A modified nitrogen budget for temperate deciduous forests in an advanced stage of nitrogen saturation

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[1] Recent advances in ecosystem descriptions associated with nitrogen (N) saturated forests allowed us to revise and improve a model of ecosystem productivity to reflect advanced N saturation. We introduce a new description of nitrogen cycling for a forest that is in stage 2 of N saturation on the basis of recent literature. We compared the accuracy of this new description to the conventional N cycling construct by assessing the degree to which each N cycle description predicted observations in a 100-year-old N-saturated watershed in the Fernow Experimental Forest. The new literature-based model of saturation outperformed the original model by more accurately predicting aboveground net primary productivity, foliar N, and stream NO_3^-. Regional estimates of forest productivity and terrestrial carbon sequestration have generally overlooked variable N availability as a vector for forest growth changes. New findings about N-saturated ecosystem processes refine productivity models and improve estimates of regional ecosystem changes in response to N saturation.

1. Introduction

[2] Anthropogenic nitrogen compounds are being distributed disproportionately around the world and this is producing a broad spectrum of nitrogen availability found among forests in temperate regions that challenges generalized nutrient-cycling models. Recent literature brings into question previous assumptions about nitrogen (N) limitation in temperate forests with evidence that forest growth responses to additional N are not always predictable and growth limitations may not always be explained by shifts in the most limiting nutrients [*Aber and Magill*, 2004; *Magill et al.*, 2004; *Elser et al.*, 2007; *Finzi et al.*, 2007]. New literature about ecosystem nitrogen balances provides an opportunity to amass empirical observations and form an alternate description of nitrogen cycling in forest ecosystems that show symptoms of nitrogen saturation [e.g., *Aber et al.*, 2002; *Lovett et al.*, 2002; *Ollinger et al.*, 2002a; *Campbell et al.*, 2004; *Gilliam et al.*, 2005; *Templer et al.*, 2005]. Descriptions of ecosystem N cycling are essential for accurate estimates of terrestrial carbon sequestration because forest ecosystem productivity is strongly coupled to ecosystem nitrogen balances.

[3] Literature that addresses forest nitrogen balances and cycling processes controlled by varying degrees of nitrogen availability in North America have increased in recent years [*Swank and Vose*, 1997; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Lovett and Rueth*, 1999; *Aber et al.*, 2002; *Lovett et al.*, 2002; *Ollinger et al.*, 2002a; *Campbell et al.*, 2004; *Gilliam et al.*, 2005; *Templer et al.*, 2005], but the majority of ecosystem process models primarily describe the nitrogen-limited extreme of the nitrogen availability spectrum. N saturation has received more attention in European nations where nitrogen deposition has been historically the highest in the world [*Dise and Wright*, 1995; *Wright and van Breemen*, 1995; *Vitousek et al.*, 1997; *MacDonald et al.*, 2002]. Nitrogen limitations on productivity are important and may become increasingly more important for biotic systems as atmospheric CO_2 increases [*Hungate et al.*, 2003; *Luo et al.*, 2004; *Finzi et al.*, 2006; *Reich et al.*, 2006]. On the other hand, deposition of N from anthropogenic emissions is increasing N availability in some forested regions [*Fenn et al.*, 1998; *Hyvonen et al.*, 2008; *Magnani et al.*, 2007; *Kulkarni et al.*, 2008; *Sutton et al.*, 2008] and therefore contributes to a dichotomy of forest nitrogen conditions that may have equally important but opposing implications for ecological productivity [*Nadelhoffer et al.*, 1999].

[4] Ecosystem process models that estimate productivity and are designed for wide geographical applications are valuable for comparing relative nutrient balances among ecosystem types, but are practically limited to ecosystems with similar characteristics and nutrient-cycling dynamics. The PnET model [*Aber and Federer*, 1992; *Aber et al.*, 1995, 1997, 2002] has been applied to answer questions about forest productivity responses to anthropogenic pollutants, including N, in a number of studies and a wide range of forest types. Early versions of PnET estimate forest growth processes based on carbon and water balances that

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are easily accessible and verifiable in watersheds with long-term historical data records. The PnET-CN version of this model suite builds on earlier versions by including nitrogen balances that are integral to forest growth [*Aber et al.*, 1997; *Ollinger et al.*, 2002b]. PnET-CN was validated in several forests across the northeastern United States and has elegantly addressed forest productivity differences associated with a variety of anthropogenic pollutants and management activities. Despite these successes, the application of PnET-CN to the Fernow Experimental Forest in Parsons, West Virginia, United States has revealed that there may be unique N balances associated with N saturation that were not accurately predicted by established process descriptions for other forest systems [*Hom et al.*, 2006].

[5] Despite many descriptions of N-saturated ecosystems in Europe [e.g., *Wright and van Breemen*, 1995; *Vitousek et al.*, 1997; *MacDonald et al.*, 2002] and the growing number of N-saturated forests in North America [*U.S. Environmental Protection Agency*, 2002], measurements that document N saturation in temperate deciduous forests of North America are few. Conceptual models of the progressive changes in relative proportions of N species that are associated with stages of N saturation have been proposed [*Stoddard*, 1994; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Jenkins et al.*, 2005] but quantitative descriptions of the processes associated with these changes and the impacts of higher N availability on ecosystem productivity are uncertain. These conceptual models describe several stages in the progression of N saturation starting with a gradual increase in foliar N and N mineralization (stage 0) followed by stage 1, with an acceleration of N mineralization and continued rise of foliar N concentrations that gives way to an increase in foliar mass and NPP [*Stoddard*, 1994; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Jenkins et al.*, 2005]. Stage 2 of N saturation is marked by an increase in nitrification rates and N leaching, reduction in seasonal variation of leachate concentrations, and abatement of NPP stimulation [*Peterjohn et al.*, 1996; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Jenkins et al.*, 2005]. There is recent evidence to suggest that N saturation is becoming more common and that it is associated with high N deposition rates [*Townsend et al.*, 1996; *Boggs et al.*, 2005; *Pregitzer et al.*, 2008]. Quantities of different N species that result with the progression of N saturation have also been documented recently [*Gilliam et al.*, 2001; *Christ et al.*, 2002; *Campbell et al.*, 2004; *Templer et al.*, 2005] but these estimates have not yet been compiled into a descriptive mathematical model for N saturation.

