

NITROGEN CONSTRAINTS ON TERRESTRIAL CARBON SEQUESTRATION,
FROM TREES TO THE GLOBE

A Dissertation

Presented to the Faculty of the Graduate School
of Cornell University

In Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

by

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January 2013

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NITROGEN CONSTRAINTS ON TERRESTRIAL CARBON SEQUESTRATION, FROM TREES TO THE GLOBE

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Cornell University 2013

Nitrogen (N) is an essential nutrient for plant growth that constrains the fixation and storage of carbon (C) in many ecosystems. Understanding how environmental change, especially increasing N deposition, carbon dioxide concentrations, and soil temperature, alters the N limitation of forest growth is critical for accurately predicting future C storage and climate change. Accurate predictions depend on developing a historical and present day evaluation of N controls on C storage and using this knowledge to assess and improve global models.

In this dissertation, I first demonstrate that N deposition has increased C storage in trees during the 1980s and 1990s across the northeastern U.S. Second, I show how integrating four different observational and experimental datasets (N fertilization experiments, N deposition gradients, ^{15}N tracer studies, and small catchment N budgets) provide unique insights for testing and improving Earth System models. By comparing model output to globally-distributed N fertilization experiments, I demonstrate that two prominent Earth System models (the CLM-CN and O-CN) differ widely in their sensitivity to step increases in N fertilization. Third, a separate analysis focused on the CLM-CN found that the model was not sensitive enough to N deposition in comparison to historical N deposition data. By comparing CLM-CN output to both ^{15}N tracer studies and small catchment N budgets, I show that

the low response to N deposition is partially due to low ecosystem retention of N. Model improvements to the CLM-CN that decreased photosynthesis and introduced a more closed N cycle (i.e., lower N inputs relative to internal cycling) increased ecosystem retention of N, decreased the productivity response to N fertilization, and increased the productivity response to N deposition, thereby yielding much more similar model predictions to observations.

Overall, this dissertation increases our knowledge of how N deposition influences C storage and is the first to explicitly benchmark C and N interactions in Earth System models using a range of observations. In addition, my work sets a foundation for estimating the impact of N cycling on climate and creates a framework for future evaluations of Earth System models.

BIOGRAPHICAL SKETCH

Robert Quinn Thomas was born to Jane and Frank Thomas and raised in the coastal North Carolina city of Wilmington. Numerous family trips camping, hiking, canoeing, and exploring forests helped develop Quinn's passion for the outdoors. One particular week-long backpacking trip during his childhood foreshadowed his future research direction. As he and his dad were hiking on the Appalachian Trail between Wayah Gap and Fontana Dam, NC, Quinn commented about how wonderful it was that these forests were preserved and that generations will be able to enjoy this hike. Though discussions with his dad over the subsequent miles of the hike, Quinn began to understand that the world is changing, as it became clear that despite being preserved, these forests were under pressure from atmospheric pollution, climate change, and pests.

Quinn graduated from John T. Hoggard High School in 2001 and attributes his embrace of nerdiness to his Advanced Placement Chemistry teacher Mr. Mac. Quinn's extra-circular activities focused on running, highlighted by a 3rd place finish in the mile run at the N.C. state championship meet, and the Boy Scouts of America, where he earned the Eagle Scout Award.

With the support of his parents, Quinn left the warm comfort of the South to venture to the North to attend Dartmouth College in Hanover, New Hampshire. At Dartmouth, Quinn was four-year member of the varsity cross country, indoor track, and outdoor track teams. Running the Hanover area was paradise with miles of trails and dirt roads. When not training, racing, or recovering, Quinn pursued his degree in

Environmental and Evolutionary Biology. As part of his major, Quinn spent ten weeks in Costa Rica and Jamaica on Dartmouth's Foreign Study Program in Biology. Of all the topics studied on the trip, forest dynamics and carbon cycling most captivated Quinn's interest, especially the dynamics of big, majestic trees. The Costa Rica trip led to an undergraduate honors thesis in David Peart's lab studying tropical forest dynamics using remote sensing. His thesis work set the stage for his current research that investigates forest dynamics from a quantitative perspective. While working in David's lab, Quinn met James Kellner, a second year graduate student. Jim's guidance and advice was the springboard into a career as an ecological scientist, and has had lasting impacts on Quinn's development as a scientist. Quinn graduated from Dartmouth College in 2005 with high honors in his major.

After finishing at Dartmouth, Quinn pursued a Masters of Science in Natural Resources at the University of New Hampshire. His desire to study forest dynamics from a "big picture" perspective led him to George Hurtt's research group in the Complex Systems Research Center. While working with George, Quinn's quantitative skills expanded by working with ecosystem models, especially the Ecosystem Demography model. Quinn's thesis combined remote sensing tools, specifically Lidar remote sensing, with his new skills in ecosystem modeling to improve carbon stock and flux estimates in the White Mountains of New Hampshire. Beyond working with George, Quinn's interactions with Scott Ollinger piqued his interest in the forest nitrogen cycle and gave an example of how to excel at combining field-based research, remote sensing, and modeling to address important environmental change issues.

Quinn's interest in forest nitrogen cycling led him to Christy Goodale's lab at Cornell. Through working in Christy's lab, Quinn's view of forest ecosystems widened, with exposure to topics ranging from soil biogeochemistry to global carbon cycling. The professional development opportunities at Cornell, especially through the Biogeochemistry and Environmental Biocomplexity Program, introduced Quinn to many of the skills needed to succeed as a scientist and educator. During his time at Cornell, Quinn spent two pivotal summers at as visiting graduate student at the National Center for Atmospheric Research in Boulder, CO.

After completing his Ph.D., Quinn will begin a one-year postdoctoral position at the National Center for Atmospheric Research, working with Gordon Bonan. He will also be an honorary fellow in the Center for Climatic Research at University of Wisconsin as part of Ankur Desai's lab group. In August 2013, Quinn will begin as an Assistant Professor of Forest Dynamics and Ecosystem Modeling in the Department of Forest Resources and Environmental Conservation at Virginia Tech in Blacksburg, VA.

To my parents, Jane and Frank, and my wife, Cayelan.

ACKNOWLEDGMENTS

My dissertation would not have been possible without the help, guidance, and support from my committee, colleagues, friends, family, and funding agencies.

First, I thank my advisor, Christy Goodale, for expanding the breadth of my scientific knowledge and providing funding sources that supported this research. Christy's vast understanding of nitrogen cycling and enthusiasm for forest ecosystems has directly contributed to my development as an ecosystem scientist, the research topics in this dissertation, and the future directions of my career. Working with Christy has challenged me to think critically about forest ecosystem processes in new ways. Christy has been incredibly supportive of how I approach ecosystem science. She has encouraged me to embrace research using quantitative methods, especially modeling, remote sensing, and analysis of large data sets. To learn these quantitative methods, Christy provided support for me as I roamed the world learning from some of the best ecosystem modelers in the field.

My dissertation committee, Natalie Mahowald and Tim Fahey, provided guidance throughout the process of completing this dissertation. Natalie was critical for facilitating my research with the National Center for Atmospheric Research. Natalie has always been a source of positive encouragement and has helped build confidence in my research and skills as a scientist. She has also been a role model for how to work in a global modeling community and in establishing a healthy work-life balance. Tim Fahey, a true forest ecologist, has kept me grounded through discussions about the details of forest ecosystem processes. When my mind was thinking about

seemingly abstract concepts at global scales, interactions with Tim have challenged me to think about observable processes in real forest ecosystems.

Outside of my committee, I have enjoyed being an honorary member of the Hairston Zoo and have benefited from Nelson's sage advice. Likewise, Monica Gerber has been a source of wisdom during my time at Cornell. Peter Hess and Natalie Mahowald provided a research group that has challenged me to think from an Earth System perspective. The support staff in EEB: Carol Damm, Patty Jordon, LuAnne Kenjerska, Dee Albertsman, and Brian Mlodzinski, made my day-to-day existence in Corson Hall run smoothly.

The second and third chapters of my dissertation would not have been possible without the support of the scientists at the National Center for Atmospheric Research in Boulder, CO. Gordon Bonan welcomed me as a summer visitor in 2010 and 2011 and has been incredibly supportive of my development as a scientist. His direct input to the content of this dissertation has been invaluable. Because of the training I received working with Gordon, I now am able to approach research from a global modeling perspective. Eric Kluzek, a software engineer at NCAR, provided hours of technical support and this dissertation would not have happened without his help. The computing support staff in the Climate and Global Dynamics at NCAR provided the computing power and support necessary for my research. Sam Levis at NCAR provided assistance with the global model simulations in Chapter 2. Others in the Terrestrial Sciences Section at NCAR- Dave Lawrence, Rosie Fisher, Peter Lawrence, and Keith Olson- have been excellent colleagues during my dissertation.

I have had the honor to work with some of the best ecological and ecosystem

modelers in the world. I thank Sonke Zaehle at the Max Planck Institute for Biogeochemistry in Jena, Germany to hosting me as a visiting scientist in January 2012 and teaching me how he approaches the modeling of carbon and nitrogen cycles at the global scale. Sonke's model simulations directly contributed to Chapter 2. In addition, I thank Ed Rastetter at the Marine Biological Laboratory in Woods Hole, MA. Ed taught me his approach to coupled nutrient cycling, and even though my research with him is not included in this dissertation, my approach to ecosystem modeling has been thoroughly influenced by his perspective. I also thank Charlie Canham at the Cary Institute for Ecosystem Studies for introducing me to statistical modeling of forest ecology and for his direct contributions to Chapter 1. I thank Kathleen Weathers, also at the Cary Institute for Ecosystem Studies, for direct contributions to Chapter 1 and for her general guidance throughout the Ph.D. process.

My friends in Ithaca have been a huge source of support during the last five years. My running buddies, Nate Senner, Jimmy O'Dea, and Jon Lambert, and I have spend hours running on the trails and roads around Ithaca. On more than one occasion, the highs and lows of completing my dissertation were a topic of discussion on runs. I especially thank Nate, who has been stride for stride with me since I arrived to Ithaca. I also thank Dan Capps, who shared hundreds of miles with me hiking the Finger Lakes Trail and an understanding of life being married to a world-traveling aquatic ecologist. I thank Danica Lombardozzi for paving the way for me to work at NCAR and being a great sounding board for research. Others at Cornell, including Thea Whitman and Susan Cook-Patton, made Ithaca an inviting and intellectually stimulating place.

My parents, Jane and Frank Thomas, have been behind my dissertation every step of the way. The pride that they have exuded throughout my Ph.D. has kept me going. Nothing beats coming home and sharing my experiences in graduate school with them. Words cannot describe the love and support that they have provided as I have chosen my way through life.

Finally, I thank my wife, Cayelan Carey, who literally was involved in every element of my dissertation. It seems trite to list the many ways she has made me a better scientist through editing my writing, supporting my travel, being a sounding board for ideas, and helping me with the many interpersonal aspects of the scientific enterprise. But, the true gift Cayelan has given to my dissertation and me has been the endless emotional support throughout all aspects of life and the persistent confidence that she has in my work and me.

The National Science Foundation awards to Christy Goodale, Peter Hess, and Timothy Fahey, the Kieckhefer Adirondack Fellowship, the National Science Foundation Biogeochemistry and Biocomplexity IGERT and National Science Foundation Cross-Scale Biogeochemistry IGERT provided funding for my dissertation research.

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CHAPTER 1
INCREASED TREE CARBON STORAGE IN RESPONSE TO NITROGEN
DEPOSITION IN THE US¹

Human activities have greatly accelerated emissions of both carbon dioxide and biologically reactive nitrogen to the atmosphere (Galloway et al. 2004, Denman et al. 2007). As nitrogen availability often limits forest productivity (LeBauer and Treseder 2008), it has long been expected that anthropogenic nitrogen deposition could stimulate carbon sequestration in forests (Melillo and Gosz 1983). However, spatially extensive evidence for deposition- induced stimulation of forest growth has been lacking, and quantitative estimates from models and plot-level studies are controversial (Magnani et al. 2007, de Vries et al. 2008, Magnani et al. 2008, Reay et al. 2008, Sutton et al. 2008, Janssens and Luyssaert 2009). Here, we use forest inventory data to examine the impact of nitrogen deposition on tree growth, survival and carbon storage across the northeastern and north-central USA during the 1980s and 1990s. We show a range of growth and mortality responses to nitrogen deposition among the region's 24 most common tree species. Nitrogen deposition (which ranged from 3 to 11 kg ha⁻¹ yr⁻¹) enhanced the growth of 11 species and decreased the growth of 3 species. Nitrogen deposition enhanced growth of all tree species with arbuscular

¹ Reprinted by permission from Nature Geoscience (Thomas, R Q, C. D. Canham, K. C. Weathers, and C. L. Goodale. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* 3:13–17). Copyright 2010, Nature Publishing Group

mycorrhizal fungi associations. In the absence of disturbances that reduced carbon stocks by more than 50%, above-ground biomass increment increased by 61 kg of carbon per kg of nitrogen deposited, amounting to a 40% enhancement over pre-industrial conditions. Extrapolating to the globe, we estimate that nitrogen deposition could increase tree carbon storage by 0.31 Pg carbon yr⁻¹.

During the 1990s, terrestrial ecosystems in the Northern Hemisphere absorbed approximately 1.7 Pg carbon (C) yr⁻¹, or ~25% of the emissions from fossil fuel combustion (6.4 Pg C yr⁻¹; Denman et al. 2007). The causes of this sink have not been quantitatively partitioned, but proposed mechanisms include forest regrowth and forest growth enhancement from climate change, CO₂ fertilization, changes in forest management and nitrogen (N) deposition (Denman et al. 2007, Reay et al. 2008). Identifying the mechanisms that control this C sink is critical for managing and predicting its future behaviour. Estimates of the magnitude of N deposition effects on global forest C balance vary greatly, with recent controversy (Magnani et al. 2007, de Vries et al. 2008, Magnani et al. 2008, Sutton et al. 2008, Janssens and Luysaert 2009) particularly focused on the plausibility of a large N-induced C sink reported for 20 (mostly European) chronosequences (>200 kg C for each kilogram of N deposited; Magnani et al. 2007, 2008).

Global biogeochemical models estimate that forest C sinks from N deposition range from 0.24 to 2.0 Pg C yr⁻¹ (Townsend et al. 1996, Holland et al. 1997, Thornton et al. 2007). In contrast, an analysis of forest inventory data from five US states discerned little growth enhancement resulting from any environmental change over the past century (Caspersen et al. 2000). Plot-level ¹⁵N tracer experiments show that most

added N is retained in soil rather than trees, leading to estimates of a small N-induced forest C sink (0.14 Pg C yr⁻¹ in trees; 0.25 Pg C yr⁻¹ in trees + soil; Nadelhoffer et al. 1999). Long-term fertilization studies show that N additions can provide modest growth enhancements (Hyvonen et al. 2008) but that N saturation can induce mortality, which decreases C storage in live biomass (Magill et al. 2004, Wallace et al. 2007) casting some doubt on both the magnitude and the direction, of future forest C responses. Spatial covariation between N deposition and patterns of tropospheric ozone and sulphur pollution may further offset N-induced growth enhancement (Ollinger et al. 2002). Here, we use spatially extensive forest inventory data to discern the effect of N deposition on the growth and survival of the 24 most common tree species of the northeastern and north-central US, as well as the effect of N deposition on C sequestration in trees across the breadth of the northeastern US.

Species-level responses to N deposition are critical to projections of how tree communities will change as a result of a range of factors, including succession, climate change and host-specific pests (Lovett et al. 2006). Individual tree growth responded to N deposition for 14 of the 24 species examined; however, the direction, shape and magnitude of the response varied by species (Fig. 1, Table 1). Three of the four most abundant species (*Acer rubrum*, *A. saccharum* and *Quercus rubra*) showed strong positive growth responses (>4% increase in C increment per kg N ha⁻¹ yr⁻¹). The largest growth enhancements (16–18% per kg N ha⁻¹ yr⁻¹) occurred in *Liriodendron tulipifera* and *Prunus serotina*, two valuable timber species.

Mycorrhizal

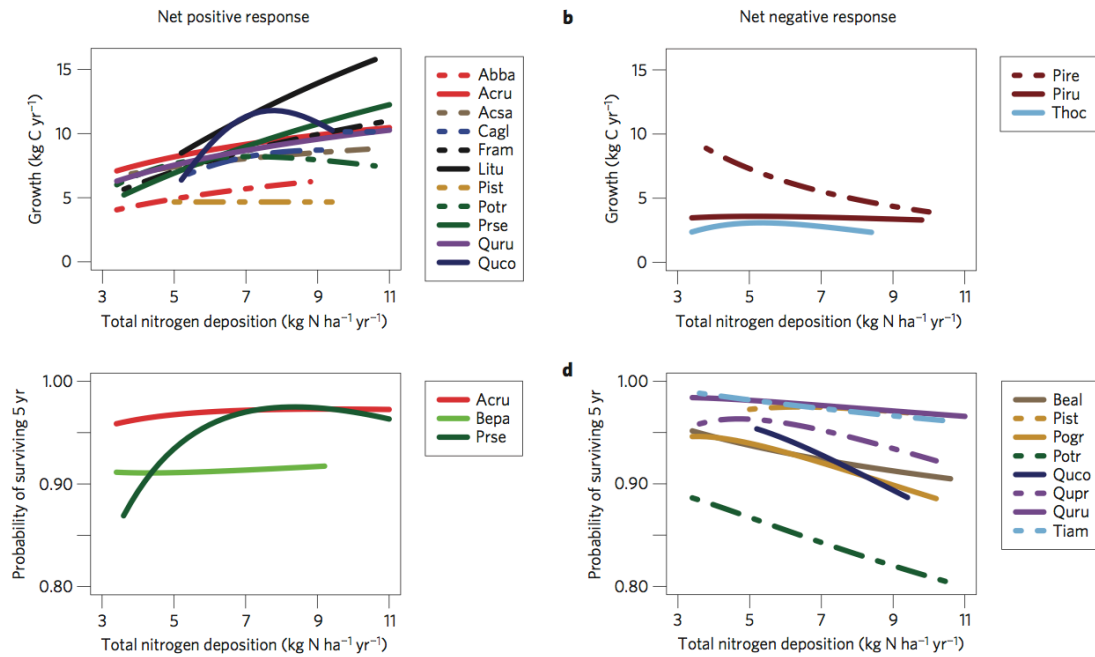


Figure 1. Growth and survival response to increasing nitrogen deposition. a–d, The annual above-ground carbon increment (a–b) and five-year survival rate (c–d) as a function of total (wet + dry) inorganic N deposition for individual trees of the 24 most common species in a 19-state region of the US. Species that did not respond to nitrogen deposition are not shown. See Table 1 for the species abbreviation codes and Supplementary Figure 1 for the survival response of *Abies balsamea*

Table 1. Species included in the analysis of individual growth and survival, with common names, sample size, ecological attributes, and results of AIC analysis.

						Growth				
Species	Abbr.	Common name	Sample Size*	% abundance	Ecological Attributes	Δ AIC Size and climate	Δ AIC Size, climate, and nitrogen deposition	R ²	Mean predicted growth rate (kg C yr ⁻¹)	% growth change per kg N ha yr ⁻¹ †
<i>Abies balsamea</i>	Abba	balsam fir	5650	3.3	EM, EC	6.79	0	0.22	10.15	12.3
<i>Acer rubrum</i>	Acru	red maple	23047	13.6	AM, DH	277.29	0	0.49	18.39	6.3
<i>Acer saccharum</i>	Acsa	sugar maple	18480	10.9	AM, DH	65.47	0	0.35	16.04	4.2
<i>Betula alleghaniensis</i>	Beal	yellow birch	3889	2.3	EM, DH	0	16.53	0.25	10.29	
<i>Betula lenta</i>	Bele	black birch	2895	1.7	EM, DH	0	58.56	0.47	14.58	
<i>Betula papyrifera</i>	Bepa	paper birch	4393	2.6	EM, DH	0	0.61	0.26	7.42	
<i>Carya glabra</i>	Caga	pignut hickory	2554	1.5	EM, DH	11.51	0	0.55	16.69	7.2
<i>Fagus grandifolia</i>	Fagr	American beech	6697	3.9	EM, DH	0	199.49	0.59	15.02	
<i>Fraxinus americana</i>	Fram	white ash	6538	3.9	AM, DH	16.03	0	0.5	18.15	13.0
<i>Liriodendron tulipifera</i>	Litu	tulip poplar	6179	3.6	AM, DH	130.16	0	0.56	29.79	16.0
<i>Pinus resinosa</i>	Pire	red pine	3333	2.0	EM, EC	62.55	0	0.31	10.82	-9.0

<i>Picea rubens</i>	Piru	red spruce	2930	1.7	EM, EC	26.66	0	0.26	7.18	-0.1
<i>Pinus strobus</i>	Pist	white pine	8272	4.9	EM, EC	0.44	0	0.32	11.69	0.9
<i>Populus grandidentata</i>	Pogr	quaking aspen	3233	1.9	EM, DH	0	32.78	0.34	14.50	
<i>Populus tremuloides</i>	Potr	trembling aspen	5462	3.2	EM, DH	31.48	0	0.39	16.30	3.4
<i>Prunus serotina</i>	Prse	black cherry	6585	3.9	AM, DH	41.41	0	0.54	24.41	18.0
<i>Quercus alba</i>	Qual	white oak	12130	7.1	EM, DH	0	127.03	0.66	15.23	
<i>Quercus coccinea</i>	Quco	scarlet oak	2406	1.4	EM, DH	157.605	0	0.63	22.81	14.4
<i>Quercus prinus</i>	Qupr	chestnut oak	8318	4.9	EM, DH	0	192.24	0.62	16.06	
<i>Quercus rubra</i>	Quru	red oak	11861	7.0	EM, DH	137.79	0	0.66	22.16	8.3
<i>Quercus velutina</i>	Quve	black oak	7328	4.3	EM, DH	0	237.11	0.61	23.86	
<i>Thuja occidentalis</i>	Thoc	white cedar	6512	3.8	EM, EC	43.25	0	0.31	6.08	-0.01
<i>Tilia americana</i>	Tiam	basswood	3450	2.0	EM, DH	0	3.27	0.48	14.51	
<i>Tsuga canadensis</i>	Tsca	Eastern hemlock	7676	4.5	EM, EC	0	5.59	0.47	11.38	

The ecological attributes include mycorrhizal association (arbuscular (AM) versus ecto (EM) mycorrhizal) and plant functional type (deciduous hardwood (DH) versus evergreen conifer (EC)). The model comparison from likelihood analysis of individual tree annual above-ground carbon increment (growth) and five-year survival rate for the 24 most common tree species is shown along with the % response per $\text{kg ha}^{-1}\text{yr}^{-1}$ of extra N deposition. Species acronyms are given for reference to the legends of the figures. AIC is the difference between the AIC of the best model ($\Delta \text{AIC} = 0$) and alternative models; a larger AIC indicates a poorer model fit. Goodness of fit (R^2) is reported for the best model. The climate effect included the most parsimonious model of annual mean temperature and precipitation, either one alone, or neither, as indicated by differences in AIC.

