MA (USA)	103	-	-	(7)	206
	Oak	WI (USA)	108	-	-	(5)	216
	Alder	WA (USA)	115	-	-	(4)	230
	Oak	WI (USA)	119	-	-	(5)	238
	Oak-Hickory	NC (USA)	142	-	-	(12)	283
		Mean	58	64	93		116
		SD	29	41	32		58
		n	67	17	9		67

Table 9. Return of plant nitrogen to soil via aboveground litterfall or belowground root turnover and predicted amounts of total nitrogen return in temperate forest ecosystems (see text). References are as follows: (1) Nadelhoffer et al. (1985), (2) Aber et al. (1983), (3) Johnson and Lindberg (1992), (4) Nadelhoffer et al. (1983), (5) Cole and Rapp (1981), (6) Gundersen (1991), (7) Joslin and Henderson (1987), (8) Mitchell et al. (1975), (9) Huff et al. (1978), (10) Hendrick and Pregitzer (1993), (11) Harris et al. (1980), (12) Lennon et al. (1985), (13) Johnson and Van Hook (1989)

Forest type	Stand type	Location	[A] Total aboveground litterfall kg N/ha per yr	[B] Return belowground kg N/ha per yr	[B:A] Ratio	Ref.	Predicted total return [A + (A x 1.6)] kg N/ha per yr
Coniferous	Pine	WI (USA)	12	20	1.67	(1)	31
	Spruce	WI (USA)	28	22	0.79	(1)	73
	Pine	MA (USA)	40	38	0.95	(2)	104
	Pine	WI (USA)	21	41	1.95	(1)	55
	Spruce	NC (USA)	11	.	.	(3)	29
	Spruce	ME (USA)	12	.	.	(3)	32
	Pine	WI (USA)	12	.	.	(4)	32
	Spruce	NC (USA)	13	.	.	(3)	34
	Pine	TN (USA)	14	.	.	(3)	36
	Fir	WA (USA)	15	.	.	(3)	38
	Pine	WI (USA)	16	.	.	(4)	42
	Fir	WA (USA)	16	.	.	(3)	43
	Pine	NC (USA)	19	.	.	(3)	49
	Fir	WA (USA)	19	.	.	(5)	49
	Fir	OR (USA)	19	.	.	(5)	49
	Hemlock	Japan	20	.	.	(5)	53
	Pine	WI (USA)	21	.	.	(4)	55
	Slash Pine	FL (USA)	22	.	.	(3)	56
	Spruce-Fir	NY (USA)	24	.	.	(3)	62
	Spruce	USSR	24	.	.	(5)	62
	Fir	WA (USA)	25	.	.	(5)	66
	Pine	NC (USA)	26	.	.	(5)	69
	Fir	WI (USA)	28	.	.	(4)	73
	Fir	Japan	32	.	.	(5)	82
	Spruce	Denmark	35	.	.	(6)	91
	Pine	TN (USA)	38	.	.	(5)	98
	Spruce	Germany	42	.	.	(5)	108
	Pine	NC (USA)	43	.	.	(3)	112
	Spruce	Germany	43	.	.	(5)	113
	Hemlock	OR (USA)	44	.	.	(5)	114
	Spruce	Germany	47	.	.	(5)	122
	Spruce	Sweden	58	.	.	(5)	151
	Pine	GA (USA)	76	.	.	(3)	198
Spruce	Denmark	100	.	.	(6)	260	
Deciduous	Oak	MO (USA)	43	22	0.52	(7)	112
	Pine	WI (USA)	16	36	2.25	(1)	42
	Oak-Hickory	NC (USA)	38	42	1.11	(8)	99
	Oak-Hickory	NC (USA)	31	42	1.38	(9)	80
	Birch	WI (USA)	25	43	1.72	(1)	65
	Maple	WI (USA)	23	47	2.04	(1)	60
	Oak	WI (USA)	26	47	1.81	(1)	68
	Hardwood	MA (USA)	41	52	1.27	(2)	107

Table 9 (continued)