[6] This study tests an alternate description of N cycling for a central Appalachian forest in stage 2 of N saturation. The nitrogen acquired, transformed, retained and lost from such a forest ecosystem does not necessarily reflect a closed N budget [*Corre et al.*, 2003]. With N highly available, volatilization and leaching are more abundant [*van Breemen et al.*, 2002] and the resident microbial community is equipped for different chemical activity that can accumulate N outside the construct of conventional N input pathways [*Aber and Magill*, 2004; *Compton et al.*, 2004; *Frey et al.*, 2004]. The new description of the N cycle introduces hypotheses that should be tested against watershed-scaled observations of N and productivity. We compared the

accuracy of predictions that were calculated using an established ecosystem productivity model with and without the new N cycle incorporated as a subroutine. If the new N cycle is a more accurate description, then the model predictions should be more similar to direct measurements of productivity and component N concentrations in a forested N-saturated watershed.

2. Methods

2.1. Site Description

[7] The Fernow Experimental Forest is located in a mixed mesophytic portion of the Appalachian Plateau [*Braun*, 1950] where extensive logging took place between the years of 1903 and 1911 [*Trimble*, 1977]. The local climate is fairly rainy and cool with an average maximum temperate of 15°C and about 146 cm of rainfall spread evenly throughout the year [*Kochenderfer*, 2006]. The watershed is composed of mixed hardwoods that have been regenerating since the early 1900s and is located at 695 to 790 m in elevation with a generally northeast aspect.

2.2. PnET-CN: Conventional N Cycling Model

[8] We chose the PnET-CN model as our control platform for a "conventional" N cycle because it was designed for application to forests that may be N-saturated [*Aber et al.*, 1997; *Ollinger et al.*, 2002b]. The first version of the PnET model was introduced in 1992 as a simple generalized process model that described the carbon and water balances that control forest productivity [*Aber and Federer*, 1992]. Belowground biomass allocation and climate change scenarios were added to the model routines in 1995 [*Aber et al.*, 1995]. Finally, a nitrogen cycling routine was added in the PnET-CN version to more completely describe ecosystem nutrient cycling and responses to N deposition or fertilization [*Aber et al.*, 1997]. Subsequent developments of the PnET model have involved hybridization with nutrient-cycling models such as Biome-BGC and DNDC [*Gbondo-Tugbawa et al.*, 2001; *Li et al.*, 2000; *Stange et al.*, 2000]. PnET-DNDC includes gaseous N fluxes from the ecosystem, but implementing this model version in the Fernow would require validation against gaseous N flux measurements and is beyond the scope of this study. We specifically wanted to make use of the historical stream chemistry data that has been recorded over 20 years (U.S. Forest Service) to simulate temporal changes in N leaching that is described by PnET-CN.

2.3. Nitrogen Cycle in PnET-CN

[9] The PnET-CN model [*Aber et al.*, 1997; *Ollinger et al.*, 2002b] defines an initial pool of nitrogen in a forest ecosystem that is available for new ecosystem processes as a percentage of nitrogen in decaying matter. This N pool is allocated to mineralization, immobilization, plant uptake, or leaching with a net loss of N from year to year (Figure 1a). The proportion of nitrogen released from decomposing organic matter is calculated on a monthly time step and becomes the estimate of gross mineralization. The proportion of mineralized nitrogen that is immobilized (NReten) is deter-
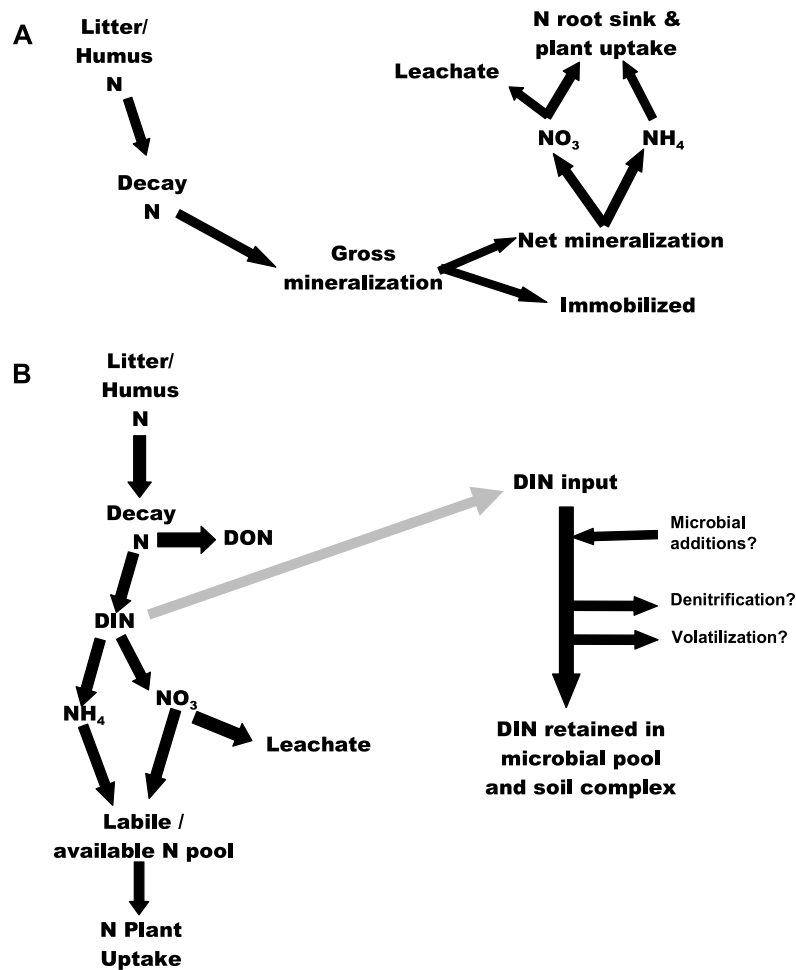
Figure 1. Conceptual diagram of soil (a) N cycle in PnET-CN (derived from *Aber at al.* [1997]) and (b) N cycle as modified in this study for PnET-CN$_{sat}$ to describe N-saturated forests. The new model distinguishes the dissolved inorganic nitrogen (DIN) pool from dissolved organic nitrogen (DON) that results from decaying matter. Nitrification rates are also defined as a site-specific percentage of overall mineralization such that NO_3^- pools are appropriately assigned to labile N pathways.