*Number of stems used in the analysis of survival (that is, alive at the time of the first census and not harvested or missing at the time of the second census).

† Assumes a linear response between the minimum and maximum nitrogen deposition observed for that species.

Table 1. Continued, survival response

	Survival			
Species	Δ AIC Size and climate	Δ AIC Size, climate, and nitrogen deposition	Mean predicted 5- yr survival rate	% 5-yr survival rate change per kg N ha yr ⁻¹ †
<i>Abies balsamea</i>	144.4	0	0.52	0.06
<i>Acer rubrum</i>	8.33	0	0.97	0.19
<i>Acer saccharum</i>	0	1.81	0.98	
<i>Betula alleghaniensis</i>	5.97	0	0.93	-0.68
<i>Betula lenta</i>	0	0.94	0.97	
<i>Betula papyrifera</i>	12.92	0	0.91	0.11
<i>Carya glabra</i>	0	2.87	0.97	
<i>Fagus grandifolia</i>	0	19.28	0.97	
<i>Fraxinus americana</i>	0	1.7	0.96	
<i>Liriodendron tulipifera</i>	0	4.26	0.98	
<i>Pinus resinosa</i>	0	3.16	0.99	
<i>Picea rubens</i>	0	11.38	0.92	
<i>Pinus strobus</i>	21.68	0	0.97	-0.08
<i>Populus grandidentata</i>	6.7	0	0.92	-0.94
<i>Populus tremuloides</i>	17.21	0	0.85	-1.30

<i>Prunus serotina</i>	10.82	0	0.97	1.47
<i>Quercus alba</i>	0	0.73	0.98	
<i>Quercus coccinea</i>	14.66	0	0.93	-1.67
<i>Quercus prinus</i>	4.82	0	0.95	-0.57
<i>Quercus rubra</i>	3.17	0	0.98	-0.24
<i>Quercus velutina</i>	0	3.16	0.95	
<i>Thuja occidentalis</i>	0	2.95	0.94	
<i>Tilia americana</i>	0.04	0	0.97	-0.39
<i>Tsuga canadensis</i>	0	1.47	0.98	

association may also influence the response to N deposition, as all five of the tree species with arbuscular mycorrhizal associations responded positively (*Acer rubrum*, *Pinus strobus*, *Thuja occidentalis*, *Prunus serotina*, *Quercus alba*). Unlike ectomycorrhizal fungi, arbuscular mycorrhizal fungi are unable to produce enzymes that break down soil organic N (Chalot and Brun 1998), thus trees with arbuscular associations may be more likely to benefit from increased availability of soil inorganic N associated with N deposition.

All three of the species with net negative growth responses were evergreen conifers (*Pinus resinosa*, *Picea rubens*, *Thuja occidentalis*). The species with the largest decline in growth (9% decrease per kg N ha⁻¹ yr⁻¹) was *Pinus resinosa*, a species shown to respond negatively to chronic N fertilization in a long-term N-addition experiment in central Massachusetts (Magill et al. 2004). The decline in growth observed here could be due to a range of factors, including N-induced leaching of soil base cations (Aber et al. 1998), increased vulnerability to secondary stressors (drought, insects) or suppression by more competitive species (Hautier et al. 2009).

The net effect of N deposition on tree C stocks depends on not only the growth responses but also the mortality response. N deposition influenced the survivorship of 11 of the 23 species examined (Fig. 1 and Table 1); three species showed increased survivorship and eight showed decreased survivorship across the range of N deposition. All eight of the species showing decreased survivorship had ectomycorrhizal associations (Table 1), further suggesting that mycorrhizal association influences tree species response to N deposition. The growth and lifespan of two tree species with arbuscular mycorrhizal associations—*Prunus serotina* and *Acer*

Table 2. ΔAIC and goodness of fit (R^2) from the likelihood analysis of plot-level annual aboveground carbon increment and annual aboveground carbon increment of the trees that survived the measurement period. N is the sample size. ΔAIC is the difference between the AIC of the best model ($\Delta AIC=0$) and alternate models. R^2 is reported for the best model. NP is the number of parameters in the best model (including any parameters estimated for the error term).

Plot-level response variable	Disturbance exclusion	Sample size	ΔAIC size, temperature, precipitation	ΔAIC size, temperature, precipitation, and nitrogen	NP	R^2	C:N Ratio
Surviving tree growth	none	4817	32.83	0	9	0.47	68:1
Net annual aboveground carbon increment	>50% net biomass lost	4686	4.15	0	9	0.08	61:1
Net annual aboveground carbon increment	none	4817	2.75	0	9	0.06	0

ΔAIC is the difference between the AIC of the best model ($\Delta AIC = 0$) and alternative models. R^2 is reported for the best model. NP is the number of parameters in the best model (including any parameters estimated for the error term).

rubrum—increased with N deposition; *P. serotina* showed especially large changes in both. No species showed reduction in both growth and survivorship.

At the stand level, the growth by all trees that survived the remeasurement period increased across the observed range of N deposition (3–11 kg C ha⁻¹ yr⁻¹; Fig. 2a and Table 2). The fertilization effects of N on tree growth presumably drove this relationship. Considering both growth and mortality responses while excluding major disturbance (that is, excluding plots that lost more than 50% of the C stock over the measurement period), annual net above-ground C increment increased nearly linearly (5.5% increase per kg N ha⁻¹ yr⁻¹) over the observed range of N deposition (Fig. 2b and Table 2). This response is steeper (5.5% versus 1.5%) than observed for two conifer species in 363 European plots spanning a larger range of N deposition (Solberg et al. 2009), perhaps owing to a greater responsiveness at the lower N deposition values observed in this study. However, the relationship between net C increment and N deposition is not present if all levels of disturbance are considered, as the variability induced by large stochastic mortality events obscured the effects of N on growth (Fig. 2a). As the response was nearly linear, there was no evidence for N saturation at the stand level at the rates of N deposition observed in this data set, although it may occur at higher rates of N deposition (Aber et al. 1998). At the species level, some species showed decreased growth or decreased survivorship at the higher levels of N deposition, suggesting that these species may be more sensitive than others to the deleterious effects of N inputs, as well as other pollutants that co-vary with N deposition (Fig. 1). N deposition explained a small amount of variation in growth, survivorship and C gain across the region, indicating that many factors affect forest C

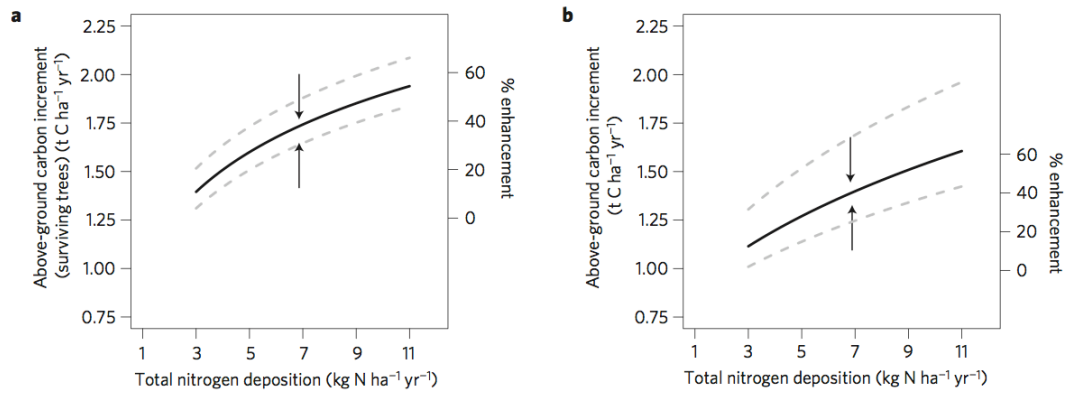


Figure 2. Annual above-ground carbon increment increases with nitrogen deposition.

a,b, The relationship between total (wet + dry) inorganic N deposition and annual above-ground growth of surviving trees (a) and net annual above-ground carbon increment (excluding plots with >50% loss of carbon stocks) (b) at the plot level. The per cent enhancement uses preindustrial N deposition (1 kg N ha⁻¹ yr⁻¹) as a baseline and a linear extrapolation of the response. The mean annual N deposition (6.9 kg N ha⁻¹ yr⁻¹) estimated for the forest inventory data is shown with the arrows. Two-unit support intervals are plotted as grey-dashed lines.

balance. Nonetheless, the statistical analyses provide strong support for a N effect on regional forest C gain in addition to the effect of climate alone (Table 2). Averaged across all plots in the 13-state subset of our study area, anthropogenic N deposition, in the absence of major disturbance, enhanced above-ground C increment in trees by 40% (37–47%; two-unit support interval, approximately a 95% confidence interval in a likelihood framework) over preindustrial conditions (calculated using a linear extrapolation to an assumed preindustrial inorganic N deposition of approximately 1 kg ha⁻¹ yr⁻¹ (Galloway et al. 2004). This response is integrative in that it includes the direct effects of N deposition on tree growth through soil fertilization, foliar N uptake and other potential interactions between N deposition and other environmental changes, including CO₂ fertilization. It greatly exceeds the <2% growth enhancement deduced from biomass and age information from similar inventory data from fewer states (Caspersen et al. 2000) , although others have highlighted uncertainties in that previous analysis (Joos et al. 2002). It also exceeds the 23% enhancement of net primary production anticipated for the year 2050 from a doubling of atmospheric CO₂ over preindustrial levels, as estimated using free-air CO₂ enrichment studies (Norby et al. 2005).

This enhancement of above-ground C storage (Fig.2b) averaged 61 kg C ha⁻¹ yr⁻¹ per kg increase in N deposition (51–82 kg C ha⁻¹ yr⁻¹ per kg; two unit support interval). This C/N response ratio does not include infrequently measured forms of N deposition, such as NH₃, NO and NO₂ gases, or organic N, nor does it include the effects of N deposition on root biomass or soil C stocks, which may have important influences on the sink (Reay et al. 2008, Janssens and Luyssaert 2009). Although

variable, below-ground tree biomass often represents roughly 20% of above-ground biomass (Jenkins et al. 2003). Therefore, the corresponding enhancement of total tree C would be 73:1(61–98:1) kg C ha⁻¹ yr⁻¹ per kg ha⁻¹ yr⁻¹. This ratio of C sequestration per unit N deposition in tree C stocks exceeds ratios estimated from European forest inventory data (20–40:1; above-ground C in trees; de Vries et al. 2008), partitioning inferred from plot-level ¹⁵N tracer studies (25:1; C in trees; Nadelhoffer et al. 1999) and plot-level fertilization studies in Scandinavia (–1 to 53:1; Hyvonen et al. 2008). The ratio is substantially lower than the whole-ecosystem (net ecosystem production) estimate of 200:1 derived from plot-level eddy flux tower and chronosequence data (Magnani et al. 2007, 2008); a 127 kg C per kg of N response in soils or dead wood would be needed to make up the difference between our tree response and the 200:1 net ecosystem production response. Although the soil response is highly uncertain, a recent review of Scandinavian N fertilization studies demonstrated soil responses that ranged from 1 to 20:1 kg C per kg of N (Hyvonen et al. 2008).

Globally, we estimate that N deposition could account for a 0.31(0.26–0.42) Pg C yr⁻¹ sink into above-ground trees. This estimate of the global sink was calculated by multiplying the C/N response measured in this study (61:1) by a conservative estimate of total N deposition to forests (5.1 Tg N yr⁻¹; Holland et al. 1997), predominately in temperate regions. Similar stoichiometric-based approaches have been used by others to obtain global estimates of the forest C sink attributed to N deposition¹ (Schindler and Bayley 1993, Janssens and Luyssaert 2009). Although there is uncertainty in applying a single C/N response to all temperate forests, such

exercises illustrate the global-scale implications of reported growth enhancements. Our estimate of a N-induced global C sink is greater.% enhancement than that estimated using plot-level ^{15}N tracers (0.14 Pg C yr $^{-1}$ in trees; Nadelhoffer et al. 1999) and a recent global biogeochemical model (0.24 Pg C yr $^{-1}$ in trees and soils; Thornton et al. 2007). In contrast, our global C sink estimate is substantially lower than the sinks in trees and soil predicted by earlier global biogeochemical models (1.5–2.0 Pg C yr $^{-1}$; Holland et al. 1997) or inferable from the 200:1 C/N response reported for 20 intensive C monitoring sites (1.02 Pg C yr $^{-1}$; Magnani et al. 2008). The latter estimates imply that most of the terrestrial C sink (1.7 Pg C yr $^{-1}$; Denman et al. 2007) can be attributed to N deposition, despite evidence that land-use history (Hurtt et al. 2002) has an important role.

Thus, we show that N deposition is an important mechanism contributing to C sequestration within these temperate forests, but is unlikely to explain all of the observed terrestrial C sink. Furthermore, forest response to N deposition depends on the species present, and N deposition will probably influence future forest demography by altering tree growth and survival.

Methods Overview

National forest inventories measure the growth and survival of individual trees, and provide an invaluable opportunity for assessing patterns of regional C balance. Here, we used forest inventory data for the 24 most common tree species occurring on 20,067 plots remeasured during the early 1980s to mid-1990s by the US Forest Service Forest Inventory and Analysis (FIA) Program. The plots span a 19-state

region bounded by Maine in the northeastern USA, to Virginia and Kentucky, and to longitude 90° west in the states of Wisconsin and Illinois. We used a model-selection approach to ask whether data on mean annual N deposition (wet NO_3^- and NH_4^+ and dry HNO_3 gas and particulate NH_4 and NO_3) improved models that predicted stand-level C increment and species-specific growth and survivorship as a function of both climate (mean annual temperature and precipitation) and C stocks at the beginning of the measurement period. The stand-level analysis was carried out using all species on a 13-state subset of the region that used fixed-radius plot designs ($n = 4,817$ plots); the six states (Indiana, Illinois, Kentucky, Michigan, Virginia and Wisconsin) with variable-radius plots were excluded. The stand-level analysis also excluded plots with trees harvested between measurement periods.

We compiled a data set on tree growth in carbon, tree survival, plot-level net C increment and plot-level C increment of living trees during the 1970s–1990s across the northeastern and north-central US. For each plot, the mean annual temperature, mean annual precipitation and mean annual total (wet + dry) inorganic (nitrate and ammonium) nitrogen deposition for each plot were estimated using the geographic location of the plot and spatially resolved data on temperature, precipitation and N deposition (see Supplementary Information for more details). For each of the independent variables (tree-level growth, tree-level survival, plot-level net C increment and plot-level C increment of living trees), we solved for the maximum likelihood estimates for model parameters in models that included the influence of climate and tree size (or plot C stock) on the variable. The climate effect included mean annual temperature, mean annual precipitation, or both, depending on which had

the lowest Akaike Information Criterion(AIC; Burnham and Anderson 2002) and was therefore the most parsimonious (that is, the best model fit for the fewest parameters). To determine whether N deposition influenced the independent variables beyond that of size and climate, we added a lognormal nitrogen deposition term to the model that included size and climate, estimated the parameters using maximum likelihood and compared the AIC between the models with and without N. If the model that included N deposition had the lowest AIC, we used the model parameters to assess the response of the variable to N deposition. Supplementary Information provides further details on the data sources, data compilation and models used in the analyses.

Acknowledgements

This research was supported, in part, by a grant to C.D.C. from the US Department of Energy, National Institute for Climatic Change Research, a Marie Tharp Fellowship, Columbia University to K.C.W., NSF-DEB award #0614099 to C.L.G. and a Kieckhefer Adirondack Foundation grant to R.Q.T. We would like to thank staff from the US Forest Service FIA Program, particularly E. LaPoint, for making the FIA data available to us, and for their considerable help in compiling this particular data set. We also thank C. Carey, J. Caspersen, W. De Vries, F. Magnani, N. Mahowald and W. Schlesinger for suggestions and comments on the manuscript.

Author contributions

R.Q.T., C.D.C., K.C.W. and C.L.G. all contributed to the development of project ideas, design, analysis interpretation and to writing of the manuscript, with

C.L.G. and R.Q.T. originating the project. In addition, C.D.C. and R.Q.T. assembled the FIA and climate data and carried out the statistical analyses, K.C.W. developed the N deposition estimates and C.L.G. and R.Q.T. provided the carbon framework

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to R.Q.T.

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SUPPLEMENTAL INFORMATION

Methods

Compiling a regional dataset on individual tree growth and survival and plot-level carbon increment

We compiled a dataset on tree growth and survival and plot-level C increment using data collected through the US Forest Service Forest Inventory and Analysis (FIA) program. FIA methodology is in the process of being standardized nationwide, but full censuses that use the national standard have not yet been completed for most states. Therefore, we used data from the last two complete censuses in the 19-state region from Maine to Wisconsin, south to Kentucky and Virginia (Supplementary Table 1). Field methods varied by state, and often from the first to the second census. The variation from the first to second census generally involved changing plot size, which permitted the use of tree remeasurement data in the smaller plot size. General descriptions of FIA methods are available on the program website <http://fia.fs.fed.us/>. Exact FIA plot locations are confidential by law, but we received true plot location data from the U.S. Forest Service under a security agreement. See <http://nrs.fs.fed.us/fia/data-tools/sds/> for information on rules about access to the spatial location of the plots. The plot location data were used to interpolate climate and N deposition data at the plot level from sources described below. The remeasurement periods varied by state and plot but the average period was 12.4 years.

The FIA program measures all trees > 12.7 cm (5 inches) diameter at breast height (DBH). We used the individual tree DBH measurements and species-specific allometric equations that related C (assuming biomass is 50% C) to DBH to determine the C stock of each tree at the time of each census (Supplementary Information Table 2; Jenkins et al. 2003). We used all trees in the 19-state region that were alive and greater than 12.7 cm DBH in both measurement periods for the tree-level growth analysis. Annual growth rate was calculated by subtracting the C stock at the first measurement from the second measurement, and dividing by the time interval between measurements. All trees with annual diameter growth rates less than -0.5 cm per year were excluded because such large negative growth rates are likely to be a product of measurement error ($<0.5\%$ of trees). We used all trees alive and >12.7 cm DBH in the first measurement period for the individual tree survivorship analysis, excluding trees that were harvested.

Annual net C increment for each plot was calculated by summing the C stock of all living trees >12.7 cm in each period and subtracting the first from the second measurement period before dividing by the length of the measurement period. Annual C increment for the surviving trees was calculated by summing the carbon increment for the individual trees that survived the measurement period. For the plot-level analysis, we used all plots without harvest from the 13 northeastern states (Maine to Ohio, south to West Virginia and Maryland) only, because differences in methods for the first and second censuses in the 6 other states (Illinois, Indiana, Kentucky, Michigan, Virginia, and Wisconsin) allowed accurate tracking of some but not all trees within plots. Other studies have used a variety of methods to attempt to correct

for the differences in methodology between states, but in our judgment those methods introduce unacceptably high levels of error to the analysis. The analysis on the surviving tree C increment used all data. The analysis on annual net C increment was performed on all data and the dataset with plots excluded based on the intensity of mortality during the measurement period. We excluded plots based on the percentage of C lost through mortality or undocumented harvesting during the remeasurement period. We used a dataset that included all plots and a dataset that excluded plots with major disturbance, which we defined as having lost >50% of C during the remeasurement period.

Nitrogen deposition data description

We estimated total (wet + dry) inorganic (nitrate and ammonium) nitrogen deposition to each of the 20,067 plots as follows:

Wet deposition: Average annual (based on 2000-2004 data) wet inorganic nitrogen ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) deposition for each FIA plot was calculated as the product of estimated average annual precipitation and kriged (Weathers et al. 2008) $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ chemistry from National Atmospheric Deposition Program site locations that bracketed our focal region (Table 1; <http://nadp.sws.uiuc.edu/>).