Forest type	Stand type	Location	[A] Total aboveground litterfall kg N/ha per yr	[B] Return belowground kg N/ha per yr	[B:A] Ratio	Ref.	Predicted total return [A + (A x 1.6)] kg N/ha per yr
	Maple	MI (USA)	55	53	0.97	(10)	142
	Oak	WI (USA)	30	62	2.07	(1)	78
	Oak	TN (USA)	34	68	1.99	(5)	89
	Liriodendron	TN (USA)	36	68	1.88	(5)	94
	Oak-Hickory	TN (USA)	36	68	1.86	(5)	95
	Maple	MI (USA)	49	72	1.47	(10)	128
	Oak	WI (USA)	31	79	2.55	(1)	81
	Poplar	TN (USA)	42	85	2.01	(11)	110
	Maple	WI (USA)	23	.	.	(4)	59
	Birch	WI (USA)	25	.	.	(4)	64
	Beech	TN (USA)	26	.	.	(3)	68
	Maple	WI (USA)	26	.	.	(12)	69
	Oak	WI (USA)	26	.	.	(4)	69
	Maple	WI (USA)	27	.	.	(12)	70
	Maple	WI (USA)	27	.	.	(12)	70
	Maple	WI (USA)	28	.	.	(12)	73
	Maple	WI (USA)	29	.	.	(12)	75
	Oak	WI (USA)	30	.	.	(4)	77
	Maple	WI (USA)	31	.	.	(12)	80
	Oak	WI (USA)	31	.	.	(4)	81
	Maple	WI (USA)	31	.	.	(12)	81
	Liriodendron	TN (USA)	31	.	.	(5)	81
Oak-Hickory	NC (USA)	34	.	.	(5)	88	
	Oak	TN (USA)	34	.	.	(13)	88
	Hardwood	NC (USA)	36	.	.	(3)	95
	Mixed	TN (USA)	38	.	.	(13)	99
	Hardwood	Ontario	40	.	.	(3)	104
	Beech	Germany	49	.	.	(5)	128
	Oak	Belgium	50	.	.	(5)	130
	Beech	Germany	52	.	.	(5)	136
	Maple-Birch	NH (USA)	54	.	.	(5)	141
	Beech	Germany	54	.	.	(5)	141
	Oak	Belgium	59	.	.	(5)	153
	Hardwood	NY (USA)	60	.	.	(3)	155
	Oak-Birch	England	64	.	.	(5)	165
	Beech	Sweden	69	.	.	(5)	179
	Alder	WA (USA)	80	.	.	(3)	208
	Alder	WA (USA)	87	.	.	(5)	226
		Mean	35	50	1.61		92
		SD	18	19	0.54		46
		n	80	20	20		80

Table 10. Functional formulation of fluxes in modified AGCHEM for forests and environmental attributes on which fluxes should be dependent.

Flux	Functional Form	Environmental Dependence
Plant Uptake: KPLNI	Saturation kinetics $\frac{U_{max} + NO_3-N}{K_s + NO_3-N}$	$U_{max} = f(\text{season, forest growth rate})$ $K_s = \text{half-saturation constant (approx. 20-50 } \mu\text{gN/L)}$
KPLAM	Saturation kinetics	same as for NO_3 , but with lower K_s , (approx. 10-20 $\mu\text{gN/L}$)
Microbial Immobilization: KIMNI, KIMAM	Saturation kinetics	similar to plant uptake, but lower U_{max}
Plant N Return: PLNTRET	Annual pulse in October (80-90% of plant uptake)	unknown
Mineralization: KAM	First-order kinetics	rate coefficient = $f(\text{temperature})$
Nitrification: KNI	First-order kinetics	rate coefficient = $f(\text{temperature})$
Denitrification: KDNI	Set to zero for well-drained forest soils	
Ammonium Partitioning (soluble/adsorbed): KADAM, KDSA	Partitioning coefficient (approx. 90% adsorbed)	unknown
Particulate Organic N Leaching: KLELORG	Partitioning coefficient (approx. 1% soluble)	unknown
KLERORG	same as for labile	unknown
Conversion to Refractory Soil N: KORGLR	First order kinetics	rate coefficient = $f(\text{temperature})$

APPENDIX A

Workshop Participants

**NITROGEN DYNAMICS IN FORESTED WATERSHEDS
FOR THE CHESAPEAKE BAY WATERSHED MODEL**

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APPENDIX B

A Simple Model of Controls on Forest Nitrogen Losses

The importance of biological controls in regulating nitrogen losses from forest ecosystems can be illustrated with a relatively simple mathematical model. The same model can be used to check the validity of estimated nitrogen pools and annual fluxes in Section 5 to determine if they yield predictions that are reasonable given our current understanding and empirical knowledge of forest nitrogen cycling.

A model of forest nitrogen cycling was built using "ithink™" software (version 1.01) on a Macintosh computer. It is similar to the conceptual model presented by Nadelhoffer et al. (1985). The model consisted of 3 pools (total plant nitrogen, unavailable soil nitrogen, and available soil nitrogen). Atmospheric deposition was the only input (to the available soil nitrogen pool) and leaching was the only output. The following set of equations described the model in Figure 1.

$$P = (k_2 \times A) - (k_1 \times P)$$

$$U = (k_1 \times P) - (k_3 \times U)$$

$$A = [(I + (k_3 \times U))] - [((k_2 \times A) + L)]$$

where

P = amount of aboveground and belowground plant nitrogen (kg/ha)

I = annual amount of atmospheric nitrogen deposition (kg/ha)

U = amount of unavailable soil nitrogen (kg/ha)

A = amount of available soil nitrogen (kg/ha)