mined by the equation

$$NReten = (NImmobA + NImmobB \times SoilPctN)/100 \qquad (1)$$

where NImmobA and NImmobB are constants defined to approximate a linear fit of a complete range of immobilization proportions that correspond to a given soil N concentration (SoilPctN). This range from 0 to 1 is assumed to correspond to soil organic matter (SOM) nitrogen percentages that range from 4.3% N to 1.5% N. The value of 151 is assigned for NImmobA and -35 is assigned for NImmobB in all forest types for which the original model was validated so that complete immobilization of N occurs when there is 1.5% N in SOM and no immobilization occurs when there is 4.3% N in SOM. The N that is not immobilized is allocated for plant uptake from pools of mineralized NO_3^- and NH_4^+. The proportion of the mineralized pool that becomes NO_3^- (NRatioNit) is defined

by the equation

$$NRatioNit = ((NRatio - 1) \times FolConRange)^2, \qquad (2)$$

where FolConRange is the range of foliar nitrogen variability in the forest canopy from year to year and NRatio is a coefficient for plant N demand. NRatio is controlled strictly by plant N pools in the equation

$$NRatio = 1 + ((PlantN/MaxNStore) \times FolConRange) \qquad (3)$$

where PlantN is the total N pool in plant matter and MaxNStore is the maximum amount of N in plant matter. Nitrate that is not allocated for plant uptake is lost from the overall N pool through leaching. A more detailed description of the equations that describe nitrogen budgets in PnET-CN is outlined by *Aber et al.* [1997].

[10] The nitrogen relationships described above are linked to the carbon budget of the forest as well through the photosynthesis versus foliar N relationship. Unlike previous versions of PnET, foliar N concentrations are predicted by PnET-CN on the basis of the plant N pool in a given year with the equation

$$BudN = (BudC/CFracBiomass) \times FLPctN$$
$$\times (1/FolNRetrans) \times Nratio \qquad (4)$$

where BudC is carbon in buds, CFracBiomass is the fraction of carbon in total biomass, FLPctN is the minimum nitrogen concentration in foliar litter and FolNRetrans is the proportion of nitrogen that is retranslocated.

2.4. Weakness of PnET-CN N Cycling for Advanced N Saturation

[11] Contrary to the carbon balance of the PnET-CN model structure, the N cycling equations do not necessarily reflect specific ecosystem processes but instead assign values that suit a particular range of N concentrations. A consequence of this "black box" type of approximation is that, over a time sequence, all of the available nitrogen becomes depleted from the modeled forest system. This reflects nitrogen limitation that occurs in mature forests and, thus, the nitrogen budget described above was validated for several forests in the northeastern United States [*Aber et al.*, 1997]. However, these equations may not be an accurate reflection of N cycling in nitrogen-saturated forest ecosystems. Specifically, we might expect the labile soil N pools of a N-saturated system to vary outside the normal ranges observed in other temperate ecosystems. There are an increasing number of studies published that describe the changes in proportions of labile N pools with N saturation and variable fates of N in such systems [*Gilliam et al.*, 2001; *Christ et al.*, 2002; *Davidson et al.*, 2003; *Campbell et al.*, 2004; *Templer et al.*, 2005; *Jenkins et al.*, 2005]. Mechanistic descriptions are still few but we can introduce empirical descriptions of N cycling from recently published literature to constrain N components according to N-saturated conditions.

2.5. Empirical Evidence of N Cycling Processes in N-Saturated Forests

[12] To reconstruct a nitrogen cycle that reflects recently published characteristics and processes of nitrogen-saturated forests, we first built a skeleton of mathematical relationships that should be defined for any ecosystem nitrogen cycle [*Paul and Clark*, 1996; *Schlesinger*, 1997]. At this initial stage of development, we identified essential components of the nitrogen cycle that were missing from the PnET-CN framework. Specifically not addressed in PnET-CN were (1) the proportion of total dissolved nitrogen that becomes inorganic nitrogen and (2) the chelation of nitrogen in soil aggregates. In PnET-CN, all dissolved N was assumed to be inorganic and plant available. Inorganic nitrogen pools have recently been reported for nitrogen-saturated forests as approximately 20% of the total dissolved nitrogen pool [*Templer et al.*, 2005]. We changed the nitrogen budget so that the total dissolved nitrogen is still a function of the decomposing organic matter pool, but only a fraction of this pool is allocated to inorganic nitrogen. This percentage is unique for advanced N saturation and defines the nitrogen that is available for plant uptake.

[13] The total inorganic nitrogen retained in nitrogen-saturated forests has been recently reported by *Campbell et al.* [2004] as 44% of nitrogen input in the Fernow Experimental Forest. This retention estimate includes chelation by soil particles as well as microbial immobilization. There is mounting evidence for abiotic retention of N [*Aber and Magill*, 2004] but this process is still not completely understood, so this is an important parameter that should be specified for a particular forest site. This site-specific retention parameter also accounts for any additional nitrogen that may be acquired through microbial activity, as has been observed but poorly quantified [*Davidson et al.*, 2003]. We replaced equation (1) with the retention percentage published by *Campbell et al.* [2004] that is unique to stage 2 of N saturation. This applies to the whole inorganic N pool and is calculated independently from plant uptake. This approach circumvents the need to have a closed nitrogen cycle that allocates nitrogen inputs until the net balance is zero. In reality, there are more pathways for nitrogen uptake (e.g., microbial inputs from atmospheric N) and release (e.g., volatilization) than we are currently able to describe mechanistically in a N-saturated forest. We expand on the importance of these other processes in the discussion. Here we use the historical stream chemistry record in the Fernow to validate predictions of N leached from a N-saturated forest. We retained the mechanistic descriptions for decomposition processes that provide N to the soil and control plant N uptake while decoupling the abiotic and microbial processes. Since we cannot accurately describe the proportions of N allocated by all processes, we instead make a coarse approximation of the total dissolved inorganic nitrogen (DIN) balance on the basis of site-specific observations of net inorganic N retention in this forest [*Campbell et al.*, 2004].

[14] We made several other modifications to the N cycle on the basis of measurements and descriptions of nitrogen cycling processes that have been published specifically for nitrogen-saturated forests [*Peterjohn et al.*, 1996; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Gilliam et al.*, 2001; *Campbell et al.*, 2004; *Jenkins et al.*, 2005]. These changes included (1) site-specific nitrification rates, (2) reduced seasonal fluctuation in N leachate, and (3) nitrogen allocated for new bud growth.

2.5.1. Nitrification

[15] We identified the method of generating nitrification rates as a limitation of the N cycle in the original PnET-CN model because predictions of nitrification are based on plant N pools instead of soil processes. With nitrogen saturation, the plant N pools would remain but soil N transformations are likely to change. Nitrification rates are typically much higher in nitrogen-saturated ecosystems but vary site to site, so we included a site-specific nitrification percentage based on measurements made in the Fernow Experimental Forest by *Gilliam et al.* [2001] and confirmed in several other studies [*Christ et al.*, 2002; *Campbell et al.*, 2004].