Precipitation data for each plot were estimated using bi-linear interpolation of 800 m resolution PRISM climate data (<http://www.prism.oregonstate.edu/>). For each plot, we averaged the interpolated annual precipitation data for each of the individual years that spanned the period from the initial to final census of a plot.

Dry Deposition: Dry inorganic N deposition ($\text{HNO}_3\text{-N}$, particulate $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) for each plot was calculated as the product of air concentrations, based on the average of 2000-2004 CASTNET air chemistry data, and deposition velocities based on vegetation cover, following the Clean Air Status and Trends Network (CASTNet) protocols (<http://www.epa.gov/castnet/>). The dry deposition velocities generated by the CASTNet were specific to forest types and leaf-off (dormant) and leaf-on (growing) seasons, where the growing season was 16-May to 15 October and the rest of the year was classified as dormant.

Each plot was classified into one of three forest types based on the relative abundance of conifers vs. deciduous species in each plot, as follows: $< 25\%$ deciduous = conifer, $> 75\%$ = deciduous, and $> 25\%$ and $< 75\%$ deciduous = mixed (Weathers et al. 2006).

For each chemical form, forest type (conifer, mixed, deciduous), and season (dormant, growing), we estimated dry deposition as the product of the spatially referenced concentration raster and the vegetation-specific deposition velocity for the cover type for the length of the entire season.

For each plot, total deposition was calculated as the sum of wet and dry deposition. Atmospheric N deposition to these plots ranged from 3-11 $\text{kg N ha}^{-1} \text{ yr}^{-1}$.

Climate data description

We compiled climate data (average annual mean temperature and average annual precipitation) for each plot using bi-linear interpolation of the 800m resolution PRISM climate data (<http://www.prism.oregonstate.edu/>). We downloaded annual

data for the period from the earliest to the latest census in the plot dataset, and then for each plot did the bi-linear interpolation using only data from the specific years between the two censuses at that plot. Average annual mean temperature ranged from 1-16°C, and average annual precipitation ranged from 750 to 2000 mm yr⁻¹.

Species level analysis methods

We tested a suite of alternate regression models to predict annual aboveground C increment (CI, in units of kg C yr⁻¹) of each of the 24 most common species in our dataset. The basic form of the model included terms for potential C increment (PCI) at optimal tree size, climate and N deposition, and multipliers that reduce potential C increment as a function of sub-optimal tree size, climate (mean annual temperature and precipitation during the specific census interval for a given plot), and nitrogen deposition:

$$CI = PCI \times \text{Size effect} \times \text{Climate effect} \times \text{Nitrogen effect} \quad (\text{Equation 1})$$

We modeled the size effect as a power law function of biomass at the first measurement period.

We modeled the nitrogen effect using a simple lognormal function that allows a range of response shapes, including a monotonic increase, a monotonic decrease, and humped responses.

$$\text{Nitrogen effect} = e^{-0.5 \left(\frac{\ln(\text{Nitrogen Deposition}/n_1)}{n_2} \right)^2} \quad (\text{Equation 2})$$

We used model selection to determine the climate variables and their functional form to include in the climate term (see below). We first determined the best model for annual mean temperature choosing among power, lognormal and logistic forms. The precipitation response was modeled using a lognormal function. The climate effect included the best model of annual mean temperature and precipitation, either one alone, or neither. The error term was normally distributed, but with a variance proportional to the mean, so the error was modeled as

$$\varepsilon = N(0, \sigma^2), \sigma = \alpha \hat{y}^\beta \quad (\text{Equation 3})$$

Where \hat{y} is the predicted value for an observation, and α and β were estimated parameters. We solved for the maximum likelihood estimates for model parameters using simulated annealing, a global parameter optimization procedure, with 50,000 iterations. We assessed the model fit for growth using two metrics: the slope of the relationship between predicted and observed, and R^2 . The Akaike Information Criterion (AIC; Burnham and Anderson 2002) was used to select the most parsimonious model (i.e., the best model fit for the fewest parameters). In particular, we used AIC to assess whether incorporating the term for N deposition improved models that predicted growth as function of tree size and climate.

Survival was modeled using a similar approach, but with a form of logistic regression in which the probability of 5 yr survival was modeled as function of a potential survival rate (PSR), and the effects of size, climate, and nitrogen deposition, with a lognormal nitrogen response (as in Equation 2) and a climate response as described above. The size effect was modeled as a lognormal function of biomass at first measurement period.

Survival = PSR \times Size effect \times Climate effect \times Nitrogen effect (Equation 4)

Since the response variable is categorical (a tree either lived or died), and the model is already probabilistic ($0 < \text{survival} < 1$), the likelihood function for the model was simply:

$$\log \text{likelihood} = \sum_{i=1}^n \left\{ \begin{array}{ll} \log(\hat{s}_i) & \text{if the individual lived} \\ \log(1 - \hat{s}_i) & \text{if the individual died} \end{array} \right\} \quad (\text{Equation 5})$$

Where \hat{s}_i was the predicted probability of survival of the i^{th} individual. We assessed the fit of the mortality model by grouping the trees into survival classes based on the predicted survival (0-10%, 10-20%, etc.) and calculating the observed survival in each group.

For growth and survival analyses, if AIC supported the inclusion of N deposition in the model, we used the estimated parameters to investigate the response of growth to N deposition. The relationship between N deposition and growth was plotted using annual mean temperature and precipitation for plots with the particular species present, and a tree size of 250 kg aboveground carbon.

Tree-level response to climate

We determined the climate response for growth and survival in Equation 1 and 4:

$$\text{CI} = \text{PCI} \times \text{Size effect} \times \text{Temperature effect} \times \text{Precipitation effect} \quad (\text{Equation 6})$$

The following is a description of the process used to determine the climate response. The “potential” was a single parameter. The size effect was a power function in the

growth analysis (Equation 7a) and a lognormal function in the survival analysis (Equation 7b):

$$\text{Size effect} = B^{b_0} \quad (\text{Equation 7a})$$

$$\text{Size effect} = e^{-0.5 \left(\frac{\ln(B)/b_0}{b_1} \right)^2} \quad (\text{Equation 7b})$$

The climate effect was determined by using AIC to compare variations of SI equation 1 with mean annual temperature (T) and mean annual precipitation (P), only mean annual temperature, only mean annual precipitation, and neither mean annual temperature nor precipitation. The temperature effect was one of three equations and AIC was used to select for the best form

$$\text{Temperature effect} = T^{t_0} \quad (\text{Equation 8a})$$

$$\text{Temperature effect} = \frac{1}{1 + \left(\frac{T}{t_1} \right)^{t_0}} \quad (\text{Equation 8b})$$

$$\text{Temperature effect} = e^{-0.5 \left(\frac{\ln(T/t_0)}{t_1} \right)^2} \quad (\text{Equation 8c})$$

Finally, the precipitation effect was modeled using the lognormal equation:

$$\text{Precipitation effect} = e^{-0.5 \left(\frac{\ln(P/p_0)}{p_1} \right)^2} \quad (\text{Equation 9})$$

The parameter estimates for the growth and survival analyses are presented in Supplementary Information Table 4 and 5.

Plot level response

We assessed whether a model that predicts plot-level aboveground C increment over the remeasurement period as a function of climate (annual mean temperature and precipitation) and stand C at the time of the first measurement period was improved by adding nitrogen deposition as an additional term. We used a functional form similar to equation (1) but with an intercept. The functional form included a lognormal size effect, a power function for the terms for annual mean temperature and precipitation, and equation (2) for the nitrogen effect. We used plot aboveground C at the first measurement period as the independent variable for the size effect. We used a normal distribution to describe the error distribution. We solved for the maximum likelihood estimates for the parameters using a simulated annealing algorithm with 50,000 iterations. AIC was used to select between the most parsimonious of the models that either included or omitted effects of N deposition. If the most parsimonious model included N deposition, we plotted C increment as a function of N deposition, holding annual temperature (8.8°C), annual precipitation (1123 mm yr^{-1}), and plot carbon stock (57 t C ha^{-1}) at the first measurement period constant at their mean values. See supporting information for parameter estimates (Supporting Information Table 3).

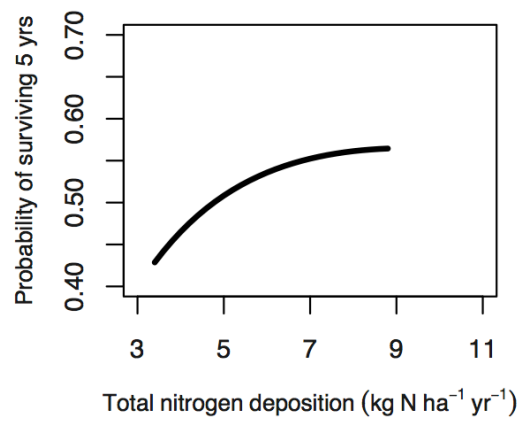
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Supplementary Information Figure 1. The 5-year survival rate for *Abies balsamea* as a function of total (wet + dry) inorganic N deposition. The curve was plotted using annual mean temperature and precipitation for plots with *A. balsamea* present, and a tree size of 250 kg aboveground carbon.

Supplementary Information Table 1. A list of the states, their census periods, and whether it was included in the species- and stand-level analysis or only the species-level analysis.

State	Census Interval	Years between measurements	Analysis that includes the state
Connecticut	1985-1998	13.7	both
Delaware	1986-1999	13.1	both
Illinois	1986-1998	12.8	species only
Indiana	1985-1997	11.4	species only
Kentucky	1988-2000	13.8	species only
Massachusetts	1985-1998	13.8	both
Maryland	1986-1999	14.1	both
Maine	1982-1995	14.1	both
Michigan	1981-1993	13.1	species only
New Hampshire	1983-1997	13.8	both
New Jersey	1987-1999	11.9	both
New York	1980-1993	13.6	both
Ohio	1979-1991	12.6	both
Pennsylvania	1978-1989	12.5	both
Rhode Island	1985-1998	14.3	both
Virginia	1990-2000	8.3	species only
Vermont	1983-1997	14.4	both
Wisconsin	1983-1995	12.3	species only
West Virginia	1989-2001	12.6	both

Supplementary Information Table 2. Coefficients used to calculate aboveground biomass for individual trees of each species (from Jenkins et al. 2003). Component ID: 2 = Whole tree, aboveground; 3 = Whole tree, above stump. Equation form ID: 1 = $\log_{10} \text{biomass} = a + b * (\log_{10}(\text{dia}^c))$; 2 = $\ln \text{biomass} = a + b * \text{dia} * c (\ln(\text{dia}^d))$; 4 = $\text{biomass} = a + b * \text{dia} + c * (\text{dia}^d)$.

Species	Component ID	Equation Form ID	a	b	c	d	Diameter	Units biomass
abba	2	2	-1.8337	0.0000	2.1283	1.0000	d.b.h. (cm)	kg
acru	2	1	-1.06	2.574	1		d.b.h. (cm)	kg
acsa	2	2	-2.192	-0.011	2.67	1	d.b.h. (cm)	kg
beal	2	1	2.1047	2.4417	1		d.b.h. (cm)	g
bele	2	1	-1.248	2.726	1		d.b.h. (cm)	kg
bepa	2	2	-2.2308	0	2.4313	1	d.b.h. (cm)	kg
cagl	2	1	-1.326	2.762	1		d.b.h. (cm)	kg
fagr	2	1	2.1112	2.462	1		d.b.h. (cm)	g
fram	3	4	3.2031	-0.2337	0.006061	2	d.b.h. (mm)	kg
litu	2	1	-1.236	2.635	1		d.b.h. (cm)	kg
pire	2	2	-2.4684	0	2.3503	1	d.b.h. (cm)	kg
piru	2	2	-1.7957	0	2.2417	1	d.b.h. (cm)	kg
pist	2	2	5.2831	0	2.0369	1	d.b.h. (cm)	g
pogr	2	2	-2.32	0	2.3773	1	d.b.h. (cm)	kg
potr	2	2	-2.6224	0	2.4827	1	d.b.h. (cm)	kg
prse	2	1	-1.247	2.663	1		d.b.h. (cm)	kg
qual	2	1	-1.266	2.613	1		d.b.h. (cm)	kg
quco	2	1	-1.283	2.685	1		d.b.h. (cm)	kg
qupr	2	1	-1.587	2.91	1		d.b.h. (cm)	kg
quru	2	1	-1.259	2.644	1		d.b.h. (cm)	kg
quve	3	2	-	0	2.65803	1	d.b.h. (in)	kg
thoc	2	4	0	0	0.1148	2.1439	d.b.h. (cm)	kg

tiam	2	1	-1.247	2.663	1		d.b.h. (cm)	kg
tsca	3	2	0.6803	0	2.3617	1	d.b.h. (in)	lb

Supplementary Information Table 3. Parameter estimates and 2-unit support intervals for the plot-level analysis. The size1 and size2 parameters are synonymous to the n1 and n2 parameters in equation 2. The temp1 and precip2 parameters refer to the exponent in the mean annual temperature and mean annual precipitation power function, respectively. These parameters yield an output in units of annual aboveground biomass increment (divide output by 2 for units in carbon).

Plot-level response variable	Disturbance exclusion	Intercept	PCI	size1	size2	temp1	precip1	n1	n2
Surviving tree growth	none	0.52 (0.47-0.58)	14.66 (14.51-14.86)	10000.00 (9800-1000)	2.53 (2.53-2.53)	0.41 (0.41-0.42)	-0.09 (-0.10--0.08)	1000.00 (950.00-1000.00)	4.13 (4.09-4.18)
Net annual aboveground carbon increment	>50% net biomass lost	1.58 (1.50-1.66)	0.66 (0.63-0.70)	9999 (9099-1000)	2.46 (2.43-2.50)	1.30 (1.28-1.32)	0.45 (1.28-1.32)	917.42 (834.85-990.82)	2.68 (2.65-2.73)
Net annual aboveground carbon increment	none	2.33 (2.23-2.44)	-100 (-100- -85.92)	10000 (9900-1000)	0.54 (0.54-0.54)	-7.28 (-7.28- -7.15)	10 (10-10)	5.39 (5.39-5.39)	0.04 (0.04-0.04)

Supplementary Information Table 4. Model detail, maximum likelihood estimates and 2-unit support intervals (below, MLEs, in parentheses) for the best models (delta AIC = 0 in Table 2) for biomass increment as a function of tree size, temperature, precipitation, and nitrogen deposition.

Species	Acronym	Sample Size	R ²	Temp Effect	Temp Form (Eqn. 3)	Precip Effect	Nitrogen Effect	Mean Temp (°C)	Mean Precip (dm)	Mean Nitrogen (kg ha ⁻¹ yr ⁻¹)
<i>Abies balsamea</i>	Abba	2587	0.22	Y	Lognormal	Y	Y	4.63	9.98	5.39
<i>Acer rubrum</i>	Acru	20819	0.49	Y	Logistic	Y	Y	8.02	10.58	7.09
<i>Acer saccharum</i>	Acsa	17051	0.35	Y	Logistic	Y	Y	7.51	10.02	6.91
<i>Betula alleghaniensis</i>	Beal	3114	0.25			Y		5.63	10.39	6.20
<i>Betula lenta</i>	Bele	2553	0.47	Y	Logistic			8.76	11.26	7.61
<i>Betula papyrifera</i>	Bepa	3257	0.26	Y	Logistic			5.45	9.68	5.99
<i>Carya glabra</i>	Caga	2311	0.55				Y	12.47	11.48	7.36
<i>Fagus grandifolia</i>	Fagr	5760	0.59	Y	Logistic	Y		8.63	11.01	7.26
<i>Fraxinus americana</i>	Fram	5690	0.50	Y	Logistic	Y	Y	9.74	10.66	7.63
<i>Liriodendron tulipifera</i>	Litu	5680	0.56	Y	Logistic	Y	Y	11.77	11.29	7.46
<i>Pinus resinosa</i>	Pire	3206	0.31	Y	Logistic	Y	Y	6.48	8.65	7.17
<i>Picea rubens</i>	Piru	2303	0.26	Y	Lognormal		Y	4.98	11.46	5.00

<i>Pinus strobus</i>	Pist	7423	0.32			Y	Y	7.50	10.51	6.29
<i>Populus grandidentata</i>	Pogr	2492	0.34	Y	Logistic	Y		7.49	9.32	7.20
<i>Populus tremuloides</i>	Potr	3507	0.39			Y	Y	5.65	8.66	6.35
<i>Prunus serotina</i>	Prse	5749	0.54	Y	Logistic	Y	Y	8.76	10.55	7.84
<i>Quercus alba</i>	Qual	10941	0.66	Y	Logistic	Y		10.83	10.80	7.54
<i>Quercus coccinea</i>	Quco	1915	0.63	Y	Logistic	Y	Y	10.96	11.32	7.07
<i>Quercus prinus</i>	Qupr	6973	0.62	Y	Logistic	Y		10.35	11.14	7.57
<i>Quercus rubra</i>	Quru	10653	0.66	Y	Logistic		Y	8.86	10.51	7.37
<i>Quercus velutina</i>	Quve	6254	0.61	Y	Logistic	Y		10.65	10.71	7.51
<i>Thuja occidentalis</i>	Thoc	5857	0.31	Y	Logistic	Y	Y	5.36	8.48	5.92
<i>Tilia americana</i>	Tiam	3050	0.48	Y	Logistic			7.21	9.27	7.11
<i>Tsuga canadensis</i>	Tsca	7186	0.47	Y	Logistic			6.91	10.64	6.67

Supplementary Information Table 4. Continued, parameter estimates and uncertainty.

	Eqn. 1	Size Parameter (SI Eqn. 7a)	Temperature Parameters (Eqns. 8a-8c)		Precipitation Parameters (Eqn. 9)		Nitrogen Parameters (Eqn. 2)		Variance Parameters (Eqn. 3)	
Species	<i>Potential</i>	b ₀	t ₀	t ₁	p ₀	p ₁	n ₀	n ₁	a	β
<i>Abies balsamea</i>	66.67 (65.34 - 68.00)	0.59 (0.55 - 0.63)	10000.00 (9900.00 - 10000.00)	1.76 (1.76 - 1.76)	10.45 (10.34 - 10.55)	0.40 (0.38 - 0.42)	150.00 (144.00 - 150.00)	2.70 (2.67 - 2.73)	1.00 (0.97 - 1.02)	0.66 (0.63 - 0.68)
<i>Acer rubrum</i>	8.09 (8.09 - 8.09)	0.71 (0.71 - 0.71)	-25.16 (-25.54 - - 24.81)	303.44 (303.44 - 303.44)	8.25 (8.17 - 8.25)	0.67 (0.65 - 0.68)	150.00 (148.50 - 150.00)	3.11 (3.11 - 3.11)	0.77 (0.77 - 0.78)	0.89 (0.88 - 0.89)
<i>Acer saccharum</i>	18.08 (18.08 - 18.08)	0.54 (0.54 - 0.54)	-13.51 (-13.69 - - 13.33)	342.90 (342.90 - 342.90)	3.95 (3.87 - 4.03)	1.68 (1.64 - 1.72)	149.80 (145.29 - 150.00)	3.60 (3.56 - 3.63)	0.75 (0.74 - 0.76)	0.81 (0.80 - 0.81)
<i>Betula alleghaniensis</i>	0.46 (0.46 - 0.47)	0.51 (0.50 - 0.52)			11.45 (11.22 - 11.85)	0.65 (0.59 - 0.71)			0.76 (0.74 - 0.78)	0.90 (0.85 - 0.94)
<i>Betula lenta</i>	0.89 (0.87 - 0.90)	0.59 (0.58 - 0.60)	-39.88 (-43.92 - - 35.23)	277.94 (277.94 - 277.94)					0.63 (0.62 - 0.64)	0.83 (0.78 - 0.87)
<i>Betula papyrifera</i>	0.35 (0.35 - 0.36)	0.59 (0.58 - 0.61)	-61.09 (-67.49 - - 56.66)	271.85(2 71.85 - 271.85)					0.66 (0.65 - 0.67)	0.80 (0.78 - 0.82)
<i>Carya glabra</i>	0.49 (0.49 - 0.50)	0.79 (0.78 - 0.79)					9.25 (8.79 - 9.62)	0.77 (0.69 - 0.95)	0.63 (0.62 - 0.65)	0.77 (0.73 - 0.79)
<i>Fagus grandifolia</i>	2.68 (2.65 - 2.71)	0.62 (0.62 - 0.63)	-29.77 (-32.54 - - 27.41)	278.02 (278.02 - 278.02)	0.07 (0.06 - 0.07)	3.52 (3.52 - 3.52)			0.67 (0.66 - 0.68)	0.81 (0.80 - 0.83)
<i>Fraxinus americana</i>	1.69 (1.67 -	0.57 (0.56 -	1000.00 (30.00 -	333.36 (290.03 -	9.93 (9.82 -	0.43 (0.41 -	148.20 (145.23 -	2.30 (2.30 -	0.65 (0.64 -	0.68 (0.66 -