L = the amount of available soil nitrogen lost each year (kg/ha)

k_1 = fractional return of plant nitrogen to soil (0.16 per year)

k_2 = fractional transfer from available soil nitrogen to plants (per year)

k_3 = fraction of unavailable soil nitrogen mineralized (0.04 per year)

The rate constants k_1 and k_3 were based on data presented in Section 5 of this report. Several other controls were important to the way the model functioned. A limit (116 kg N/ha per year) was set on nitrogen uptake by plants. This value corresponded to

the estimated average total nitrogen uptake by forest biomass (Section 5). Plants assimilated all of the available soil nitrogen (i.e., $k_2 = 1.0$) if the uptake flux ($A \times k_2$) was less than this limit. Consequently, there were no leaching losses from this model forest when plant demands exceeded available supplies. When the limit was reached, then excess available soil nitrogen was lost by leaching. Excess available soil nitrogen (E) was calculated as:

$$E = (I + (k_3 \times U)) - (k_2 \times A).$$

With nitrogen deposition set to zero, the model state variables reached expected equilibrium values for total soil nitrogen ($U + A = 2313$ kg N/ha) and total plant nitrogen (560 kg N/ha). The model predictions compared with a mean (\pm SD) of 2055 ± 927 kg N/ha in surface soils at 10 sites in the Integrated Forest Study and a mean (\pm SD) of 579 ± 253 kg N/ha in temperate forest plant biomass (see Section 5). The equilibrium values for the state variables were slightly higher with nonzero nitrogen deposition. Plant nitrogen reached equilibrium at 730 kg N/ha and soil nitrogen reach equilibrium at 3016 kg N/ha (both values were still within ± 2 SD of the expected mean value).

The importance of biological controls (i.e., plant uptake) to nitrogen losses from the model forest can be demonstrated by three experiments where nitrogen inputs and fluxes within the model were manipulated.

- Hypothesis 1: Increasing atmospheric nitrogen deposition will increase the amounts of nitrogen lost from the forest and will decrease the time to nitrogen saturation as indicated by nitrogen leaching.

Nitrogen deposition was varied between 0 and 25 kg N/ha per year. At low rates of nitrogen deposition (0 to 5 kg N/ha per year) there were no nitrogen losses from this model forest for at least 150 simulated years. As deposition rates increased from 10 to 25 kg N/ha per year, then the amount of nitrogen lost at steady state increased and the time to the beginning of nitrogen loss decreased (Figure 2). With

the minimum level of control imposed upon forest nitrogen cycling in this model, nitrogen outputs equaled nitrogen inputs at steady state.

- Hypothesis 2: A disturbance that increases net nitrogen mineralization will increase nitrogen losses from the forest.

With nitrogen deposition set at 10 kg/ha per year, a disturbance was simulated by doubling the rate of net nitrogen mineralization after 150 simulated years (i.e., k_3 changed from 0.04 to 0.08 per year). Nitrogen losses from the model forest increased sharply in response to an increase in net nitrogen mineralization and then returned to a steady state value ≈ 50 simulated years following the disturbance (Figure 3). Steady state amounts of total soil nitrogen declined by $\approx 50\%$ as a result of the change in k_3 .

- Hypothesis 3: A disturbance that decreases the plant uptake of available soil nitrogen will increase nitrogen losses from the forest.

With nitrogen deposition set at 10 kg/ha per year, a disturbance to plant uptake was simulated 150 years into the model run by reducing the limit on plant uptake (116 kg N/ha per year) by 33%. Nitrogen losses from the model forest increased sharply in response to this disturbance and then returned to steady state ≈ 50 years later (Figure 4). Steady state amounts of soil nitrogen and plant nitrogen both declined by $\approx 33\%$ following disturbance to plant uptake.

Although many processes which may contribute to variability in nitrogen losses from forests are ignored (see e.g., Vitousek and Melillo 1979) and the model is a gross oversimplification of controls on nitrogen losses from forest ecosystems, the qualitative behavior of the model is reasonable in all of the following respects: (1) there is minimal nitrogen leaching from the model forest over relatively long time periods at low (1 to 5 kg N/ha per year) deposition rates, (2) the time to nitrogen saturation decreases with increasing atmospheric nitrogen deposition (Figure 2), (3) disturbances that cause nitrogen supplies to exceed forest demands (i.e. increased rates of net nitrogen mineralization or reduced plant uptake) result in a sudden

increase in nitrogen leaching followed by a return to steady state (Figures 3 and 4). More sophisticated process oriented models are needed for quantitative predictions of nitrogen outputs from forests, but O'Neill's (1976) suggestion that "simple mathematical constructs, quantifiable from available data and amenable to direct analysis, have much to offer in increasing our understanding of ecosystem function" is just as true today as it was almost 20 years ago.

Appendix B References

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