2.5.2. Reduced Seasonal Variation in N Leaching

[16] The original PnET-CN model assumed a strong seasonal fluctuation in dissolved nitrogen output as is often observed in N-limited ecosystems. This fluctuation is controlled by plant N demand that is much higher during the growing season. A reduction in this seasonality of N leachate has been observed repeatedly in N-saturated forests, and this has been used as an identifying characteristic to define stage 2 of N saturation [*Stoddard*, 1994; *Fenn et al.*, 1998; *Aber et al.*, 1998; *Jenkins et al.*, 2005]. We modified the retention and leaching equations of PnET-CN to reflect a more modest seasonal fluctuation in dissolved nitrogen output [*Peterjohn et al.*, 1996; *Aber et al.*, 1998; *Jenkins et al.*, 2005] by using a generic algorithm that proportionally redistributes excess labile nitrogen throughout the year. More specifically, our modified model simulates retention of half of the labile N during the first four months of the year that is later released during the growing season months. Then in the last two months of the year, during early winter months, half of the leachable nitrogen is again retained. While the mechanism that controls this seasonal retention is unknown, the equations serve as a testable hypothesis for the generalized proportions of leachate and are based on repeated observations [*Peterjohn et al.*, 1996; *Aber et al.*, 1998; *Jenkins et al.*, 2005].

2.5.3. N Allocated to New Bud Growth

[17] In order to correct for the imbalance in nitrogen allocated to foliage when nitrogen is highly available, our final revision of PnET-CN involves modifying the equation that describes nitrogen in tree buds (BudN), as described in equation (4) above. In PnET-CN, foliar N is estimated as a proportion of bud N such that when there is highly available nitrogen, this equation overpredicts the proportion of N allocated to leaves. Retranslocated N is already applied to the plant N pool in the model so further allocation of retranslocated N to BudN inflates estimates of foliar N. This inflation of foliar N is magnified with higher N availability and drives model predictions outside normal biological ranges of foliar N. To correct for this, we rewrote the equation for BudN as

$$BudN = (BudC/CFracBiomass) \times ((1.3 \times FLPctN) \times NRatio) \tag{5}$$

and thus, the entire foliar pool of nitrogen is not recycled each year; instead 30% of litterfall N is allocated for BudN. This coefficient may need to be calibrated for other forest sites, but reflects observed proportional differences between foliar and litter N concentrations (data not shown).

2.6. Summary of Difference Between Proposed and Conventional N Cycle

[18] Figure 1 depicts the conceptual model of conventional N cycling in PnET-CN and an alternative N cycle, PnET-CN$_{sat}$, based on the empirical evidence that we have described. The differences in the new model can be summarizes as follows: (1) Dissolved nitrogen inputs are divided into organic and inorganic pools [*Templer et al.*, 2005]. (2) Inorganic N is partitioned into NO_3^- and NH_4^+ on the basis of site-specific nitrification rates [*Gilliam et al.*,

2001; *Christ et al.*, 2002; *Campbell et al.*, 2004]. (3) Total inorganic soil N retention is specified for the site to account for N in soil aggregates and additional microbial inputs [*Campbell et al.*, 2004]. Other changes to the N cycle that are not shown in this conceptual diagram include (1) reduced seasonal fluctuation in N leachate [*Peterjohn et al.*, 1996; *Aber et al.*, 1998; *Jenkins et al.*, 2005] and (2) nitrogen allocated for new bud growth.

[19] The dissolved inorganic N cycle is calculated independently of the soil-plant N interactions. We retained the original equations for soil organic matter input to the N-cycling subroutine as well as the output routines that allocate nitrogen back to the plant N pool in the system. Dissolved organic nitrogen recycles to the total soil N pool monthly.

3. Comparison of N Cycling Models

3.1. Parameterizing Model Runs

[20] We tested the two different N cycling descriptions against on-site measurements of five output variables in a 100-year-old watershed of the Fernow Experimental Forest that shows symptoms of stage 2 N saturation [*Peterjohn et al.* 1996]. Both model runs included the same site-specific climate records and climate change scenarios. Climate data was available for the site starting in 1952, and climate was reconstructed for the years prior to 1952 using monthly averages. The model runs started in 1900, and included a 70% biomass removal in response to logging in 1908 and 25% biomass removal in response to the Chestnut Blight in 1935. No harvesting or disturbance has been documented since those events. Atmospheric CO_2 was gradually ramped according to Mauna Loa estimates (http://www.esrl.noaa.gov/gmd/ccgg/trends/) and N deposition was ramped up to concentrations reported in 2000 by the National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu) from the baseline value starting in 1940.

[21] Seventeen site-specific input parameters were applied to the model runs and defined by on-site field measurements or previously measured data (Table 1). The same parameters were used in model runs with different N cycling descriptions. The exception is two input parameters, Nitr and NReten, which only applied to the new N cycle model (PnET-CN$_{sat}$). Data for all measured parameters were collected during the growing season of 2006. Soil and litter variables were collected monthly from May through September in six plots randomly located in the 100-year-old watershed. Three samples were obtained from each plot and then homogenized. Woody and leaf litter components were separated for analysis of N content. All soil and litter samples were dried for 48 h at 65°C, ground in an amalgamator for 20 s and then wrapped in tin for analysis through Dumas combustion in a Carlo Erba CN autoanalyzer (CE Instruments, Milan, Italy). The minimum N concentration observed in foliar litter and woody litter over the five month sampling period was applied as the minimum foliar litter [N] (FLPctN) and the minimum woody litter [N] (WLPctN) respectively. Soil organic matter N (HON) was estimated from average [N] in soil samples collected over the growing season. Specific leaf weight of

Table 1. Model Parameters Used in Comparative Model Runs[a]

Modeling Method	Input Parameter	Value	Source of Estimate	Definition
PnET-CN and PnET-CN$_{sat}$	AmaxA	41.1	*Reich et al.* [1998]	Intercept of foliar N versus A_{max} relationship
	AmaxB	42.3	*Reich et al.* [1998]	Slope of foliar N versus A_{max} relationship
	SLWmax	73	measured on site, 2002, 2006	Specific leaf weight at the top of the canopy
	GDDFolStart	340	R. Hicks, unpublished data, 2003	Sum of degrees above 0 before leaf growth
	GDDFolEnd	960	R. Hicks, unpublished data, 2003	Sum of degrees above 0 at end of leaf growth
	GDDWoodStart	507	R. Hicks, unpublished data, 2003	Sum of degrees above 0 before wood growth
	GDDWoodEnd	3045	R. Hicks, unpublished data, 2003	Sum of degrees above 0 at end of wood growth
	Latitude	39	measured	Latitude of site
	WHC	7	from *Christ et al.* [2002]	Water holding capacity
	FLPctN	0.01512	measured on site, 2006	Minimum N concentration in leaf litter
	WLPctN	0.00877	measured on site, 2006	Minimum N concentration in woody litter
	MaxNStore	76	*Adams et al.* [2004]	Maximum N in plant pool
	FolNRetrans	0.3	measured on site, 2006	Percent of N retranslocated from leaves
	NRatio	1.9	from *Peterjohn et al.* [1996]	Mobile N ratio to maximum plant N
	HON	451	measured on site, 2006	N in humus organic matter
PnET-CN$_{sat}$ only	NReten	0.44	*Campbell et al.* [2004]	Proportion of inorganic N retained in soil
	Nitr	0.92	*Gilliam et al.* [2001]	Nitrification:mineralization ratio