	1.71)	0.58)	1000.00)	100000.0 0)	10.03)	0.48)	150.00)	2.30)	0.65)	0.70)
<i>Liriodendron tulipifera</i>	5.52 (5.47 - 5.58)	0.58 (0.57 - 0.59)	526.43 (2.18 - 1000.00)	95805.73 (958.06 - 100000.0 0)	2.67 (2.64 - 2.70)	1.31 (1.30 - 1.33)	65.84 (65.18 - 66.50)	1.58 (1.58 - 1.58)	0.97 (0.96 - 0.98)	0.56 (0.55 - 0.57)
<i>Pinus resinosa</i>	1.60 (1.57 - 1.62)	0.44 (0.43 - 0.46)	-999.18 (-1000.00 - 9689)	0.00 (0.001 - 276.83)	8.66 (8.57 - 8.74)	0.31 (0.29 - 0.33)	0.62 (0.60 - 0.62)	1.65 (1.64 - 1.65)	0.59 (0.57 - 0.60)	0.86 (0.83 - 0.89)
<i>Picea rubens</i>	973.88 (954.41 - 1000.00)	0.65 (0.63 - 0.67)	10000.00 (10000.00 - 10000.00)	0.88 (0.88 - 0.88)			5.18 (4.97 - 5.34)	1.90 (1.71 - 2.14)	0.63 (0.61 - 0.65)	0.79 (0.76 - 0.81)
<i>Pinus strobus</i>	0.69 (0.68 - 0.70)	0.54 (0.52 - 0.55)			785.26 (698.88 - 887.35)	6.34 (6.21 - 6.47)	149.69 (122.75 - 150.00)	7.01 (6.59 - 7.47)	0.59 (0.58 - 0.59)	0.57 (0.55 - 0.60)
<i>Populus grandidentata</i>	6.10 (5.99 - 6.22)	0.54 (0.52 - 0.56)	-11.80 (-12.05 - -11.54)	330.80 (330.80 - 330.80)	143.56 (127.77 - 160.69)	4.08 (3.92 - 4.25)			0.59 (0.58 - 0.60)	0.81 (0.74 - 0.86)
<i>Populus tremuloides</i>	0.88 (0.87 - 0.89)	0.54 (0.53 - 0.56)			58.34 (54.84 - 62.11)	2.73 (2.64 - 2.81)	7.09 (6.74 - 7.53)	0.93 (0.82 - 1.07)	0.58 (0.57 - 0.59)	0.72 (0.67 - 0.76)
<i>Prunus serotina</i>	307.06 (303.99 - 310.13)	0.67 (0.67 - 0.68)	-11.80 (-11.95 - - 11.64)	425.51 (425.52 - 425.51)	10.40 (10.29 - 10.50)	0.35 (0.33 - 0.37)	150.00 (147.00 - 150.00)	2.04 (2.04 - 2.04)	0.75 (0.74 - 0.76)	0.82 (0.79 - 0.83)
<i>Quercus alba</i>	11.07 (10.95 - 11.07)	0.73 (0.73 - 0.73)	-17.65 (-17.93 - - 17.39)	319.71 (319.71 - 319.71)	0.92 (0.91 - 0.93)	1.79 (1.79 - 1.79)			0.68 (0.68 - 0.69)	0.68 (0.67 - 0.69)
<i>Quercus coccinea</i>	15.65 (15.49 - 16.00)	0.71 (0.71 - 0.72)	-11.65 (-11.91 - - 11.35)	332.60 (332.60 - 332.60)	0.43 (0.42 - 0.44)	2.26 (2.260 - 2.28)	7.76 (7.68 - 7.84)	0.36 (0.34 - 0.39)	0.64 (0.63 - 0.66)	0.80 (0.77 - 0.83)
<i>Quercus prinus</i>	26.70 (26.44 - 26.97)	0.72 (0.72 - 0.72)	-27.59 (-27.97 - -27.23)	319.01 (319.01 - 319.01)	945.12 (916.77 - 982.93)	3.83 (3.83 - 3.83)			0.59 (0.58 - 0.60)	0.90 (0.88 - 0.92)
<i>Quercus</i>	3.90	0.69	-16.86	293.26			150.00	2.77	0.67	0.77

<i>rubra</i>	(3.86 - 3.90)	(0.69 - 0.69)	(-17.40 - - 16.37)	(293.26 - 293.26)			(147.00 - 150.00)	(2.77 - 2.77)	(0.67 - 0.68)	(0.76 - 0.77)
<i>Quercus velutina</i>	1.05 (1.04 - 1.06)	0.65 (0.66 - 0.65)	-90.62 (-96.08 - - 84.33)	278.72 (278.72 - 278.72)	9.65 (9.56 - 9.75)	0.39 (0.37 - 0.41)			0.84 (0.83 - 0.85)	0.65 (0.63 - 0.65)
<i>Thuja occidentali s</i>	16.77 (16.60 - 16.96)	0.65 (0.64 - 0.67)	-1.21 (-1.23 - - 1.19)	1312.05 (1298.93 - 1325.17)	9.37 (9.28 - 9.46)	0.45 (0.41 - 0.50)	5.32 (5.21 - 5.43)	0.62 (0.59 - 0.67)	0.78 (0.77 - 0.79)	0.81 (0.78 - 0.83)
<i>Tilia americana</i>	7.72 (7.61 - 7.88)	0.65 (0.65 - 0.66)	-15.51 (-15.80 - - 15.22)	332.53 (332.53 - 332.53)					0.80 (0.78 - 0.81)	0.81 (0.78 - 0.84)
<i>Tsuga canadensis</i>	3.69 (3.65 - 3.72)	0.65 (0.65 - 0.66)	-16.08 (-16.34 - - 15.80)	319.18 (319.18 - 319.18)					0.60 (0.59 - 0.60)	0.70 (0.68 - 0.72)

NOTES ON PARAMETER RESCALING: To improve the efficiency and accuracy of parameter estimation with the global optimization routine, several of the independent variables were rescaled for the purposes of fitting the models. Figures in the paper have been displayed in more traditional units of degrees C, mm precipitation, and size in K. Temperature is in units of degrees Kelvin (i.e. degrees C + 273.15) . Precipitation is in units of dm (i.e. mm/100). Initial Tree Size is in units of hundreds of kg (i.e. kg/100). Mean temperature (degrees C), precipitation (dm) and N deposition (kg/ha/yr) are also reported - these are the means across all of the plots in which a species was present, and were used in displaying the curves in Figures 1-3

Supplementary Information Table 5. Model detail, maximum likelihood estimates and 2-unit support intervals (below MLEs, in parentheses) for the best models (delta AIC = 0 in Table 2) for survival as a function of tree size, temperature, precipitation, and nitrogen deposition.

Species	Acronym	Sample Size	Temp Effect	Temp Form (Eqn. 3)	Precip Effect	Nitrogen Effect	Mean Temp (°C)	Mean Precip (dm)	Mean Nitrogen (kg ha ⁻¹ yr ⁻¹)
<i>Abies balsamea</i>	Abba	5650			Y	Y	4.63	9.98	5.39
<i>Acer rubrum</i>	Acru	23047			Y	Y	8.02	10.58	7.09
<i>Acer saccharum</i>	Acsa	18480			Y		7.51	10.02	6.91
<i>Betula alleghaniensis</i>	Beal	3889				Y	5.63	10.39	6.20
<i>Betula lenta</i>	Bele	2895					8.76	11.26	7.61
<i>Betula papyrifera</i>	Bepa	4393	Y	Lognormal	Y	Y	5.45	9.68	5.99
<i>Carya glabra</i>	Caga	2554					12.47	11.48	7.36
<i>Fagus grandifolia</i>	Fagr	6697	Y	Lognormal	Y		8.63	11.01	7.26
<i>Fraxinus americana</i>	Fram	6538	Y	Lognormal			9.74	10.66	7.63
<i>Liriodendron tulipifera</i>	Litu	6179	Y	Lognormal			11.77	11.29	7.46
<i>Pinus resinosa</i>	Pire	3333			Y		6.48	8.65	7.17
<i>Picea rubens</i>	Piru	2930	Y	Lognormal			4.98	11.46	5.00
<i>Pinus strobus</i>	Pist	8272	Y	Lognormal		Y	7.50	10.51	6.29
<i>Populus grandidentata</i>	Pogr	3233			Y	Y	7.49	9.32	7.20

<i>Populus tremuloides</i>	Potr	5462			Y	Y	5.65	8.66	6.35
<i>Prunus serotina</i>	Prse	6585	Y	Lognormal		Y	8.76	10.55	7.84
<i>Quercus alba</i>	Qual	12130	Y	Lognormal	Y		10.83	10.80	7.54
<i>Quercus coccinea</i>	Quco	2406			Y	Y	10.96	11.32	7.07
<i>Quercus prinus</i>	Qupr	8318	Y	Logistic		Y	10.35	11.14	7.57
<i>Quercus rubra</i>	Quru	11861	Y	Lognormal		Y	8.86	10.51	7.37
<i>Quercus velutina</i>	Quve	7328	Y	Lognormal			10.65	10.71	7.51
<i>Thuja occidentalis</i>	Thoc	6512			Y	Y	5.36	8.48	5.92
<i>Tilia americana</i>	Tiam	3450			Y	Y	7.21	9.27	7.11
<i>Tsuga canadensis</i>	Tsca	7676			Y		6.91	10.64	6.67

Supplementary Information Table 5. Continued, parameter estimates and uncertainty.

	Eqn. 4	Size Parameters (Eqn. 7b)		Temperature Parameters (Eqns. 8a - 3c)		Precipitation Parameters (Eqn. 9)		Nitrogen Parameters (Main text eqn. 2)	
Species	<i>Potential Survival</i> (/5 yr)	b_0	b_1	t_0	t_1	p_0	p_1	n_0	n_1
<i>Abies balsamea</i>	0.94 (0.93 - 0.94)	0.44 (0.40 - 0.48)	2.52 (2.34 - 2.69)			13.72 (13.44 - 14.25)	1.06 (1.00 - 1.13)	9.35 (9.17 - 9.64)	1.36 (1.31 - 1.42)
<i>Acer rubrum</i>	1.000 (1.00 - 1.00)	5.01 (4.46 - 5.71)	9.11 (8.39 - 9.80)			2.03 (1.93 - 2.09)	7.06 (6.84 - 7.19)	9.32 (8.20 - 11.01)	5.86 (4.57 - 7.51)
<i>Acer saccharum</i>	1.00 (1.00 - 1.00)	4.48 (4.06 - 5.01)	7.68 (7.22 - 8.35)			4.27 (4.14 - 4.40)	4.396 (4.26 - 4.57)		
<i>Betula alleghaniensis</i>	1.00 (1.00 - 1.00)	2.71 (2.14 - 3.34)	6.03 (5.31 - 7.03)					0.29 (0.25 - 0.33)	8.29 (7.96 - 8.65)
<i>Betula lenta</i>	0.97 (0.97 - 0.97)	4.15 (3.40 - 4.94)	5.75 (5.12 - 6.72)						
<i>Betula papyrifera</i>	1.00 (1.00 - 1.00)	1.90 (1.54 - 2.72)	5.64 (4.74 - 8.68)	9604.20 (0.00 - 10000.00)	763.06 (137.35 - 1000.00)	74.30 (68.36 - 79.86)	5.13 (4.98 - 5.33)	4.30 (4.13 - 4.63)	1.74 (1.58 - 2.04)
<i>Carya glabra</i>	0.97 (0.97 - 0.97)	2.89 (2.17 - 3.92)	7.58 (6.37 - 9.52)						
<i>Fagus grandifolia</i>	1.00 (1.00 - 1.00)	1.69 (1.32 - 1.99)	9.19 (8.27 - 9.79)	283.48 (283.48 - 283.48)	0.06 (0.06 - 0.06)	1.50 (1.28 - 1.80)	10.25 (9.43 - 11.14)		

<i>Fraxinus americana</i>	1.00 (1.00 - 1.00)	6.104 (5.19 - 7.16)	6.48 (5.83 - 7.34)	266.49 (266.49 - 266.49)	0.21 (0.20 - 0.22)				
<i>Liriodendron tulipifera</i>	0.99 (0.99 - 0.99)	14.23 (12.38 - 17.59)	8.93 (8.04 - 9.41)	283.96 (283.96 - 283.96)	0.08 (0.06 - 0.12)				
<i>Pinus resinosa</i>	1.00 (1.00 - 1.00)	1.46 (1.07 - 2.22)	11.47 (9.41 - 20.37)			7.82 (7.58 - 8.17)	1.32 (1.16 - 1.54)		
<i>Picea rubens</i>	1.00 (1.00 - 1.00)	2.11 (1.75 - 2.53)	4.35 (3.70 - 5.28)	289.45 (289.45 - 289.45)	0.11 (0.10 - 0.11)				
<i>Pinus strobus</i>	1.00 (1.00 - 1.00)	3.36 (3.09 - 4.09)	6.85 (6.10 - 7.25)	291.42 (291.42 - 291.42)	0.18 (0.16 - 0.18)			6.40 (5.50 - 7.84)	3.57 (2.28 - 5.83)
<i>Populus grandidentata</i>	1.00 (1.00 - 1.00)	3.51 (2.78 - 4.54)	5.71 (4.91 - 6.96)			3.87 (3.63 - 4.06)	2.70 (2.54 - 2.89)	3.54 (3.26 - 3.83)	2.91 (2.62 - 3.26)
<i>Populus tremuloides</i>	0.92 (0.92 - 0.92)	3.37 (2.16 - 4.47)	6.83 (5.67 - 9.08)			22.93 (19.95 - 25.81)	4.11 (3.70 - 4.79)	2.05 (1.90 - 2.25)	3.53 (3.32 - 3.84)
<i>Prunus serotina</i>	0.98 (0.98 - 0.98)	15.91 (13.20 - 19.26)	9.92 (9.23 - 10.72)	280.70 (280.7 - 280.7)	0.05 (0.05 - 0.06)			8.37 (7.53 - 8.82)	1.76 (1.48 - 2.72)
<i>Quercus alba</i>	1.00 (1.00 - 1.00)	8.27 (7.61 - 9.26)	7.10 (6.74 - 7.44)	300.48 (297.47 - 300.48)	0.54 (0.48 - 0.71)	5.56 (5.39 - 5.87)	3.85 (3.65 - 4.16)		
<i>Quercus coccinea</i>	1.00 (1.00 - 1.00)	3.88 (2.56 - 6.11)	7.63 (5.88 - 11.20)			31.91 (28.40 - 34.80)	3.71 (3.45 - 4.18)	3.96 (3.77 - 4.23)	2.15 (1.98 - 2.44)
<i>Quercus prinus</i>	1.00 (1.00 - 1.00)	5.94 (4.81 - 6.85)	7.21 (6.70 - 8.14)	291.71 (291.71 - 291.71)	0.11 (0.10 - 0.11)			4.70 (4.46 - 4.93)	2.63 (2.37 - 2.94)
<i>Quercus rubra</i>	1.00 (1.00 - 1.00)	6.07 (5.52 - 6.61)	7.03 (6.61 - 7.44)	275.98 (275.98 - 275.98)	0.12 (0.11 - 0.13)			3.04 (2.80 - 3.28)	6.61 (6.01 - 7.21)

	1.00)	6.86)	7.63)	275.98)	0.13)			3.43)	7.60)
<i>Quercus velutina</i>	1.00 (1.00 - 1.00)	9.40 (8.37 - 11.28)	6.46 (5.81 - 6.85)	217.72 (215.54 - 219.89)	0.90 (0.87 - 0.93)				
<i>Thuja occidentalis</i>	0.98 (0.98 - 0.98)	0.24 (0.19 - 0.33)	10.79 (9.50 - 12.68)			7.45 (7.30 - 7.72)	1.24 (1.13 - 1.39)		
<i>Tilia americana</i>	1.00 (1.00 - 1.00)	4.73 (4.07 - 5.57)	5.56 (4.90 - 6.07)			7.94 (6.28 - 10.48)	3.33 (1.83 - 8.98)	1.09 (0.89 - 1.22)	8.18 (7.36 - 8.66)
<i>Tsuga Canadensis</i>	1.00 (0.99 - 1.00)	2.31 (1.92 - 2.85)	8.81 (7.75 - 10.48)			89.30 (78.59 - 102.95)	11.85 (11.14 - 12.64)		

CHAPTER 2

GLOBAL PATTERNS OF NITROGEN LIMITATION: CONFRONTING TWO GLOBAL BIOGEOCHEMICAL MODELS WITH OBSERVATIONS¹

Abstract

Predictions of climate change using biogeochemical models coupled to climate models depend on accurately modeling the feedbacks among the carbon (C) cycle, nitrogen (N) cycle, and climate system. To explore why C-N-climate feedbacks vary considerably among models and how they compare to field observations, we initiated a model inter-comparison that assessed the consequences of sustained N additions in a set of global N fertilization simulations. Here, we present results from two global biogeochemical models (CLM-CN and O-CN) that use different approaches to modeling C-N interactions. On the global scale, the CLM-CN was substantially more nitrogen limited than the O-CN. By comparing to nitrogen fertilization experiments in temperate and boreal forests, we showed that the aboveground primary productivity in the CLM-CN and O-CN were 82% more responsive and 75% less responsive to nitrogen fertilization than observations, respectively. The most striking difference between the two models occurred in humid tropical forests, where the CLM-CN

¹A version of this chapter is in preparation for submission to the journal *Global Change Biology*: Thomas, R. Q., S. Zaehle, P. M. Templer, and C. L. Goodale. Global patterns of nitrogen limitation: Confronting two global biogeochemical models with observations.

predicted a 62% increase in primary productivity at the highest N addition level, while the O-CN predicted a 2% decrease in primary productivity due to N fertilization increasing plant respiration. Despite the low response to nitrogen fertilization, the O-CN model accurately simulated the ecosystem retention of N and the fate of added nitrogen to vegetation and soil when compared to ^{15}N tracer studies. In contrast, the CLM-CN predicted lower N retention and partitioned more losses of N as gas than observed in small catchment N budgets. The substantial differences in N limitation suggest that previously reported N limitation of CO_2 fertilization is too strong in the CLM-CN and too weak in the O-CN. Overall, this study is the first to explicitly benchmark C and N interactions in Earth System models using multiple types of observational data, provides a foundation for future inter-comparisons, and helps identify field observation and experiment needs.

1. Introduction

Biogeochemical cycling on the land surface directly influences global climate by controlling greenhouse gas concentrations in the atmosphere (Denman et al. 2007). Consequently, land surface representations of Earth System models have included the carbon (C) cycle (Friedlingstein et al. 2006) and increasingly, also the nitrogen (N) cycle (Sokolov et al. 2008, Thornton et al. 2009, Zaehle and Friend 2010). Models with both the C and N cycles have shown that N availability limits the capacity of many terrestrial ecosystems to store C (Sokolov et al. 2008, Jain et al. 2009, Thornton et al. 2009, Zaehle et al. 2010b, Zaehle and Dalmonech 2011).

The control of the land C cycle by N availability in model simulations reflects

what has long been established in the ecosystem research community: C and N cycles are tightly coupled in most terrestrial ecosystems. N limitation of primary productivity is widespread (Vitousek and Howarth 1991, LeBauer and Treseder 2008). In temperate and boreal regions, N enrichment from several different sources can increase plant growth, including atmospheric N deposition (Magnani et al. 2007, de Vries et al. 2009, Thomas et al. 2010), accelerated N mineralization by warming soil (Melillo et al. 2011), and experimental N additions (LeBauer and Treseder 2008). N limitation can also constrain net primary productivity responses to elevated atmospheric CO₂ (Oren et al. 2001, Norby et al. 2010) due to progressive N limitation (Luo et al. 2004). Therefore, predictions of climate change are sensitive to processes that govern coupled C and N cycling (Thornton et al. 2009).

Recently developed global biogeochemical models with coupled C and N cycles have produced a range of predictions describing how the N cycle impacts the C cycle and climate (Sokolov et al. 2008, Jain et al. 2009, Thornton et al. 2009, Zaehle et al. 2010b). Differing predictions of C-N feedbacks among models reflect their divergent approaches to modeling C and N interactions (Zaehle and Dalmonech 2011). Fundamental processes that govern C-N coupling vary among models, including the incorporation of flexible C:N ratios in vegetation and soils, competition between plants and microbes for mineral N, the process of N fixation, and controls on N export (Jain et al. 2009, Thornton et al. 2009, Gerber et al. 2010, Zaehle et al. 2010b). Furthermore, even processes that are generally similar among models use different methods for simulating the processes, especially for decomposition of detritus and plant uptake of N (Jain et al. 2009, Thornton et al. 2009, Gerber et al. 2010, Zaehle et

al. 2010b). Given the range of approaches to modeling C and N interactions in global biogeochemical cycles and the increasing number of global biogeochemical models coupled to climate models, there is a need for a systematic data-model comparison, such as the one we present here, that tests the strengths and weaknesses of each model against globally distributed observational data.

The disparate approaches to modeling C-N interactions, described briefly above, prevent the use of a common metric of N limitation to compare across models from existing global simulations. Instead, we used perturbation simulations with N additions to directly test N limitation in the models and compared the response of the modeled productivity to a database of field studies. There is a wealth of field studies examining N limitation and N cycling, especially in temperate and boreal ecosystems, that allow for globally distributed assessment of model predictions of N limitation. However, such assessments require not only N fertilization experiments to test plant responses to increased N uptake, but also additional data to examine the mechanisms governing N limitation (i.e., the fate of added N and processes that control N loss).