[a]Local climate data were used for each site and included measured precipitation, temperature, and radiation records starting in 1949 and reconstructed back to 1900.

the top canopy leaves (SLWmax) was calculated from canopy foliage that was collected from dominant canopy trees in July of 2002 (N = 22) and 2006 (N = 25). Small branches were retrieved with a shotgun from tree species that included *Acer saccharum, Fagus grandifolia, Liriodendron tulipifera, Prunus serotina,* and *Quercus rubra.*

3.2. Validation Test: Theory Comparison

[22] The validation test of both model runs included a comparison of modeled output variables to on-site measurements of aboveground woody net primary productivity (WoodNPP), aboveground net primary productivity (ANPP), historical stream [N], historical streamflow, foliar [N], and woody litter [N] from Watershed 13 (WS 13) in the Fernow Experimental Forest. On-site measurements of WoodNPP were made by collecting increment cores from trees in six 10m radius plots located randomly in watershed 13. We identified all of the trees in each plot to species, measured the diameter at breast height (DBH), and collected two increment cores from all trees > 10cm DBH within each plot. We also cored all standing dead trees, though only a subset of these cores was suitable for further analysis. Tree increment cores were brought back to the lab where they were mounted and sanded with increasingly finer grades of sandpaper up to 2000 grit. All cores were cross-dated using skeleton plots [*Stokes and Smiley,* 1968] in order to assign biomass estimates to the appropriate year. Species-specific allometric equations [*Tritton and Hornbeck,* 1982; *Brenneman et al.,* 1978] were used to estimate aboveground biomass at annual increments from tree ring analysis. Litterfall collections were made monthly during 2001 and the sum of all new litter biomass was used to estimate annual foliar mass production. Litterfall estimates were then combined with tree ring data to estimate ANPP of the 100-year-old watershed in the Fernow Experimental Forest, and litterfall was assumed to be a constant proportion of the aboveground net primary productivity over the years for which woody biomass estimates were available.

[23] Historical records of streamflow and stream N concentrations in the watershed were obtained from USDA Forest Service public data sets (Northeastern Research Station, unpublished data, 2004). Streamflow records were only recorded for 15 years in WS 13, so we compared model outputs to the long-term streamflow record of a nearby watershed (WS 4) that has also been maintained as an unharvested forest. Some differences exist in the hydrology of the two watersheds, so a validation against both watersheds is a more robust test of modeled streamflow predictions.

[24] As described above, canopy foliage of the dominant tree species was sampled with a shotgun in 2002 (N = 22) and 2006 (N = 25). Nitrogen concentrations of these samples were measured and compared to model predictions of foliar [N]. Leaf tissue was dried for 48 h at 65°C, ground, and analyzed for N in a Carlo Erba CN autoanalyzer (CE Instruments, Milan, Italy) using the Dumas combustion method. The average N concentration of woody litter samples collected monthly as described above (N = 30) was also compared to model predictions of woody litter [N]. It should be noted that this is independent of the input parameter WLPctN, which specifies the minimum wood litter N concentration that was measured over the entire growing season. Model estimates of foliar and woody litter N concentrations for the last 5 years of the model run were averaged and compared to the on-site measurements of foliar [N] and woody litter [N]. Methods for estimating foliar [N] and woody litter [N] were compared using a one-way analysis of variance (ANOVA) (SAS-JMP software version 5.1).

4. Results
4.1. Results of Conventional Model

[25] In the first model run, we fully parameterized the original PnET-CN model to include site-specific carbon, water and nitrogen balance parameters in the Fernow Experimental Forest (Table 1). Overall, in this scenario,
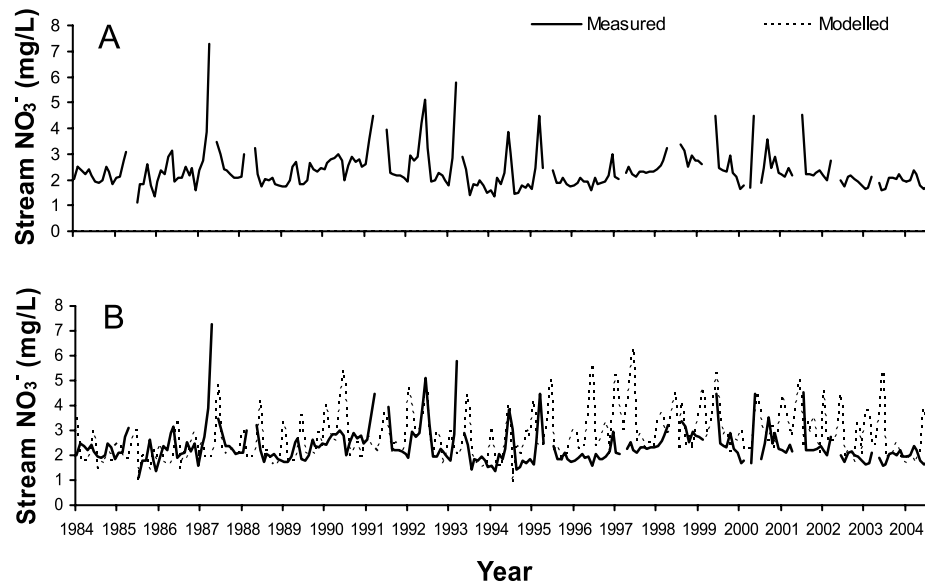
Figure 2. Measured (solid) and modeled (dashed) estimates of NO$_3$ in streamflow in a 100-year-old watershed in the Fernow Experimental Forest (Parsons, West Virginia, United States). Modeled estimates were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (a) and using PnET-CN$_{sat}$ with full on-site parameterization including a modified N balance subroutine (b); PnET-CN predicted no NO$_3$ was leached over 20 years, but regression of measured estimates on PnET-CN$_{sat}$ modeled estimates over a 20-year period was significant ($r^2 = 0.03$, $p = 0.0067$).