Here, we use a series of recent syntheses of N fertilization experiments, ¹⁵N tracer studies, and catchment N budgets, described in detail below, to benchmark global biogeochemical models and diagnose differences in model responses to perturbations to the N cycle. Specifically, we assessed model predictions of N limitation using a series of global N fertilization simulations, designed to span a range of N responses from small changes in N inputs associated with low-levels of anthropogenic N deposition to large changes associated with field-based N fertilization experiments. Our framework for model benchmarking provides an

extension of previous data-model comparison (or benchmarking) that has focused on the C cycle (e.g., Schimel et al. 1997, Randerson et al. 2009), but thus far has not focused on the N cycle and C-N interactions. We present results from two global biogeochemical models coupled to climate models: the Community Land Model – CN (Thornton et al. 2007, 2009) and the O-CN (Zaehle et al. 2010a, Zaehle and Friend 2010), models that have contrasting approaches to modeling C-N interactions. Based on our data-model comparison, we aim to identify why and how they arrive at contrasting responses to perturbation of the N cycle, highlight key areas for future model improvements, offer suggestions for future field experiments that can improve model evaluation, and provide insight into the mechanisms that control the simulated responses to CO₂ fertilization and N deposition.

2. Methods

The sections below describe the two models used in this study (CLM-CN and O-CN), the global N fertilization simulation protocol, the observational datasets, and data-model comparison procedure.

2.1 CLM-CN model

The CLM-CN 4.0 model is the land surface model within the Community Earth System Model (release 1.0) (Thornton and Rosenbloom 2005, Thornton et al. 2007, and Thornton et al. 2009). The model uses fully prognostic terrestrial C and N cycles calculated on a 30-minute time step. N and C are cycled through the following pools: 1) three litter pools, based on the chemical composition of the inputs (e.g.,

labile, cellulose, lignin pools), with stoichiometry that varies with the stoichiometry of litter inputs and different decomposition rates, 2) one coarse woody debris pool with constant stoichiometry, 3) four soil organic matter pools with differing decomposition rates and with C:N ratios that vary by pool but are constant over time, and 4) six vegetation pools (leaves, live stem, dead stem, live coarse roots, dead coarse roots, and fine roots) with time-invariant C:N ratios that differ by pool and among plant functional types. All plant functional types within a grid cell share the same soil environment. Plant uptake of N directly depends on the demand set by gross primary productivity. Microbial uptake of N is a function of the decomposition rate, C use efficiency, and the difference between the C:N ratio of the donor and receiving pool, based on the Biome-BGC model (Thornton et al. 2002, Thornton and Rosenbloom 2005). When the demand for N by both the microbes and vegetation exceeds the available inorganic N pool, both GPP and decomposition rates are reduced in proportion to their N demand relative to total N demand so that total N demand matches available N. All C and N uptake and competition occurs at the 30-minute time step. Allocation of C and N among plant tissues is based on fixed allocation ratios, with one exception: the ratio of stem allocation to leaf allocation increases with NPP. Leaf area is determined through the balance between C allocation and turnover through litter fall or fire. N inputs into the CLM-CN include N deposition and N fixation. N fixation is calculated as a saturating relationship with annual NPP, based on Cleveland et al. (1999) and varies over time and space. N outputs include hydrologic N leaching, N gas production calculated as a proportion of net mineralization, N gas production when N availability exceeds plant and microbial

demand, N volatilization by fire, and N removal during harvesting. As a community land model, the CLM-CN is continually undergoing model development. In this study we use the most recently released version (v. 4.0) that corresponds to the version used in published studies that report on C-N interactions (Thornton et al. 2009). It also corresponds to the version that will be used in the Intergovernmental Panel on Climate Change fifth assessment report. It does not include model modifications to how the CLM-CN simulates the scaling of radiative transfer and leaf photosynthesis, as described in Bonan et al. (2011, 2012), although we discuss below the potential implications of these modifications on the results described in this study.

2.2 O-CN model

Like the CLM-CN, O-CN has fully prognostic C and N cycles and is described in more detail in Zaehle and Friend (2010), Zaehle et al. (2010a) and Zaehle et al. (2011). In the O-CN model, C and N cycle through the following pools: 1) four litter pools (above- and below-ground metabolic and structural), 2) two coarse woody debris pools, 3) four soil pools (surface, active, slow, and passive), and 4) nine vegetation pools. The soil organic dynamics are based on the Century approach (Parton et al. 1993). All pools have variable C-N ratios. The C-N ratio in the vegetation depends on the balance of labile C to labile N, and all of the C:N ratios in the vegetation pools vary in proportion to variation in foliar C:N ratios. Foliar C:N ratios determine how GPP is influenced by N availability (i.e., increasing GPP with increasing foliar N). N uptake by vegetation is a function of the availability of inorganic N, root C, plant N demand, and the abiotic environment. As labile N builds

up relative to labile C, root uptake of N is reduced. Each plant functional type within a grid cell has a unique soil environment. Microbial uptake of N is based on the Century model (Parton et al. 1993) and depends on the decomposition rate, C:N ratio of the donor and receiving pools, and inorganic N availability. Soil organic matter has a flexible stoichiometry that depends on inorganic N concentrations in the soil. When plant and microbial demand for N exceeds inorganic N availability, N is first allocated to microbes, and plants receive the remaining N in excess of microbial demand. The allocation of C and N to plant tissues varies in the O-CN as a function of the labile C and N ratios, with the allocation to fine roots increasing with N stress. The allocation to leaves depends on the pipe-model theory (Shinozaki et al. 1964, Zaehle et al. 2006), resulting in a theoretical maximum leaf area index (LAI) based on the light environment. N inputs into the O-CN include N deposition and N fixation, with the latter a prescribed input that varies over space but not time and is based on the relationship between evapotranspiration and N fixation (Cleveland et al. 1999). N export includes N leaching, gaseous emissions, and harvesting. Gaseous emissions are based on the LPJ-DyN simplification of the DNDC model (Xu-Ri and Prentice 2008) and depend on the availability of nitrate, soil organic C, and soil water (Zaehle et al. 2011).

2.3 Model simulations

We used a series of N fertilization simulations to predict the globally distributed response of terrestrial ecosystems to increased N inputs and thereby to assess the nature of N limitation and how NPP saturates with elevated N inputs in each

model. Our control simulations build off the “Trendy” model inter-comparison protocol (Sitch et al. 2008, Le Quere et al. 2009), where each model simulates trends in ecosystem dynamics from an assumed steady-state using common climate drivers (1901-2009, CRU-NCEPv4, <http://dods.extra.cea.fr/data/p529viov/cruncep/>) and with transient land-use, N deposition, and atmospheric CO₂. Branching off from this control run, we performed five N addition simulations which added N to all global land surfaces at different rates (0.5, 2.0, 4.0, 10.0, and 30.0 g N m⁻² yr⁻¹, respectively) for 25 years (1985-2009). Together, the 0.5 – 30.0 g N m⁻² yr⁻¹ created a response function to N addition and tested where N saturation occurred. N was added to the N deposition input field as 50% NH₄⁺ and 50% NO₃⁻ and was distributed evenly throughout the year. The CLM-CN model was run at 0.5° x 0.5° resolution using half-hourly climate inputs. The O-CN model was run at 2.5° x 3.75° resolution using monthly climate inputs, disaggregated to half-hourly values using a weather generator (Zaehle et al. 2010a). N deposition inputs included in CLM-CN were based on Lamarque et al. (2005) and the inputs used in the O-CN were from TM5 (Dentener et al. 2006). Both models required initial conditions to start the 1860-2009 transient simulations. We simulated the initial conditions by spinning up each model to approximate steady-state in 1860, using 1860 N deposition rates, 1860 atmospheric CO₂, and repeatedly cycling through the climate data from 1901 to 1920 in lieu of having 1860 climate data.

2.4 Field observations and model comparison

The model simulations were compared to three sets of observations that included N fertilization experiments, ^{15}N tracer studies, and small catchment N budgets. The observations represented 296 studies from 237 sites distributed globally. The majority of the sites were in the Northeastern U.S. and Western Europe (Figure 1), both regions with a history of elevated N deposition, with few sites in the tropics. Figure 1 shows the locations of the data used for the model-data comparison. Some additional observations were available but were not used because they did not have a corresponding grid-cell in both models (e.g., the coarse-resolution of the O-CN model excludes the Hawaiian islands, where several N fertilization experiments have occurred).

2.4.1 N Fertilization Experiments

We used observations of net primary production responses to N additions in grasslands and in temperate and boreal forests. The N addition rates ranged from 2.5 - 57.2 g N m⁻² yr⁻¹ over 1-6 years in the grassland studies and from 0.9 – 15.0 g N m⁻² yr⁻¹ over 2 - 30 years in the forest studies. The grassland data were obtained from the meta-analysis by LeBauer and Treseder (2008) and included 39 N fertilization experiments. The forest data were assembled through a literature review and included only experiments with multiple years of N addition (≥ 2 years), had a fertilization treatment that included N alone, and that reported a measure of production (NPP, ANPP, volume production, or basal area increment). We included all fertilization dosages at a single site if available, and excluded studies that only reported litterfall.

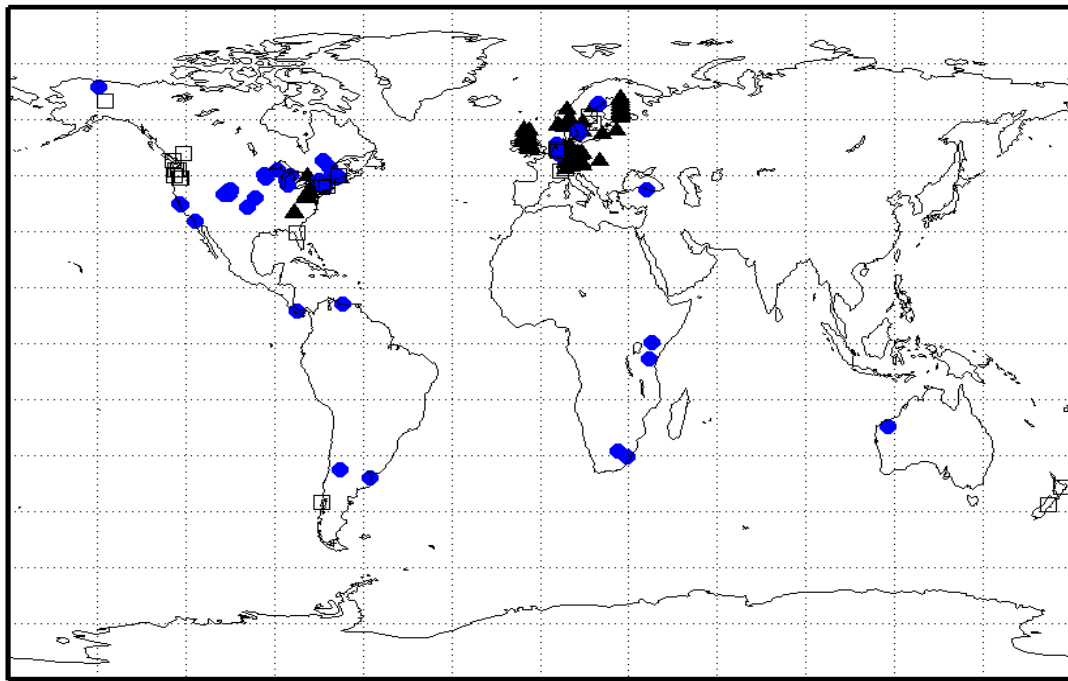


Figure 1: A map of the nitrogen fertilization experiments (circles), ^{15}N tracer studies (squares), and small catchment nitrogen budgets (triangles) used in the model-data comparison.

We also excluded studies if the N fertilization plots grew slower than the control plots to avoid including harmful effects of soil acidification that can be associated with fertilization studies (e.g., Magill et al. 2004); we discuss the implications of excluding the studies with negative growth responses below. A total of 32 experiments in forest ecosystems were used, all in temperate and boreal forests. Data on primary production responses to N fertilization were limited in the tropics, especially outside the Hawaiian Islands, and as a result, we excluded the few tropical sites from this analysis. Information on the forest sites included in the analysis is in Supplemental Information Table 1 and information on sites not included in the analysis is in Supplemental Information Table 2.

To compare measured N responses to model simulations, we used the percentage change of aboveground net primary productivity (ANPP) between the N addition and control treatment. Within each model output, we located the grid cell that contained the field observations and calculated the ANPP response for corresponding plant functional type (i.e., grass, temperate deciduous broadleaf, or needleleaf evergreen) and the simulation with the dosage that best corresponded to the field experiment. The model NPP response was calculated for the same time duration of the field observations. In the model, we began all fertilization experiments in 1985; experimental initiation in the field ranged from 1971 to 2004. We describe the responses of GPP, NPP, foliar C:N ratio, plant N content, and LAI responses to N fertilization for temperate broadleaf and boreal needle leaf forests separately.

2.4.2 ¹⁵N Tracer Studies

The application and recovery of isotopically labeled N to ecosystems examines the fate of N added to the ecosystem (Nadelhoffer et al. 1999, Templer et al. 2012). In a typical experiment, a low dosage of N highly enriched in ¹⁵N is applied to the soil surface. Ecosystem pools (i.e., soil, litter, wood, leaves, roots, etc.) are then sampled following the N addition. When all pools are measured, the total amount of added ¹⁵N that is recovered corresponds to the N retention in the ecosystem. Consequently, the fate of the recovered ¹⁵N in plant and soil pools can be used to infer the impact of added N on C cycling (e.g., Nadelhoffer et al. 1999).

In this study, we used results from a recent meta-analysis of ¹⁵N tracer studies in temperate and boreal forests (Templer et al. 2012). The meta-analysis reported the recovery of ¹⁵N in soil (the sum of litter, organic soil, and mineral soil) and vegetation (foliage, branches, stem, fine root, coarse roots, and total plant). Not all ecosystem components were sampled in each study; the number of studies with data on ¹⁵N recovery in vegetation, soil, and total ecosystem were 18, 17, and 16, respectively. Here, we only use data for studies that report recovery between 3 months and 2 years following ¹⁵N addition to test the initial fate of added N in the models. We only included studies with ambient N inputs (e.g., no ¹⁵N tracer additions to N fertilization studies).

Neither of the global models simulated redistribution of tracer ¹⁵N or natural ¹⁵N fractionation processes. In lieu of directly simulated ¹⁵N in the two models, we used the ecosystem retention and fate of added N in the N fertilization simulations. We used the 0.5 g N m⁻² yr⁻¹ simulation to represent ambient N deposition (non-

fertilized) ^{15}N tracer studies. The fertilization effects within the first 2 years in the $0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ simulations were minimal, suggesting that it was appropriate to match predictions from the $0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ simulations to data from the non-fertilized ^{15}N field studies. The total ecosystem retention of added N and the recovery in soil and vegetation were calculated for each grid cell that contained the plot locations of a ^{15}N study. For sites where only a subset of the ecosystem components were measured or ecosystem retention was measured but not divided into components, the model-data comparison only included the measured components. Because different components were measured at different sites, it is possible for the sum of the mean percent recovery and retention to exceed 100%.

2.4.3 Small-catchment N budgets

In addition to ^{15}N tracer studies, small catchment N input/output budgets can be used as a measure of ecosystem N retention (Aber et al. 2003, MacDonald et al. 2002). We used data that described the percentage of N deposition lost through leaching from a recent meta-analysis that included 209 sites across the northeastern U.S., Western-Central Europe, and Scandinavia (see Aber et al. (2003), MacDonald et al. (2002), and Goodale (personal communication) for more information on the N budget data). The N budgets measured N deposition inputs into small catchments and N exports through the leaching of dissolved inorganic and organic N. As most data on N inputs and exports in forests were from upland (i.e., well-drained) ecosystems with no symbiotic N-fixing species present, it is assumed that inputs through N fixation were minimal. N losses through denitrification were recognized, but rarely if ever

quantified at annual timescales or large spatial scales. The small catchment studies were included because they describe the percentage of N deposition that is lost through leaching and help elucidate the partitioning of N losses in models.

We used results from the control simulations (no N added other than N deposition) to compare to the catchment observations. For each model grid cell that contained a field observation, we calculated the ratio of N leaching to N deposition. The mean ratio of leaching to deposition across all sites was compared to the observations using a standard t-test. Based on the leaching loss results described below, we also ran a simulation in the O-CN without transient N deposition (1860-2009) to isolate the contribution of N deposition to the leaching losses. We used this additional simulation to subtract the background leaching due to excess N fixation from the total leaching losses.

3. Results and Discussion

The CLM-CN and the O-CN had the same mean global terrestrial NPP (1985-2009) in the control simulation of 50 Pg C yr^{-1} , but the models had key spatial differences. In the tropical latitudes, NPP was higher in the CLM-CN than the O-CN model (Figure 2ab). In contrast, the high latitudes and Western Europe had higher NPP in the O-CN than the CLM-CN model (Figure 2ab).

The NPP response to N fertilization indicates that the CLM-CN model was more N-limited than the O-CN model. Furthermore, the spatial patterns and magnitude of the NPP response to N fertilization differed substantially between

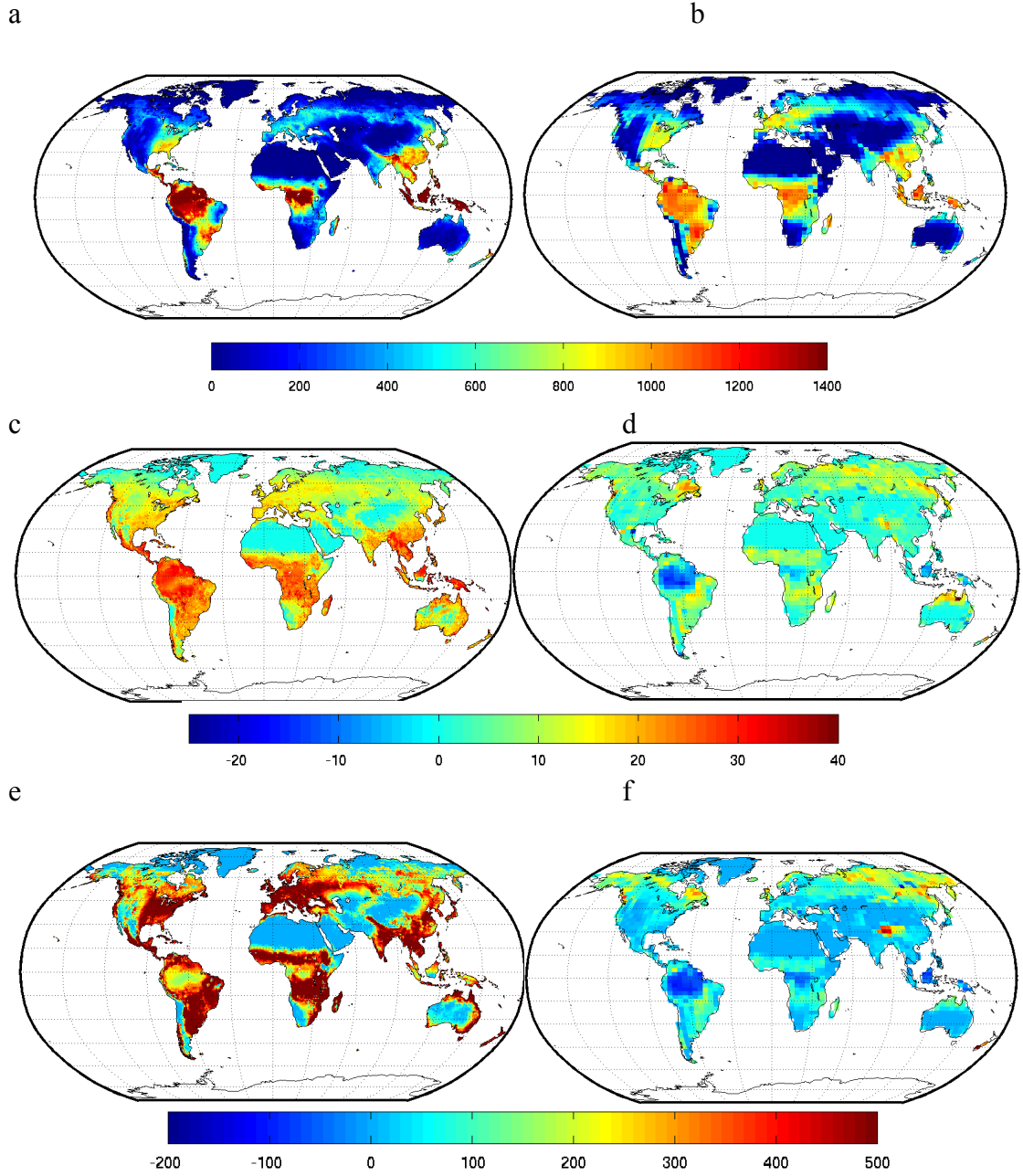


Figure 2: Geographically explicit NPP (1985-2009) in the CLM-CN (a,c,e) and O-CN (b,d,f). The control experiments without nitrogen added (a,b), the 0.5 g N m⁻² yr⁻¹ experiment (c,d), and the 30 g N m⁻² yr⁻¹ (e,f) are shown. All values are g C m⁻² yr⁻¹.

models (Figure 2cd). In the global low fertilization simulations ($0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$), the absolute increase of 25-yr mean NPP in response to N fertilization in the CLM-CN was largest across all tropical ecosystems, especially the humid tropics (Figure 2c). At the highest N fertilization level simulation ($30 \text{ g N m}^{-2} \text{ yr}^{-1}$), the NPP increase in the CLM-CN was largest in temperate forests and dry tropical forests (Figure 2f). In tropical, mid-latitude and high latitude forests, NPP response to N fertilization in the CLM-CN did not saturate within the set of N fertilization rates used in the study ($0 - 30 \text{ g N m}^{-2} \text{ yr}^{-1}$; Figure 3a). While the absolute increase in NPP from N fertilization was largest in tropical regions in the CLM-CN (Figure 3a), the enhancement of NPP in response to fertilization in forest ecosystems was highest in mid- and high- latitude forests, due to lower productivity in the control simulations (Figure 3b).

In contrast to the CLM-CN, the 25-yr mean NPP in the O-CN model had the largest NPP response to N fertilization in the high latitude and dry tropical regions (figure 1df). In the O-CN, the humid tropical regions (a highly responsive region in the CLM-CN) had lower NPP in the N fertilization simulations than in the control simulations. The NPP response to N fertilization in mid-latitude forests saturated between 0 and $10 \text{ g N m}^{-2} \text{ yr}^{-1}$, while high latitude forests continued to exhibit increasing NPP in the $30 \text{ g N m}^{-2} \text{ yr}^{-1}$ simulation (Figure 2a). The O-CN model predicted similar spatial patterns for both absolute and relative NPP responses to N addition (O-CN NPP response: boreal forests > temperate forests > tropical forests: Figure 2b).

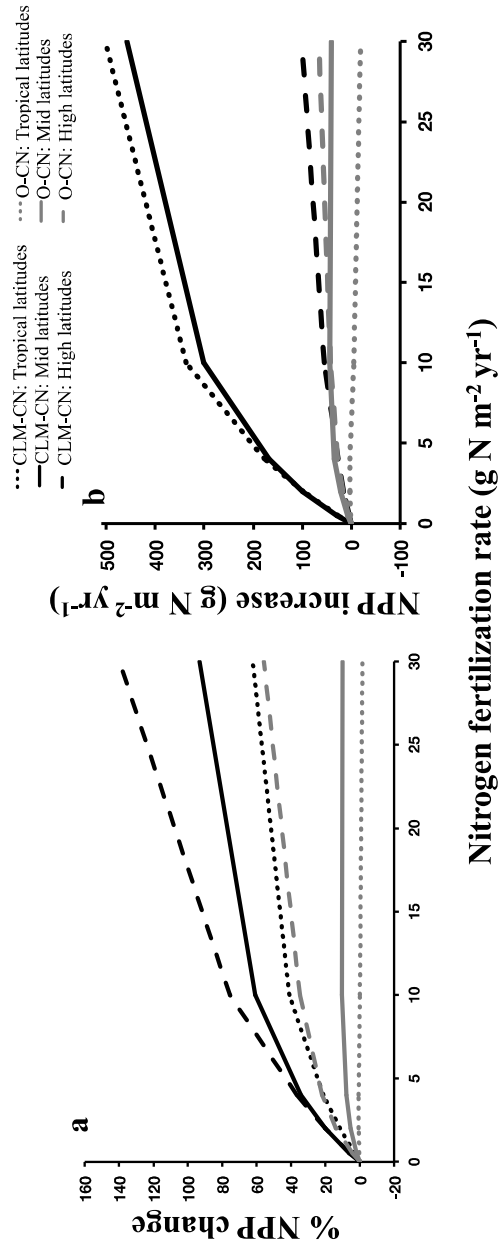


Figure 3: NPP responses to nitrogen fertilization for the CLM-CN (gray solid lines) and the O-CN (black dashed lines). The absolute increase (a) and the relative increase (b) of NPP in response to the 5 levels of nitrogen fertilization are shown for low latitude ($< |23^\circ|$; triangles), mid-latitude ($> |23^\circ|$ and $< |50^\circ|$; circles), and high latitude ($> |50^\circ|$; squares) forests.

In the N fertilization simulations, the most striking difference between the CLM-CN and O-CN in the NPP response to N addition occurred in humid tropical regions, where the two models predicted opposite responses to N fertilization. In the CLM-CN, high potential GPP and low N availability in the control simulations led to strong N limitation and a positive NPP response. In the O-CN, the control simulation was light-limited, so N fertilization did not increase photosynthesis. Rather, the extra N absorbed into plant tissue in the N fertilization simulations contributed to higher respiration, decreasing the NPP response.

Unfortunately, the availability of N fertilization field experiments in mature lowland tropical rainforest is limited, thus precluding our ability to systemically compare model predictions to observations. For example, a meta-analysis describing global patterns of nitrogen limitation only included three non-Hawaiian tropical nitrogen fertilization studies and none specifically reporting NPP responses (LeBauer and Treseder 2008). However, two recent N fertilization studies have found little evidence of limitation by N alone in lowland tropical forests (Cusack et al. 2011; Wright et al. 2011) with one of the two studies suggesting co-limitation with potassium (Wright et al. 2011). Overall, understanding limitations on forest growth in the humid tropics is critical, as N deposition is expected to increase in tropical regions over the next century (Galloway et al. 2004), and tropical forests are predicted to be large C sinks (Pan et al. 2011). Future research studying the limitations to lowland tropical rainforest productivity is necessary, especially N fertilization studies with plot sizes adequate to robustly measure NPP (see Wright et al. 2011) and total plant respiration response to N addition.

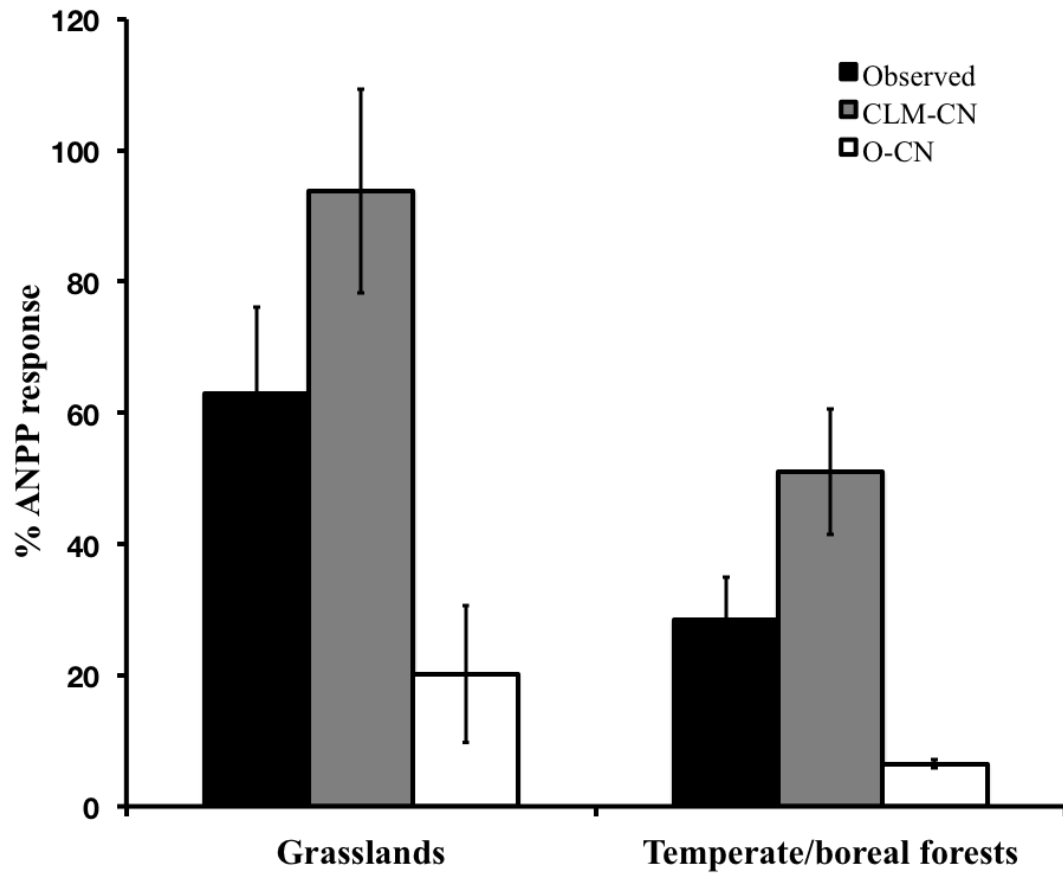


Figure 4: Aboveground net primary productivity response to nitrogen fertilization t in grassland ($n = 39$) and temperate and boreal forests ($n = 32$). The observations are from the set of nitrogen fertilization experiments and the model response is from the grid cells that contain field experiments. The model fertilization matched the duration and magnitude of nitrogen fertilization in the field experiment.

Table 1. Model predictions of carbon and nitrogen cycle responses to nitrogen fertilization. The values are 25-year mean for the grid-cells that contain field nitrogen fertilization experiments. See Supplemental Information Table 1 for the nitrogen fertilization input levels and timing.

Model (Treatment)	GPP	NPP	ANPP	ANPP/ NPP	Foliar C:N	Vegetation N	LAI
<i>Broadleaf temperate</i> <i>n = 10</i>							
CLM-CN (control)	974 (142)	553 (94)	328 (63)	0.59	25 (0)	40.8 (6.9)	4.9 (0.7)
CLM-CN (fertilized)	1197 (116)	705 (79)	399 (53)	0.57	25 (0)	43.9 (6.6)	5.6 (0.7)
O-CN (control)	1435 (168)	736 (56)	457 (43)	0.62	28.9 (1.8)	72.2 (10.3)	4.6 (0.3)
O-CN (fertilized)	1501 (163)	774 (52)	488 (40)	0.63	27.1 (1.8)	73.7 (10.2)	4.8 (0.3)
<i>Needle leaf boreal</i> <i>n = 22</i>							
CLM-CN (control)	1181 (428)	294 (156)	177 (97)	0.60	39.2 (1.7)	28.2 (11)	4.2 (1.5)
CLM-CN (fertilized)	1480 (375)	407 (163)	258 (108)	0.63	39.2(1.7)	32.9 (10)	5.2 (1.2)
O-CN (control)	1405(226)	808 (77)	456 (61)	0.56	48.3 (4.0)	45.0 (10)	5.2 (0.4)
O-CN (fertilized)	1466 (207)	838 (67)	485 (52)	0.58	44.7(3.4)	47.2(10)	5.3 (0.3)

The observed ANPP increase in N fertilization experiments for thirty-nine grassland and thirty-two temperate/boreal forests sites was $60 \pm 13\%$ and $28 \pm 7\%$, respectively. The CLM-CN predicted larger increases in ANPP than observed in N fertilization experiments, simulating $94 \pm 16\%$ and $51 \pm 10\%$ increases in ANPP at the grassland and temperate/boreal forest sites, respectively. In contrast, the O-CN model predicted lower ANPP response to N fertilization than observed in grassland ($20 \pm 10\%$) and temperate/boreal forests ($7 \pm 1\%$).

For the boreal and temperate forest sites with N fertilization experiments, both models predicted an increase in gross primary productivity, net primary productivity, and LAI that paralleled the increase in ANPP (Table 1). However, the GPP, NPP, and ANPP in the control simulations were lower in broadleaf forests in the CLM-CN than the O-CN (Table 1). In the O-CN, the N fertilization treatments had slightly lower foliar C:N ratios than the control treatments, while the CLM-CN was not designed to simulate dynamic foliar C:N ratios (Table 1). Total plant N increased with fertilization in both models for both temperate and boreal forests (Table 1). However, the CLM-CN had less total N in plant tissue than the O-CN (Table 1).

3.1 CLM-CN

The large NPP response to N fertilization in the CLM-CN may partially be due to overly large partitioning of added N to plant tissues, as indicated by the comparison to ^{15}N tracer experiments (Figure 5). In eighteen ^{15}N tracer studies, $16 \pm 4\%$ of added

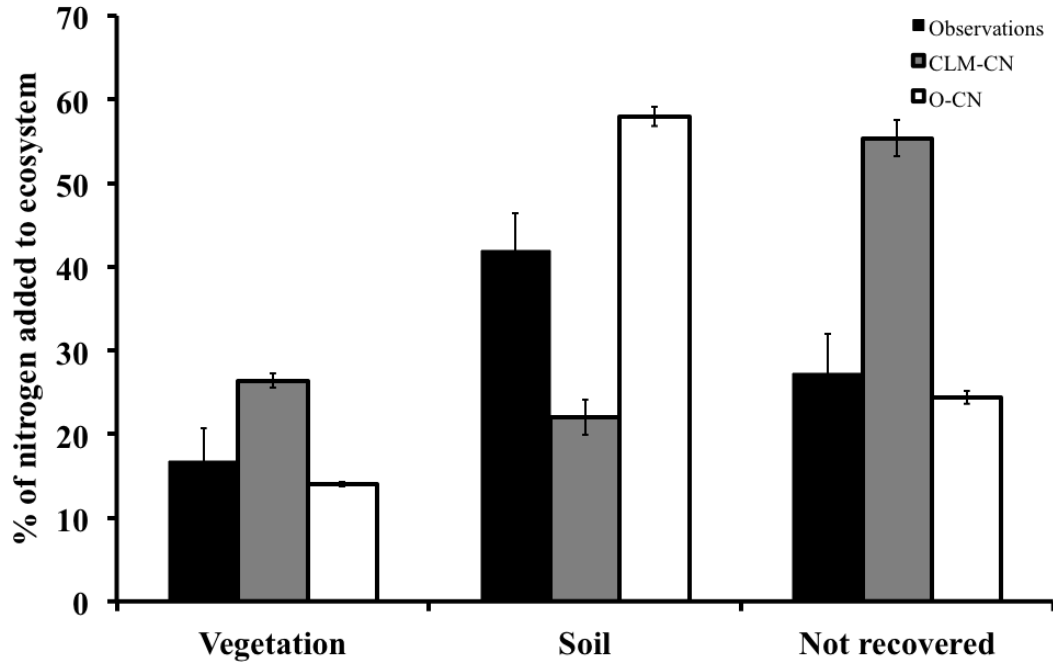


Figure 5: The short-term (1-3 year) fate of added nitrogen to soil organic matter, vegetation, and loss processes from the forest ecosystem. Observational data are from ^{15}N tracer studies in temperate and boreal forests. The model values represent the fate of nitrogen in the first 1-3 years of the $0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ nitrogen fertilization simulation. The model values correspond to the grid cells and duration of the ^{15}N tracer studies.

N was recovered in vegetation shortly after the tracer was added (3 month – 2 years) (Figure 5). In the CLM-CN simulations, $25 \pm 1\%$ of added N was accounted for in vegetation (Figure 5). However, another study that used the CLM-CN to investigate the multi-decadal fate of N deposition at a single site found less partitioning of added N to vegetation and more to soils than we report (Thornton et al. 2009). Different time scales (1-3 years in this study and decades in Thornton et al. (2009)), may explain the contrasting results, as the N initially taken up by vegetation cycles into the soil over time. Understanding what mechanisms govern the partitioning of added N, such as competition between plants and microbes for N and plant internal allocation of N, is important for further diagnosing the NPP response to N fertilization.

The large simulated N fertilization response may also be explained by erroneously high productivity when N is not limiting. In the case of the CLM-CN, especially in mesic temperate and boreal forests, the next most limiting resource after nitrogen is light. Therefore, accurately simulating canopy light use efficiency is critical for simulating NPP responses to nitrogen fertilization. Canopy light use efficiency and the photosynthetic rate of shaded leaves have known biases in the CLM-CN 4.0 and there is uncertainty associated with the values used for maximum leaf-level photosynthetic capacity (Bonan et al. 2011, 2012). Recent revisions to the photosynthetic parameterization in the CLM-CN reduced global estimates of GPP to values supported by observations from eddy flux towers and reduced the photosynthetic rates of shaded leaves (Bonan et al. 2011, 2012). The impacts of these changes on C-N interactions have not yet been investigated but are likely to reduce the

nitrogen fertilization response by decreasing non-N limited NPP, thus decreasing the response in fertilization simulations.

The CLM-CN not only has an overall large response to N fertilization, but it also continued to yield substantial NPP responses even at high fertilization inputs (30 g N m⁻² yr⁻¹), except in the humid tropics. Compared to ¹⁵N tracer studies, the persistence of N limitation even at high N inputs may be partially due to high N losses. Field observations from ¹⁵N tracer studies measured 73% retention of N deposition, while the CLM-CN, despite being strongly N-limited, only retained 45% of N deposition (Figure 5). The high N losses in the CLM-CN prevented the build-up of N in the ecosystem and maintained plant N limitation. Comparing against catchment N budgets further indicates that future versions of the CLM-CN should increase N retention processes, while also accounting for a stronger loss term associated with hydrologic processes. That is, hydrologic leaching amounted 40 ± 4% of N deposition measured at 209 temperate and boreal forest catchments, but was negligible (always <0.2%) in the CLM-CN (Figure 6). Without data on whole forest ecosystem N gas loss, it is difficult to test whether the N gas loss predictions are too high in the CLM-CN. However, increasing the hydrologic N losses in the CLM-CN requires either reducing the N gas losses or increasing the total N outputs, with the latter likely leading to even greater N limitation than currently predicted. Overall, improvements that increase N retention must be in parallel with improvements that decrease the potential (non-N-limited) GPP to prevent high and unrealistic fertilization responses to low N inputs.

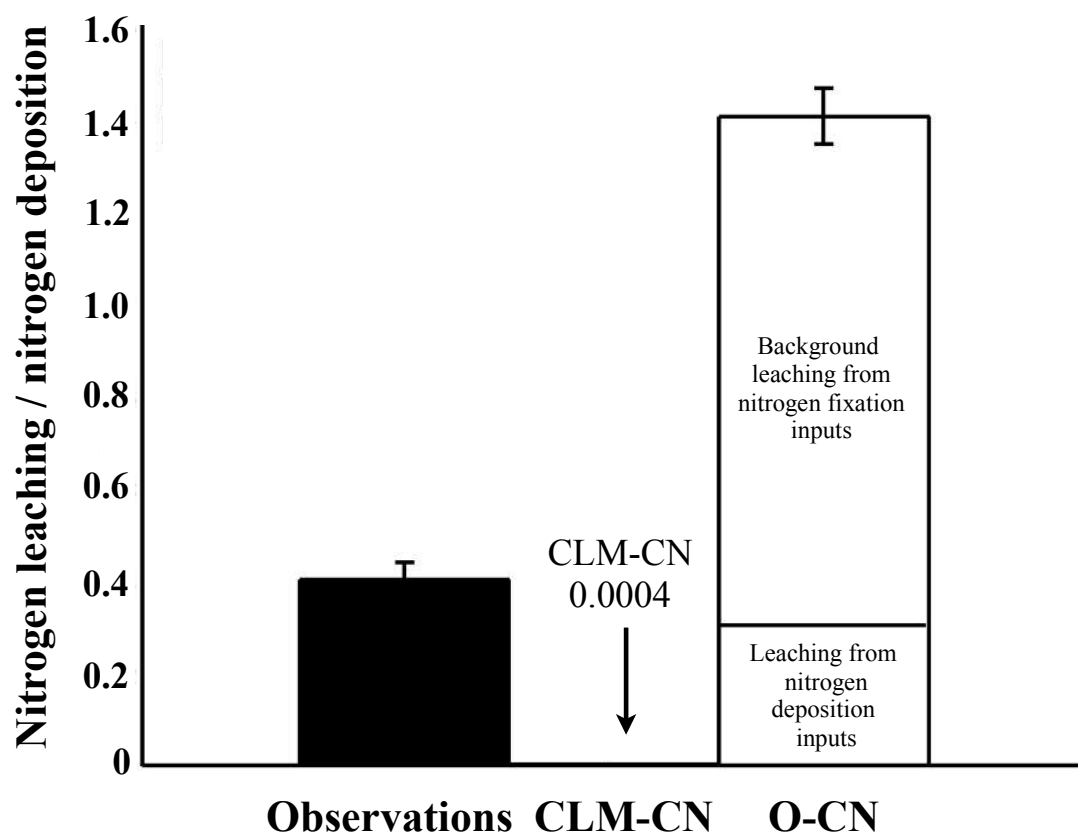


Figure 6: The proportion of nitrogen deposition lost through hydrologic leaching in observations of plot or small catchment nitrogen budgets in temperate and boreal forests and the corresponding grid cells in the CLM-CN and O-CN model. Model values are from the control simulation without nitrogen fertilization. Model values from the O-CN simulation where nitrogen deposition was held constant at 1860 levels is shown to isolate the leaching that is due to excess nitrogen fixation.

3.2 O-CN

In contrast to the high sensitivity to N additions in the CLM-CN, primary productivity in the O-CN model was relatively unresponsive to N addition. However, previous studies have reported that the C sequestration response to nitrogen deposition in the O-CN was 36 kg of C storage per kg N received in atmospheric deposition (range: 2 – 79 kg C kg N⁻¹) (Zaehle and Friend 2010), a response that compares well to observations (de Vries et al. 2009; Sutton et al. 2008). What can explain this apparent contradiction, i.e., a response to N fertilization that is lower than observations but good correspondence to observations that N deposition increases C sequestration? A simple explanation is that the ecosystem response to historical N deposition substantially reduced N limitation in the O-CN during the last decades of the 20th century. Consequently, ecosystems that were previously N-limited may now be limited by other resources, and thus have little capacity to respond to N fertilization.