the model showed a poor validation with measured ecosystem attributes of the N-saturated forest. Contrary to measurements of stream N, PnET-CN predicted that no nitrogen was leached from the watershed over the past 20 years (Figure 2a). Modeled foliar N was 19% and 38% greater than foliar N measured in 2002 and 2006, respectively, and the long-term foliar N estimates over the 103 years modeled were 36% and 58% greater than measured foliar N in 2002 and 2006 (Figure 3). On the other hand, modeled woody litter N was not significantly different from measured woody litter N ($p = 0.2320$; Figure 4). On average, PnET-CN overestimated WoodNPP by 40% and ANPP by 12% over a 30-year period (Figure 5a) even though the relationships between measurements and predictions were significantly correlated (WoodNPP: $r^2 = 0.13$, $p = 0.0446$; ANPP: $r^2 = 0.20$, $p = 0.0124$). Streamflow estimates from PnET-CN accurately reflected the measured streamflow since 1952 and modeled and measured data sets were significantly correlated (WS 4: $r^2 = 0.76$, $p < 0.0001$; WS 13: $r^2 = 0.93$, $p < 0.0001$; Figure 6a).

[26] The equations that describe soil N balances in PnET-CN become an evident source of error when applying the model to a nitrogen-saturated watershed. The error is inflated primarily because nitrogen is not gradually depleted in a nitrogen-saturated system, and secondarily because high nitrification rates are likely to change the balance between plant uptake and nitrogen leaching in a forest with high nitrogen availability [Peterjohn et al., 1996; Aber et al., 1998; Fenn et al., 1998; Jenkins et al., 2005]. Using PnET-CN, the modeled nitrogen pool was depleted rapidly because the high nitrate supply was drained from the

system. At the same time, excessive nitrogen was allocated to new foliar growth each year.

4.2. Results of the New N Cycling Description

[27] We fully parameterized the modified model, PnET-CN$_{sat}$, to include site-specific carbon, water and nitrogen balance parameters in the Fernow Experimental Forest (Table 1). This included two site-specific parameters (NReten and Nitr; Table 1) not used in the parameterization of the original PnET-CN. Estimates of all five output variables from PnET-CN$_{sat}$ were validated against on-site measurements. The average stream NO$_3^-$ leached over 20 years was 19% higher than average measured NO$_3^-$ leached (Figure 2b) but there was a significant correlation between measured and modeled stream NO$_3^-$ ($p = 0.0067$). Foliar N (Figure 3) and woody litter N (Figure 4) concentration estimates from PnET-CN$_{sat}$ were not significantly different from measurements made in the forest ecosystem. A 5-year average of foliar N using PnET-CN$_{sat}$ was 6% higher than the measured foliar N in 2002 and 23% higher than 2006 measurements and the long-term foliar N average over the 103 years modeled was 4% lower and 11% higher than 2002 and 2006 foliar N measurements respectively (Figure 3). PnET-CN$_{sat}$ modeled woody litter N concentration was only 7% greater than the woody litter [N] measured in 2006 (Figure 4). These differences were not significant ($p > 0.05$) and the magnitude of difference between PnET-CN$_{sat}$ predictions and on-site measurements were substantially less than those observed between PnET-CN estimates and on-site measurements. In addition, PnET-CN$_{sat}$ predictions for WoodNPP and ANPP were more similar to measured NPP on average; overestimates were reduced to
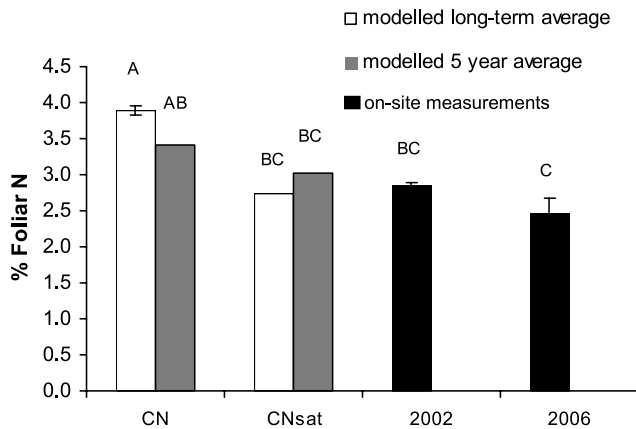
Figure 3. Measured (solid), modeled long-term average (clear), and modeled short-term average (shaded) estimates of canopy foliage N concentration in a 100-year-old watershed in the Fernow Experimental Forest (Parsons, West Virginia). Modeled estimates represent means of output for the last 5 years modeled and were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (CN), and using PnET-CN_{sat} with full on-site parameterization including a modified N balance subroutine (CNsat). Measured estimates reflect means of foliar N concentration of sun leaves collected from the five dominant tree species in the Fernow watershed during 2002 and 2006. Bars denoted by different letters are significantly different according to a one-way analysis of variance (ANOVA) with $F = 58.14$ and $p < 0.0001$ (SAS-JMP software version 5.1).

28% and 5.8% for WoodNPP and ANPP predictions relative to tree ring estimates (Figure 5b). There was a trend suggesting that modeled WoodNPP was predictive of measured WoodNPP ($r^2 = 0.12$, $p = 0.0605$) and there was a significant correlation of measured and modeled ANPP estimates ($r^2 = 0.18$, $p = 0.0177$). Streamflow estimates from PnET-CN_{sat} accurately reflected the measured streamflow since 1952 (Figure 6b) and modeled and measured data were significantly correlated (WS 4: $r^2 = 0.76$, $p < 0.0001$; WS 13: $r^2 = 0.93$, $p < 0.0001$).

5. Discussion and Conclusion

[28] The new approach to N cycling (PnET-CN_{sat}) more accurately predicts variables associated with forest carbon and nitrogen balances than the traditional approach (PnET-CN) for N-saturated forest ecosystems. However, site-specific nitrification and N retention must be assessed for the forested sites to which this model version is applied. The new model is appropriate for forests that are in stage 2 of the nitrogen saturation, currently defined as when biologically available nitrogen is excessive year-round and nitrification occurs all year as well [*Stoddard*, 1994; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Jenkins et al.*, 2005]. The open N cycle approach allowed for more accurate estimates of five validation variables relative to the conventional step-by-step reduction of nitrogen. PnET-CN_{sat} more comprehen-

sively describes ecosystem N balances that contribute to productivity changes. This is the first data set from a chronosequence spanning two decades of N-saturated conditions to be compared with a process driven ecosystem model of N saturation. The comparable model projections suggest that this new description of the N cycle may be used to further develop hypotheses about processes that are not well understood in N-saturated forests.