The small NPP response to N fertilization in the O-CN also seems to contradict excellent correspondence of N retention between the O-CN and observational data from ¹⁵N tracer studies (Figure 5) and catchment N budgets (Figure 6). The O-CN model predicted that $76 \pm 1\%$ of added N was retained at the ≤ 3 year time scale, with the ¹⁵N tracer field studies measuring a $73 \pm 5\%$ retention of added N (Figure 5). Similarly, $30 \pm 6\%$ of N deposition was accounted for in hydrologic N losses from 209 temperate and boreal forest catchments in the O-CN, with $40 \pm 4\%$ of N deposition accounted for in observed N budgets. This high N retention in the O-CN would have led to the retention of historical N deposition and a substantial reduction of N limitation in previously N-limited ecosystems. Therefore, the ability of

N fertilization in the O-CN to further increase NPP depends the strength of limitation by the next most limiting resource (i.e., light or water). Reducing the strength of light or water limitation would likely increase the capacity of the O-CN to respond to N fertilization.

Another mechanism in the O-CN model that contributed to the low ANPP response to N addition was that the increase in the ratio of above- to belowground C allocation in response to N fertilization was too low. A larger shift of NPP from belowground to aboveground NPP would have increased the response of ANPP to N fertilization without requiring an additional increase in GPP. This mechanism is similar to observations from a set of N fertilization experiments across a climate gradient in Michigan, USA (Talhelm et al. 2011), which found that N fertilization increased ANPP, but did not increase leaf-level photosynthesis. The results indicated that the ANPP response was primarily due to a reallocation of NPP, rather than increased GPP. The O-CN model does include mechanisms through which elevated soil mineral N decreases the allocation of NPP to fine roots, and the ratio of ANPP to NPP did show a small increase in the simulated N fertilization experiments (Table 1). However, the mechanisms that govern dynamic NPP allocation in the O-CN model are probably too strongly buffered against changes in N availability. Global parameterization and applicability of the model may be setting limits to the plasticity of the allocation response to N fertilization.

The O-CN partitions most of the added N to soil organic matter ($58 \pm 1\%$; Figure 5), which exceeds the observations from the ^{15}N tracer studies ($42 \pm 4\%$). The retention of N in soil organic matter is due to processes associated with decomposition

(either due to increased litter N concentration or microbial N immobilization). The model does not include any explicit mechanism of abiotic N incorporation to soil organic matter (Davidson et al. 2003). In contrast, the CLM-CN retains little of the added N in soil. One primary difference in belowground N cycling between the CLM-CN and O-CN model is that the CLM-CN has constant soil organic matter C:N ratios while the O-CN model has soil organic matter C:N ratios that decrease with increasing soil N availability. The decreasing soil C:N ratios in the O-CN model can absorb additional N without requiring an increase in soil decomposition rates, thereby decreasing the N available for plants.

3.3. Implications

Here, we show that patterns of N limitation vary widely between two global biogeochemistry models that have contrasting approaches to representing C-N interactions. In particular, the CLM-CN was substantially more N limited than the O-CN and the N limitation in grassland and temperate/boreal forests from field observations was bounded by the two model predictions. These differences in N limitation provide a context for interpreting the projections of coupled terrestrial C and N cycles in these models.

First, the N limitation of CO₂ fertilization is likely too strong in the CLM-CN while the N limitation of CO₂ fertilization is too weak in the O-CN. This parallels previous simulations that reported that CO₂ fertilization between 1850 and 2100 was reduced by 74% in the CLM-CN (Thornton et al. 2007) and 50% in the O-CN (Zaehle et al. 2010b) when N limitation was included in the simulations.

Second, the results from our study also suggest that the C sequestration response to N deposition needs to be more closely evaluated in the models. In the O-CN, this study provides insight into predictions of carbon sequestration response to nitrogen deposition in the 21st century. As discussed above, the carbon sequestration response to historical (20th century) N deposition compares well to observations. However, the small response to fertilization in the O-CN demonstrated in this study indicates that N deposition to date has saturated the capacity to respond to additional N deposition unless environmental change (e.g., increased CO₂ and altered land use) induces greater N limitation. In contrast to the O-CN, the high N fertilization response in the CLM-CN could imply that the nitrogen deposition response is too high. However, low ecosystem retention of N deposition in the CLM-CN may balance or overcome the strong N limitation to yield realistic or even low predictions for C storage attributable to N deposition. An analysis of both N deposition and N fertilization responses in five temperate forest sites using the CLM-CN corroborates the high sensitivity to N fertilization and the low N retention in this study, while also showing that the CLM-CN is not sensitive enough to historical N deposition in temperate forests (See Chapter 3).

3.4 Building a foundation for future model-data comparisons

Overall, the combination of N fertilization experiments, ¹⁵N tracer studies, and catchment N budgets helped identify mechanisms for model improvement that would not have been possible with each dataset in isolation. The N fertilization data was the cornerstone dataset that specifically assessed the models' C-N interactions by testing

each model NPP response to N addition. However, the use of N fertilization experiments for such an evaluation is not without caveats.

In the field, N fertilization can cause soil acidification that reduces plant productivity (e.g., Hogberg et al. 2006, Wallace et al. 2007) via mechanisms not included in global biogeochemical models (e.g., base cation depletion). Therefore, caution should be used when examining the N response to fertilization. For the observations used in this study, soil acidification effects were likely minimal, as we intentionally excluded many N fertilization studies that reported harmful effects to vegetation. If we had included these studies, the observed NPP response to N fertilization would have been smaller, leading to a larger mismatch with CLM-CN simulations. The O-CN response would have compared better with observations, but the improved model predictions would have only been due to incorrectly representing the mechanisms that governed the low NPP response. Future N fertilization experiments aimed at helping improve global biogeochemical models should isolate the effects of N fertilization from acidification, while model applications should recognize the potential adverse consequences of excess N addition.

While the N fertilization experiments used in this study provided information on the NPP response to N addition, we used ^{15}N tracer studies to understand whether mismatched NPP responses were due to error in the partitioning of added N or error in the variability of plant tissue N concentrations. The ^{15}N data clearly demonstrated that the CLM-CN does not retain sufficient N in temperate and boreal ecosystems. Furthermore, comparing model predictions with small catchment N budgets showed that the CLM-CN underestimates hydrologic N losses and greatly overestimates N gas

loss. Overall, this model-data comparison demonstrates how multiple data sources can be used to isolate specific areas of model improvement in global land surface models.

We tried to minimize the effects of specific site conditions on the model-data comparison by pooling as many experiments as possible together and by comparing appropriate combinations of climate, N deposition, and levels of additional N input. However, the response of a particular ecosystem will always be affected by its initial state and history, requiring large sample sizes to develop a landscape- to regional-scale understanding of N limitation that is necessary to compare to global model simulations. A sample size of 32 forest sites is unlikely to be fully representative of the average temperate and boreal response at the biome level. There is an especially strong need for further experiments in under-sampled regions (e.g., tropical forests) to close gaps in the observational constraints of N limitation and N addition responses. Additionally, remote sensing of evapotranspiration and plant productivity may aid in scaling N limitation from plot-scale N fertilization studies to landscape, regional and global scales (Fisher et al. 2012).

Future N fertilization experiments will be important for informing global land surface models with C-N interactions, especially since differences between models were clear within the time-scale (~5 years) of a typical study (Supplemental Information Figure 1). Fertilization experiments with a relatively high addition rate may provide a measure of the non-N-limited NPP, while experiments with multiple fertilization dosages can further inform the slope of the N-NPP response, which is important to determine the trajectory of an ecosystem towards N saturation. However, the most informative experiments include measurements that isolate the specific

mechanisms that contribute to an observed NPP response to fertilization. For example, experiments should determine whether photosynthetic rates increased as a result of N additions. Talhelm et al. (2011) provide an example of how leaf-level photosynthesis measurements in N-fertilized plots show that ANPP response was due to reallocation of belowground C, rather than an increase in photosynthesis. Experiments that would be most helpful for the evaluation of N limitation in ecosystem models would include not only a measure of the response of aboveground productivity to N addition, but at the same time provide information about shifts in the total belowground C allocation (e.g., Janssens et al. 2010) and the fate of the added N in the ecosystem.

Beyond understanding whether or under which conditions GPP increases as a result of N fertilization, studies should establish whether C use efficiency changes as a result of fertilization. Assessing C use efficiency is especially important in humid tropical forests because the O-CN predicts that N fertilization increases respiration more than GPP, while the CLM-CN predicts a large increase in GPP and a smaller increase in respiration. Plant respiration is a function of tissue N concentrations in most land surface models (based on Ryan 1991). Accurately modeling the mechanisms that contribute to N fertilization requires understanding whether total N stocks in vegetation increase, whether respiration increases with greater N stocks, and whether the relationship between tissue N content and respiration changes as a result of N enrichment.

Most model-data comparisons that have systematically assessed the performance of terrestrial biosphere models have focused on water and C cycling (e.g.,

Schimel et al. 1997, Randerson et al. 2009). Here, we present the foundation for model-data comparisons that investigate C-N interactions and N cycling in global biogeochemical models. We propose that our approach to model-data comparisons, which uses three different sets of measurements (N fertilization experiments, ^{15}N tracer studies, and catchment N budgets), provides a novel and rigorous framework to assess the magnitude and mechanisms of N limitation in global biogeochemical models. Given the tight coupling of C-N dynamics and the control of N on C responses to climate, continued systematic evaluations of the nature of N limitation is vitally important across the new generation of global biogeochemical and Earth System models that include N dynamics.

5.0 Acknowledgements

We would like to thank Cayelan Carey, Timothy Fahey, and Natalie Mahowald for helpful comments on the manuscript. Sam Levis provided assistance with the CLM-CN simulations. National Science Foundation (NSF) awards to Christy Goodale and Peter Hess, the NSF IGERT in Cross-Scale Biogeochemistry and Climate, Cornell Biogeochemistry and Environmental Biocomplexity Small Grant Program, and the NSF INTERFACE Research Coordination Network financially supported the project. We would also like to thank the participants that the March 2011 INTERFACE meeting at Captiva Island for feedback on project development.

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SUPPLEMENTAL INFORMATION

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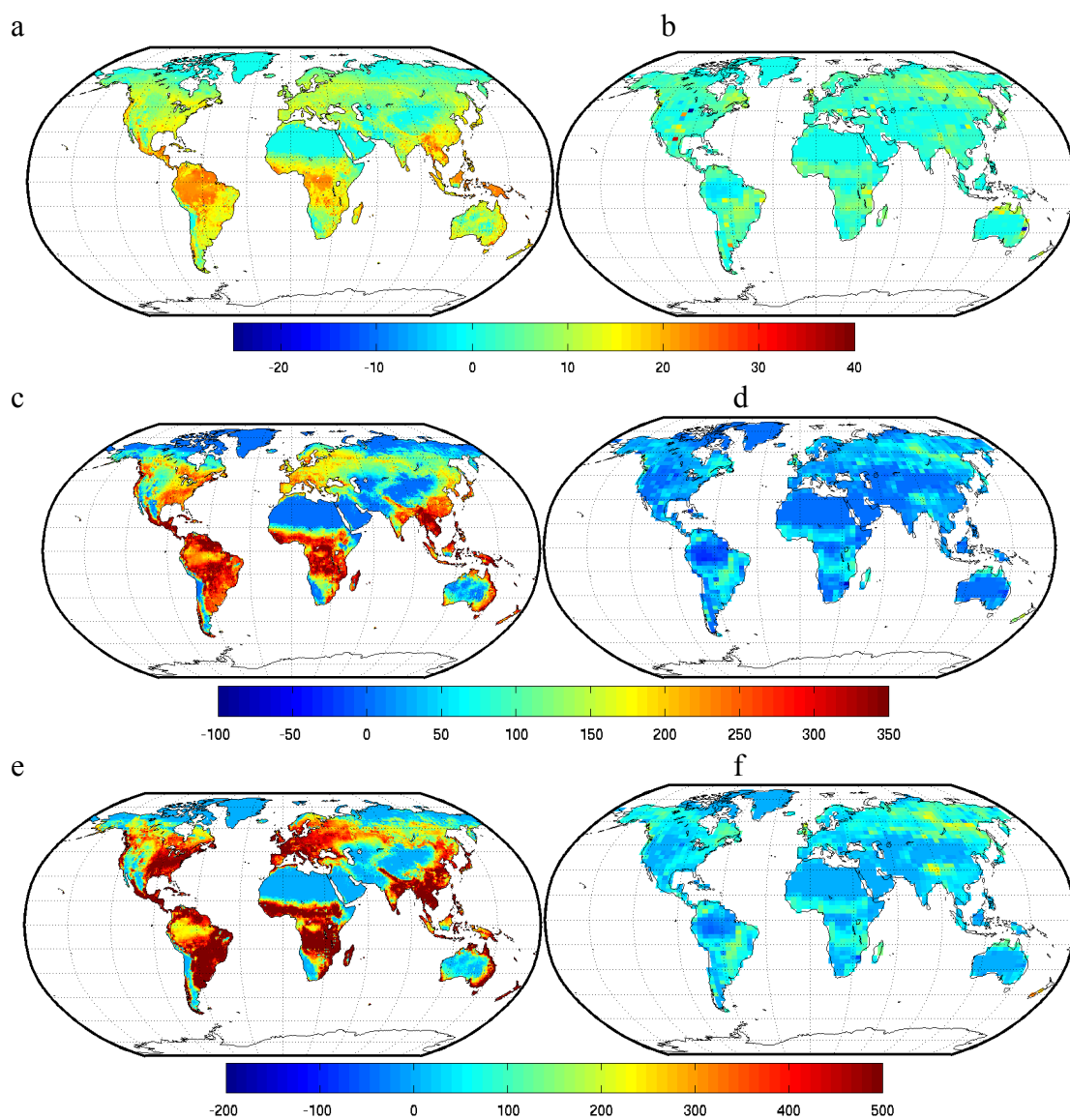
Supplemental Information Table 1. Forest nitrogen fertilization experiments used in model-data comparison. Simulation level refers to the fertilization inputs used in the model simulations. ANPP, Aboveground net primary productivity

Citation	Forest Type	Latitude	Longitude	Duration (years)	Fertilization Level ($\text{g N m}^{-2} \text{ yr}^{-1}$)	Simulation Level ($\text{gN m}^{-2} \text{ yr}^{-1}$)	Type of measurement
Magill et al 2004 (Hardwood +5)	Broadleaf temperate	43.4 N	72.2 W	16	5	4	ANPP
Magill et al 2004 (Hardwood +15)	Broadleaf temperate	43.4 N	72.2 W	16	15	10	ANPP
Pregitizier et al 2008 (Site A)	Broadleaf temperate	46.7 N	88.9 W	10	3	4	ANPP
Pregitizier et al 2008 (Site B)	Broadleaf temperate	45.6 N	84.9 W	10	3	4	ANPP
Pregitizier et al 2008 (Site C)	Broadleaf temperate	44.4 N	85.8 W	10	3	4	ANPP
Pregitizier et al 2008 (Site D)	Broadleaf temperate	43.7 N	86.2 W	10	3	4	ANPP
Magill et al 1996 (+ 2.5)	Broadleaf temperate	44.9 N	68.1 W	3	2.5	2	ANPP
Magill et al 1996 (+5.6)	Broadleaf temperate	44.9 N	68.1 W	3	5.6	4	ANPP
Finzi 2009 (Sugar maple – ash)	Broadleaf temperate	42 N	73.3 W	2	15	10	ANPP
Finzi 2009 (Oak-beech-hemlock)	Broadleaf temperate	42 N	73.3 W	2	15	10	ANPP
Kulmatiski et al 2007 (Big Moose)	Needleleaf evergreen	43.8 N	74.9 W	6	10	10	ANPP
Kulmatiski et al 2007 (Hubbard Brook)	Needleleaf evergreen	43.92 N	71.7 W	6	10	10	ANPP
Högberg et al 2006 (+3.4)	Needleleaf evergreen	64.4 N	19.8 E	30	3.4	4	Volume increment
Högberg et al 2006	Needleleaf	64.4 N	19.8 E	30	6.4	4	Volume increment

Houllé and Moore 2008 (Spruce + 3)	Needleleaf evergreen	49.2 N	73.7 W	3	3	4	Basal Area Increment
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Supplemental Information Table 2. Forest nitrogen fertilization experiments identified but not used in model-data comparison. Nitrogen fertilization experiments in tropical forests are not listed.

Citation	Reason for exclusion
Gage et al. 2007	No growth data reported
Wallace et al. 2007	Growth decline
De Walle et al. 2006	No stand level productivity reported
Magill et al. 2004 (Pine stand)	Growth decline; significant mortality
McNulty et al. 2005 (all treatments)	Growth decline
Emmett et al. 2004 (all treatments)	Growth decline; no stand-level growth data reported
Hyvonen et al. 2008 (Skogaby)	Growth decline
Schleppi et al. 2004	Growth decline
Elvir et al. 2003	No growth data reported
Gundersen 1998	Grid cell with site not simulated at O-CN resolution



Supplemental Information Figure 1. 5-yr mean NPP responses in the CLM-CN (a,c,e) and O-CN (b,d,f) for $5 \text{ g N m}^{-2} \text{ yr}^{-1}$ (a,b), $10 \text{ g N m}^{-2} \text{ yr}^{-1}$ (c,d) and $30 \text{ g N m}^{-2} \text{ yr}^{-1}$ (e,f) global nitrogen fertilization simulations.

CHAPTER 3

EVALUATING ALTERNATIVE APPROACHES TO MODELING TERRESTRIAL C AND N INTERACTIONS USING OBSERVATIONS OF ECOSYSTEM RESPONSES TO NITROGEN DEPOSITION AND EXPERIMENTAL FERTILIZATION¹

Abstract

In many forest ecosystems, nitrogen (N) deposition is increasing the uptake of carbon dioxide and reducing climate warming from fossil fuel emissions. Therefore, accurately modeling how forest carbon (C) sequestration responds to N deposition is critical for understanding how future changes in N availability will influence climate. Here, we use observations of how forest C responded to both N fertilization experiments and N deposition gradients to test and improve a global biogeochemical model (CLM-CN 4.0). We focus on quantifying how model predictions of the C response to N inputs differs across three primary modifications to the CLM-CN model that 1) reduce N fixation and N gas loss, 2) buffer plant N uptake and soil N availability for plants and microbial processes, and 3) alter the scaling of canopy

¹ A version of this chapter is in preparation for submission to the journal

Biogeosciences: Thomas, R. Q, G. B. Bonan and C. L. Goodale. Evaluating alternative approaches to modeling terrestrial C and N interactions using observations of ecosystem response to nitrogen deposition and experimental fertilization.

photosynthesis. Across five temperate forest sites, the set of modifications improved the correspondence between model predictions and observational data by increasing the C storage in response to historical N deposition (1850-2004) and decreasing the response to N fertilization experiments. The increased model sensitivity to N deposition was primarily attributable to greater retention of N deposition associated with modifications that decreased total N inputs and outputs (i.e., a less open N cycle) and increased the buffering of plant N uptake. In contrast, the decreased sensitivity to N fertilization was attributable to increased light limitation from the modifications to canopy photosynthesis and the buffered N plant N uptake. Furthermore, the modified model showed a greater role of synergy between N deposition and rising atmospheric CO₂ as a mechanism governing the change in temperate forest primary production over the 20th century. Based on our results, we suggest that N retention and the strength of light limitation of plants are important attributes that should be investigated in global biogeochemical model inter-comparisons. By simulating C storage sensitivity to observational data from both N deposition gradients and N fertilization experiments, we show that non-linearities in ecosystem response to N addition led to different assessments of sensitivity to N inputs in the these two types of observations. Therefore, testing models with both the response to gradual increases in N inputs over decades (N deposition) and N pulse additions of N over multiple years (nitrogen fertilization) allows for greater understanding of the mechanisms governing C-N coupling.

1. Introduction

Reactive nitrogen (N) from fossil fuel combustion and agricultural activities influences global climate by altering atmospheric chemistry, aerosols, and greenhouse gas concentrations (Butterbach-Bahl et al. 2011, Pinder et al. 2012). However, the direction of the climate impact of reactive N primarily depends on the balance of opposing processes: positive radiative forcing from emissions of N₂O, a greenhouse gas, and negative radiative forcing from altered atmospheric chemistry and carbon dioxide (CO₂) storage in N-fertilized forests (Arnth et al. 2010, Pinder et al. 2012). Reactive N deposited on forest ecosystems can increase primary production if the forest is N-limited (Nadelhoffer et al. 1999, Magnani et al. 2007, Thomas et al. 2010), which results in less CO₂ in the atmosphere and consequently reduced climate warming. Recent estimates show that this reduction in climate warming has a similar magnitude as the increase in warming from N₂O emissions, indicating that the forest sink of CO₂ has an important role in global climate (Zaehle et al. 2011, Butterbach-Bahl et al. 2011, Pinder et al. 2012).

Accurately predicting how carbon (C) storage in forest ecosystems will respond to the changing deposition of reactive N is critical for developing climate change targets for reducing emissions and air pollution. Global biogeochemical models coupled to climate and atmospheric chemistry models are powerful tools for exploring this carbon-nitrogen-climate interface (Sokolov et al. 2008, Thornton et al. 2009, Yang et al. 2009, Zaehle and Friend 2010), but it is paramount to build confidence in predictions of how C uptake and storage respond to changing N inputs.