[29] The primary uncertainty of the new N cycle model is the fate of N retained with the reduced seasonal fluctuation in dissolved nitrogen output that is observed in N-saturated forest ecosystems. *Peterjohn et al.* [1996] estimated that seasonal variability in stream N discharge was reduced in stage 2 of N saturation, but no mechanistic descriptions of the seasonal reduction have been quantified. Several hypotheses have been proposed for what may happen to this nitrogen pool. One potential explanation is the loss of N to the atmosphere through volatilization [*van Breemen et al.*, 2002; *Venterea et al.*, 2003], a process that has been identified as increasing in the most advanced stages of N saturation [*Aber et al.*, 1998; *Jenkins et al.*, 2005]. *Neilsen et al.* [2001] found that volatilization and release of N_2O is greater immediately following soil thaw and it stands to reason that an atmospheric N sink would increase in the early winter season when temperature fluctuations are likely to induce short freeze-thaw periods more frequently than during other times of the year. Recent literature suggests that gaseous N losses are important for balancing N budgets in N-saturated ecosystems [*Pilegaard et al.*, 2006; *Kulkarni et al.*, 2008], and the seasonal imbalance we detect here could be hypothesized as a gaseous flux that might be
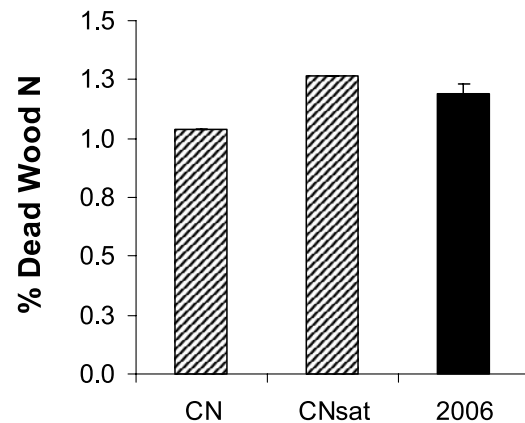

Figure 4. Measured (solid) and modeled (striped) estimates of % N in woody litter in a 100-year-old watershed in the Fernow Experimental Forest (Parsons, West Virginia). Modeled estimates represent means of output for the last 5 years modeled and were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (CN) and using PnET-CN_{sat} with full on-site parameterization including a modified N balance subroutine (CNsat). The measured estimate reflects mean woody litter N concentration collected in the watershed in 2006. There were no significant differences among means according to a one-way ANOVA with $F = 1.52$ and $p = 0.2320$ (SAS-JMP software version 5.1).
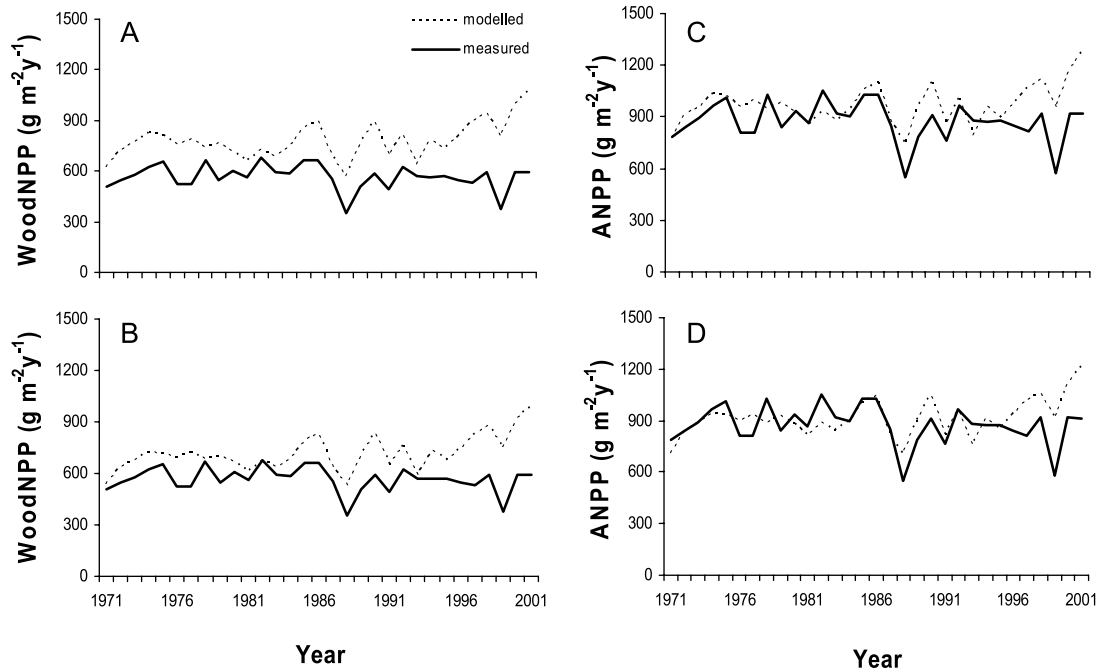
Figure 5. Measured (solid) and modeled (dashed) estimates of woody net primary productivity (WoodNPP) (left) and aboveground net primary productivity (ANPP) (right) in a 100-year-old watershed in the Fernow Experimental Forest (Parsons, West Virginia). Modeled estimates were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (a, c), and using PnET-CN$_{sat}$ with full on-site parameterization including a modified N balance subroutine (b, d).

measured over time and compared with estimates from PnET-DNDC [*Stange et al.*, 2000]. With validated estimates from both PnET-CN$_{sat}$ and PnET-DNDC, further information may be deduced about the hierarchical control of N cycling in N-saturated forests.

[30] Because of the large percentage of N that is retained, we suggest that there may be more than one pathway for the additional nitrogen retention. *Aber et al.* [1998] identified three classes of soil processes that are likely explanations for N retention under high nitrogen conditions; two of these processes involve organic nitrogen accumulation by microbial activity. Tree and understory species composition changes over time may also affect nitrification and leaching processes [*Fenn et al.*, 1998; *Lovett and Rueth*, 1999; *Lovett et al.*, 2002; *Templer et al.*, 2005], but these probably have less of an influence on seasonal dynamics than microbial community changes. Fungal species can dominate heterotrophic nitrification processes so they may be key regulators of the available soil nitrogen pools. *Schimel et al.* [1984] observed that the potential for heterotrophic nitrification was higher than that of autotrophic nitrification in forests. *Duggin et al.* [1991] found that heterotrophic and autotrophic processes were equally important for controlling nitrification in forests. *Pedersen et al.* [1999] found that autotrophic nitrification can be more important in recently clear-cut forests, but heterotrophic processes dominate nitrification in mature forest ecosystems. Little is known about seasonal fluctuation of soil microbial biomass in temperate deciduous forests, but *North et al.* [1997] found

that standing crops of hypogeal fungi increased in the fall season while consumption by animals was low and that consumption resumed in the winter period. If higher trophic level organisms increase consumption of fungal nitrogen in the early winter season, they may also export that nitrogen through emigration. Since we do not have a solid mechanistic explanation of the seasonal maintenance of NO_3^- discharge, we applied an equation that presents a general description of NO_3^- discharge patterns that can be compared to mechanistic hypotheses in the future.

[31] An important uncertainty in both the conventional and new N cycle is the description of N that is allocated to new bud growth and foliage. With high N availability, the original bud N equation greatly overestimated foliar N concentrations in a N-saturated forest which, in turn, significantly overestimates productivity. We found that a fairly large reduction in the amount of N that was recycled from the foliar litter N pool was necessary for accurate predictions of foliar N concentrations. This suggests that the amount of nitrogen allocated to foliage becomes more dependent on nitrogen availability and less dependent on recycling of nitrogen from foliage in nitrogen-saturated forests. *May et al.* [2005] measured species-level N resorption and found that nitrogen use efficiency was less important for N availability with accumulating N additions. Recent observations of nitrogen dynamics in forests treated with elevated atmospheric CO_2 concentrations have also challenged the traditional view that resource allocation is more important that nitrogen uptake [*Finzi et al.*, 2007].
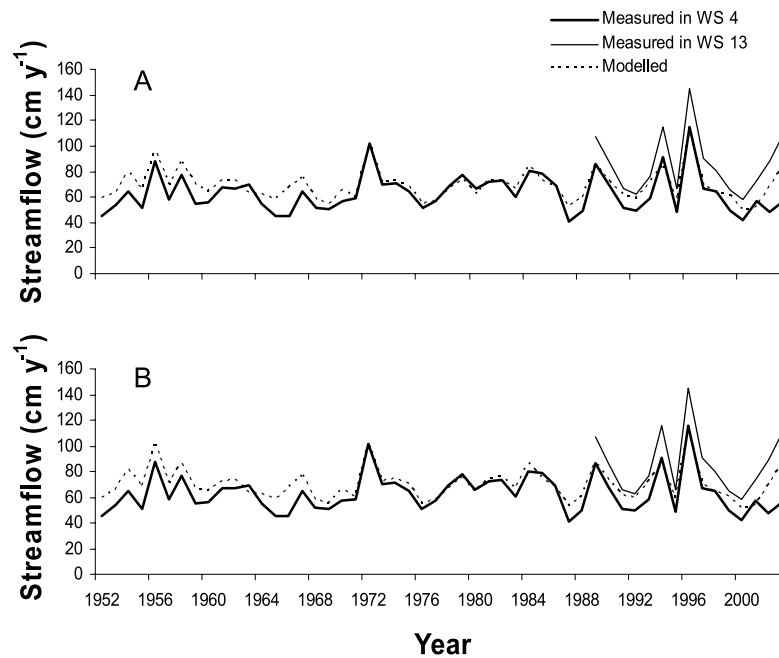
Figure 6. Measured (solid) and modeled (dashed) estimates of N in streamflow in a 100-year-old watershed in the Fernow Experimental Forest (Parsons, West Virginia). Modeled estimates were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (a) and using PnET-CN$_{sat}$ with full on-site parameterization including a modified N balance subroutine (b). Regressions of measured estimates against PnET-CN and PnET-CN$_{sat}$ modeled estimates over a 20-year period were significant (PnET-CN versus WS 4: $r^2 = 0.76$, $p < 0.0001$; PnET-CN$_{sat}$ versus WS 4: $r^2 = 0.76$, $p < 0.0001$; PnET-CN versus WS 13: $r^2 = 0.93$, $p < 0.0001$; PnET-CN$_{sat}$ versus WS 13: $r^2 = 0.93$, $p < 0.0001$).

[32] The overprediction of WoodNPP and ANPP by PnET-CN$_{sat}$ may be partially explained by ozone damage. Tropospheric ozone concentrations are correlated with N deposition [*Ollinger et al.*, 2002b] and may play an important role in plant processes of forests like the Fernow that have high historic rates of N deposition. To illustrate this, we conducted an experimental run of PnET-CN$_{sat}$ and included the ozone routine that *Ollinger et al.* [1997] developed to reflect ozone damage in plant tissues. Such ozone damage can lead to abatement of growth stimulation in response to N and CO_2 additions [*Ollinger et al.*, 2002b]. With ozone damage included in the PnET-CN$_{sat}$ model, predictions of WoodNPP were only 11% higher than measured WoodNPP and predicted ANPP was 5.5% higher that measured ANPP. The predicted WoodNPP is considerably more accurate than the 28% overprediction without ozone and suggests that this may be an important variable to consider in N saturation models for ecosystems.

[33] We focused our efforts on explaining the DIN portion of the nitrogen cycle in this study because DIN stream exports are indicative of ecosystem N status [*Campbell et al.*, 2000]. Dissolved organic nitrogen (DON) can be a substantial component of stream N, but shows less of a response to terrestrial biologic processes and seasonality. *Jones et al.* [2005] concluded that most of the DON exchange from soil to plants was a quick-cycle recovery of plant DON losses so the net acquisition of nitrogen by plants was not largely impacted. Although stream DON concentration can be very high, outputs of DON to stream water are also typically in balance with inputs from precipitation [*Campbell et al.*, 2000]. In the new N cycle presented here, DON is recycled to the soil N pool monthly. In the conventional N cycle, there is no accounting for the DON component in the soil N pool. Proportional quantities of leached dissolved organic nitrogen relative to the soil DON pool at varying degrees of N saturation would further refine N cycling descriptions, but it is likely a small component of change in the overall soil-plant N balance.

[34] There are increasing numbers of forested sites in the eastern United States that are considered nitrogen-saturated [*Jenkins et al.*, 2005]. Regional estimates of forest productivity and terrestrial carbon sequestration have generally overlooked variable N availability as a vector for forest growth changes. Such large-scale estimations will become even more inaccurate as nitrogen saturation spreads across the region because of anthropogenic nitrogen sources. The new N cycle presented here improves N descriptions in an N-saturated forest and provides a foundation for formulating new hypotheses about unknown mechanisms associated with nitrogen-saturated forests.

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