Fortunately, a variety of observational and experimental data are available to test and improve the sensitivity of global biogeochemical models to changes in N deposition and the resulting C sequestration. Studies have generally shown that elevated N inputs often increase plant growth and soil C sequestration (Magnani et al. 2007, Hyvonen et al. 2008, de Vries et al. 2009, Janssens et al. 2010, Thomas et al. 2010), although some ecosystems have been harmed by chronic elevated N inputs that led to soil acidification and saturation (Aber et al. 1998, Hogberg et al. 2006, Wallace et al. 2007). The current range of estimates quantifying the additional C sequestered per unit of N added (kg C per kg N; or dC/dN) is broad, in part due to the myriad of approaches used to quantify dC/dN . These approaches include N fertilization studies (Hyvonen et al. 2008, Liu and Greaver 2009), where large inputs of N are added to forests over short time scales, and N deposition gradient studies (Magnani et al. 2007, de Vries et al. 2009, Thomas et al. 2010), where spatial variation in N deposition and forest growth are used to estimate the impact of gradual increases N deposition on C storage over multiple decades. Furthermore, there can be variation among studies in the C pools being measured, as some studies calculate the dC/dN of aboveground stem C (de Vries et al. 2009, Thomas et al. 2010), soil organic matter (Janssens et al. 2010), or net ecosystem production (NEP; Magnani et al. 2007, Sutton et al. 2008). Finally, the observations span regions with very different historical N deposition loads (i.e., the U.S. compared to Western Europe). Successfully using the available data to test and improve global biogeochemical models requires directly accounting for the variation in magnitude and time-scale of N additions in the observational and experimental data.

Many different approaches have been used to model key processes influencing C and N cycle interactions in terrestrial ecosystems (Zaehle and Dalmonech 2011). For example, N fixation has been modeled as a function of net primary production (NPP) (Thornton et al. 2007), evapotranspiration (Yang et al. 2009, Zaehle and Friend 2010) or N demand (Gerber et al. 2010). Similarly, N uptake has been represented as a direct function of photosynthesis and C:N stoichiometric constraints on building plant tissue (Thornton et al. 2002, 2007) or based on allocation of carbon to plant roots (Gerber et al. 2010, Zaehle and Friend 2010). Soil and plant buffering of the C cycle to daily to annual changes in N availability also differs among models (Gerber et al. 2010, Zaehle and Friend 2010). Despite these differences, global biogeochemical models predict reasonable levels of global NPP (Thornton et al. 2007, Gerber et al. 2010, Zaehle et al. 2010a), suggesting that the representation or parameterization of one process may compensate for the representation or parameterization of another. Understanding how the different model structures or parameterizations influence the prediction of how ecosystems respond to N deposition requires isolating key processes that govern C and N interactions. Unfortunately, inter-model comparisons can be limited by broad differences in model structure that make it difficult to isolate particular processes that differ among models. One approach to this problem is to compare different representations of particular C and N cycle processes within the same general model, thereby obtaining a better understanding of which processes influence predictions of how terrestrial C storage and climate respond to changing N availability.

Here, we explored the influence of alternative approaches to modeling C and N interactions on the sensitivity of C storage to N inputs in temperate forest ecosystems. To isolate the alternative approaches, we implemented multiple alternative assumptions about C and N cycling within a single global biogeochemical land surface model (CLM-CN 4.0). We focused on three key assumptions about the N cycle in the CLM-CN 4.0: 1) the extent to which the N cycle is open, based on N fixation inputs and N losses relative to internal N cycling, 2) the buffering of the soil mineral N pool and buffering of how plants take up N, and 3) the canopy scaling of photosynthesis. Alternative model structures of the CLM-CN were compared to observations of forest C response in N fertilization experiments and across N deposition gradients, specifically simulating differences in the magnitude and time-scale of N additions among the observational studies.

2.0 Methods

2.1 Baseline model description

We used the CLM-CN 4.0 as the baseline model (Thornton and Rosenbloom 2005, Thornton et al. 2007, 2009, Bonan and Levis 2010) in our study (hereafter, referred to as the “clm4cn” model). The clm4cn is a global biogeochemical and land surface model coupled in the Community Earth System Model (Gent et al. 2011). A complete model description can be found elsewhere (Thornton et al. 2002, Thornton and Rosenbloom 2005, Thornton et al. 2007, 2009), while a description of the key processes that relate to new model modifications are described below.

In the clm4cn model, the C and N cycles are coupled through litter and soil organic matter decomposition and through plant dynamics. The primary C and N coupling occurs on the 30-minute time scale, as plants compete for N with microbial immobilization into soil organic matter, where N comes from a generic soil inorganic N pool (i.e., NH_4 and NO_3 are combined). Plant N demand is based on the N needed to match the demand set by non-N limited photosynthesis and plant tissue C:N stoichiometric constraints. If the combined N demand exceeds the available N, plant uptake and microbial immobilization are reduced in proportion to the available N and their relative demands.

Sources of new N into the clm4cn model include N fixation and N deposition. N losses include denitrification, leaching, fire, and harvest. N fixation is a saturating function of NPP based on Cleveland et al. (1999). Fixation and deposition are both directly added to the soil inorganic N pool. The clm4cn model includes both denitrification and leaching processes; however, the vast majority of N is lost as N gas in most ecosystems in the model (Supplemental Information Table 3.SI.2). Therefore, the two loss pathways for N gases in the clm4cn model are very important: 1) a constant 1% of net mineralization is lost as N gas and 2) the soil mineral N that exceeds plant uptake and immobilization is denitrified at a rate of 50% per day.

2.2. Modified model description

The overall model modifications (referred to as “clm4mod”) build on recent improvements to the calculations of canopy photosynthesis in the clm4cn (Bonan et al. 2011, 2012) by adding processes that buffered the C cycle coupling to N availability,

and reducing N inputs to create an N cycle with lower N inputs and outputs relative to internal N cycling (i.e., a less open N cycle) in mature temperate and boreal forests. This less open N cycle in the clm4mod reflects the understanding that symbiotic N fixation is low in mature temperate and boreal forests (Crews 1999). This is in contrast the clm4cn that includes both symbiotic and free-living bacteria in all ecosystems. Furthermore, the modifications within the clm4cn reflect differences between the clm4cn and other global biogeochemical models, specially models that have greater buffering of the N cycle than the clm4cn (O-CN; Zaehle and Friend 2010) and less N fixation in temperate and boreal forests than the clm4cn (LM3V; Gerber et al. 2010). As described below, the key modifications included plant N uptake, internal N cycling, N loss, and biological N fixation. A full description of the modifications is found in the supplemental information.

2.2.1 Internal N cycling

Plant N Uptake in the clm4mod model is based on Michaelis–Menten kinetics, where the rate of N uptake depends on a maximum uptake rate per gram of fine root C, as well as the concentration of soil mineral N in NH_4 and NO_3 pools (see Supplemental Information for detailed information; NH_4 and NO_3 pools were added in the modified model). Plant uptake increases with soil temperature and as the internal plant pool of N decreases relative to a maximum internal pool. The formulation of N uptake is similar to that used in other global biogeochemical models (Gerber et al. 2010, Zaehle and Friend 2010) and differs from the clm4cn by allowing the N uptake to be decoupled from photosynthesis at short time scales (i.e., seconds to days); longer

term N uptake (i.e., at days to years) remains ultimately coupled to photosynthesis. The maximum internal plant N pool is equal to one year of live plant tissue N turnover (Gerber et al. 2010). In the clm4mod model, the maximum uptake rate is assumed to be equal for NH_4 and NO_3 , as implemented in other models (Gerber et al. 2010, Zaehle and Friend 2010). N uptake occurs any time during the growing season (i.e., when leaves were present on the plant), rather than only during the day within the growing season, as implemented in the clm4cn version. Plant uptake is assumed to be less competitive for N than soil immobilization of N, in that plant uptake occurs after soil microbial immobilization demands are met. The clm4mod includes a plant labile N pool that is used to buffer the demand for N from photosynthesis from the uptake of N by roots. The buffering occurs by allowing only 2% of the N labile pool to be available for combining with photosynthesized C to build plant tissue. The 2% buffering capacity leads to a two-day turnover time of labile plant N. The clm4cn does not include buffering of labile plant N, although recent model improvements to the clm4cn include a buffered labile N pool (Thornton et al. personal communication).

2.2.2 N losses

The clm4mod model introduces a nitrification algorithm, an alternative denitrification algorithm, and a simple algorithm describing the production and hydrologic loss of dissolved organic matter, including dissolved organic N (DON). Nitrification is a function of soil NH_4 , soil temperature, soil water, and net mineralization based on Parton et al. (2001) with 2% of nitrification lost as N_2O (Parton et al 2001). Denitrification is a function of soil NO_3 , soil water, and soil

heterotrophic activity based on Bradbury et al. (Bradbury et al. 1993, Yang et al. 2009). To buffer the availability of soil mineral N and approximate short term cation exchange processes, 10% of total soil NH_4 is available for immobilization, plant uptake, nitrification, and leaching (Gerber et al. 2010), and, since NO_3 is highly mobile in soils, 100% of NO_3 is assumed to be available for soil, plant, and loss processes. Dissolved organic matter is produced at a constant proportion (2%) of the organic matter transfer between the slow litter pool (lignin-based) and its receiving soil organic matter pool (based on Gerber et al. 2010). Both dissolved organic C and N are lost in proportion to hydrologic export, similar to leaching loss of mineral N in the Clm4cn model. The clm4cn does not include separate consideration of NO_3 and NH_4 cycling, nor does it include DOC and DON losses.

2.2.3 *N inputs*

In clim4cmod N fixation is a function of actual evapotranspiration, based on the central relationship in the Cleveland et al. (1999) review of N fixation measurements, rather than a function of NPP, as implemented in clm4cn. In addition, symbiotic and non-symbiotic sources of N fixation are separated. Symbiotic N fixation is assumed to be zero in mid- to late-successional temperate and boreal forests (i.e., when leaf area index (LAI) > 1) and non-symbiotic N fixation increases with actual evapotranspiration (see Supplemental Information SI.1.6). Both sources of fixation are assumed to occur in grasslands and tropical forests. This N fixation routine reduces the overall N inputs to mid- to late-successional extra-tropical forests

(see Table 3.SI.1 for the magnitude of change in N fixation). A pathway for N fertilization was also added to facilitate the simulation of N fertilization experiments.

2.2.4 Canopy photosynthesis

Finally, the clm4mod model includes changes to the canopy scaling of photosynthesis, maximum photosynthetic rates, radiative transfer, leaf photosynthesis, and stomatal conductance as described in Bonan et al. (2011) and (2012). Bonan et al. (2012) introduced a multi-layer canopy scaling approach that solved photosynthesis throughout the canopy rather than using a whole canopy (two stream) approximation. The model updates in Bonan et al. (2011, 2012) decreased GPP and effectively reduced the photosynthetic potential of shaded leaves, but the impact of the changes on C-N interactions has not been investigated. The clm4mod model also includes specific values of maximum photosynthetic rate for each plant functional type from a synthesis of a plant trait database (Kattge et al. 2009), although they only differed slightly from the values in the clm4cn model for the temperate broadleaf plant type used in this study (clm4cn, 52; clm4mod, 58; $\mu\text{mol m}^{-2} \text{s}^{-1}$).

2.3 Simulations

The clm4cn and clm4mod models were used to simulate forest biogeochemistry at five sites in North American broadleaf temperate deciduous forests. The five sites were chosen based on the presence of long-term forest productivity measurements (10+ years), long-term N fertilization experiments (10+ years), and are contained within the geographic boundaries of the analysis of forest

inventory data by Thomas et al. (2010), which estimated how forest C storage has responded to N deposition across the northeastern U.S. (see below). Basic descriptions of the sites are included in Table 1. Four of the five sites were in Michigan, USA, with each site receiving a $3 \text{ g N m}^{-2} \text{ yr}^{-1}$ experimental addition of N over ten years (Pregitzer et al. 2008; 1995-2005). The other site was at Harvard Forest in Massachusetts, USA (Magill et al. 2004) and included two different 14-year fertilization additions (5 and $15 \text{ g N m}^{-2} \text{ yr}^{-1}$; 1988-2002). All data used in this study for the five sites and six N fertilization experiments can be found in Magill et al. (2004) and Pregitzer et al. (2008).

We simulated ecosystem response to transient N deposition and N fertilization at each of the five sites using the *clm4cn* and *clm4mod* models. The simulations involved running each model from 1850 to 2004 at each of the five sites with different combinations of forcing data. The baseline simulation used transient N deposition (NH_x and NO_y ; Lamarque et al. 2005), atmospheric CO_2 , land use (based on stand age at the five sites), and climate. N deposition and atmospheric CO_2 had forcing data for the entire simulation (1850-2004). A 57-year meteorological dataset was available to force the model (1948-2004; Qian et al. 2006). We spatially interpolated the global gridded data to create site-level meteorological data. We used the data from 1948-1972 for the 1850-1972 simulation years, and the 1973-2004 meteorological dataset was used for the 1973-2004 simulation years. Each simulation needed initial conditions that were attained by running the model to equilibrium using 1850 values for N deposition and atmospheric CO_2 and the 1948-1972 time-series for meteorological data. All wildfire was excluded in the spin-up and other simulations

due to uncertainties using the statistical fire model at a single point location.

Simulations used site-specific soil texture (Magill et al. 2004, Pregitzer et al. 2008).

We isolated the influence of transient N deposition on C cycling at each site by repeating the baseline simulation described above except for holding N deposition at 1850. We also tested whether C cycle sensitivity was different for larger inputs of N deposition than included in the baseline simulation. The high N deposition simulation used a N deposition trajectory with 1995 – 2004 mean deposition levels at the five sites of $2.2 \text{ g N m}^{-2} \text{ yr}^{-1}$ rather than their actual N deposition rates that ranged from $0.68 - 1.18 \text{ g N m}^{-2} \text{ yr}^{-1}$.

Because the NPP response to rising atmospheric CO_2 is constrained by nitrogen availability, we tested whether the sensitivity of NPP to rising atmospheric CO_2 changed as a result of the modifications to clm4cn. To test this sensitivity we performed two additional simulations at the five sites using the clm4cn and clm4mod: a simulation that held both N deposition and atmospheric CO_2 constant at 1850 levels and a simulation that held CO_2 constant at 1850 levels but included 1850-2004 N deposition levels.

Finally, we simulated the six N fertilization experiments (Table 1; four sites with one experiment each and one site with two experiments) by adding N fertilization to the baseline simulation to best approximate the field experiments by specifying the start year, duration, magnitude and intra-annual distribution of N application.

2.4 N fertilization and deposition analysis and observations

The model comparison to observations focused on NPP, net ecosystem productivity (NEP), and annual aboveground net C increment (ACI) in plants because these were the variables measured in the N fertilization experiments and across the N deposition gradients. The model response to N fertilization was assessed by comparing mean annual aboveground NPP (ANPP) in the control and N-fertilized simulations to ANPP data from the corresponding control and fertilized treatments in the field data. In both the models and observations, ANPP corresponded to the sum of mean leaf and stem productivity over the course of the observational data. We also report ACI for the fertilization experiments (the change of aboveground C stock between years). ACI differs from NPP and ANPP in that ACI does not include the production and turnover of wood or leaves within a year that are included in NPP measurements. However, ACI includes the losses of C from mortality that are not included in NPP measurements. We report the ACI response to fertilization by dividing by the N added ($dC_{ACI}/dN_{fertilization}$).

We compared the model response to N deposition to observations from the literature. We calculated average ACI between 1994 and 2004 in the simulations with and without transient N deposition (both including transient CO_2). The ACI response to N deposition was expressed as the ACI difference divided by the difference in mean N deposition over the same time period ($dC_{ACI}/dN_{deposition}$). We also report the difference in NEP divided by the difference in N deposition ($dC_{NEP}/dN_{deposition}$). We compared the above metrics of N deposition response to the corresponding metrics reported in analyses listed in Table 2.

Table 1: Descriptions of sites used in model simulations.

Site	Harvard Forest	Michigan gradient A	Michigan gradient B	Michigan gradient C	Michigan gradient D
Code	HF	MI-A	MI-B	MI-C	MI-D
Latitude (N)	42° 30' N	46° 52'	45° 33'	44° 23'	43° 40'
Longitude (W)	72° 10' W	88° 53'	84° 51'	85° 50'	86° 09'
Stand Age (years) [^]	52	97	91	92	96
MAT* (°C)	7.1	4.7	6.0	6.9	7.6
MAP [#] (mm)	1120	873	871	888	812
Aboveground carbon (g C m ⁻²) [^]	6597	14,700	14,150	15,800	14,450
Vegetation type	temperate deciduous broadleaf	temperate deciduous broadleaf	temperate deciduous broadleaf	temperate deciduous broadleaf	temperate deciduous broadleaf
Years of experiment	1988-2002	1995-2004	1995-2004	1995-2004	1995-2004
Nitrogen fertilization rate (g N m ⁻² yr ⁻¹)	5 & 15	3	3	3	3
Nitrogen deposition (g N m ⁻² yr ⁻¹)	0.8	0.68	0.91	1.17	1.18
Citation	Magill et al. 2004	Pregitzer et al. 2008	Pregitzer et al. 2008	Pregitzer et al. 2008	Pregitzer et al. 2008

* Mean annual temperature

Mean annual precipitation

[^] Age and carbon stocks in the year 1994

Table 2. Model simulations and observations of the vegetation and ecosystem carbon increment response to nitrogen deposition and fertilization.

Response metric	Carbon measurement	Nitrogen input	clm4cn model	clm4mod model	Observations	Citation
$dC_{ACI}/dN_{deposition}$	Aboveground carbon increment	U.S. deposition gradient	14.0±1.1	34.2±3.0	50 (41-66)	Thomas et al. 2010*
$dC_{ACI}/dN_{deposition}$	Aboveground carbon increment	E.U. deposition gradient	11.8±0.8 [#]	26.2±2.6 [#]	15-40	DeVries et al. 2009
$dC_{ACI}/dN_{fertilization}$	Aboveground carbon increment	Fertilization experiments	10.7±1.3	10.6±4.5	4±2.7	Magill et al. 2004, Pregitzer et al. 2008
$dC_{NEP}/dN_{deposition}$	Net ecosystem production	U.S. deposition gradient	30.0±1.8	74.1±8.17	no data	
$dC_{NEP}/dN_{deposition}$	Net ecosystem production	E.U. deposition gradient	24.5±1.5	49.5±4.4	50-75	Sutton et al. 2008
$dC_{NEP}/dN_{fertilization}$	Net ecosystem production	Fertilization experiments	27.9±2.8	23.2±9.4	31 ± 10	Magill et al. 2004, Pregitzer et al. 2008

* The reported 61 dC/dN was divided by a factor of 1.23 to account for unmeasured nitrogen deposition. See Pinder et al. (2012) for more information.

[#] These model simulations used higher N deposition (1994-2004 mean = 2.2 g N m⁻² yr⁻¹) to approximate nitrogen deposition in regions that have experience higher historical N deposition loads.

We also assessed the contribution of N retention to the N deposition response in the clm4cn and clm4mod models. The total N deposition retained between 1970 and 2004 and between 2000 and 2004 was calculated to determine the long- and short-term retention of N deposition, respectively. Over each time period, we calculated total deposition retained in the ecosystem and the fate of N deposition into soil organic matter (including litter and coarse woody debris) and vegetation.

In addition, we assessed the relative contribution of CO₂ fertilization to how NPP responds to N deposition for each site using the method developed by Churkina et al. (2009) and Zaehle et al. (2010b). That is, we isolated the pure N deposition (i.e., N deposition enhancement without an interaction with CO₂ fertilization), the pure CO₂ fertilization, and the synergistic effect of CO₂ fertilization and N deposition on NPP by calculating the mean NPP (1994-2004) in the simulations with 1) N deposition and atmospheric CO₂ at pre-industrial levels, 2) only transient N deposition, 3) only transient CO₂, and 4) both transient N deposition and CO₂ (i.e., control simulation described above). The pure N deposition response was the difference in NPP between simulations 1 and 2, while the pure CO₂ fertilization response was the difference between 1 and 3. The additional NPP needed to reach the difference between 1 and 4 was the synergy between N deposition and CO₂ fertilization.

2.5 Sensitivity Analysis to model structure

To better isolate the general mechanisms that contributed to the differences in $dC_{ACI}/dN_{deposition}$ and ANPP response to N fertilization between the clm4cn and clm4mod models, we created a set of intermediate models that isolated key

mechanisms (Table 3). The intermediate models represented a series of cumulative changes to the clm4cn that first isolated the canopy photosynthesis changes in Bonan et al. (2012; Model B); second, the soil buffering of mineral N (Model C); third, an N cycle with reduced N fixation and N losses relative to internal N cycling (i.e., a less open N cycle; Model D); fourth, changes to plant N uptake, nitrification, and denitrification (Model E); and finally, plant buffering of labile N (the full clm4mod model). Table 3 describes the isolated mechanisms and the Supplemental Information describes the model changes and parameterizations for each of the intermediate models. To test the sensitivity of $dC_{ACI}/dN_{\text{deposition}}$, we repeated the simulations for each intermediate model with and without transient N deposition at a single site (Harvard Forest) to test the sensitivity of $dC_{ACI}/dN_{\text{deposition}}$ to the alternative approaches to modeling N cycling. To test the sensitivity of the ANPP response to N fertilization, we simulated the $5 \text{ g N m}^{-2} \text{ yr}^{-1}$ N fertilization experiment at Harvard Forest in each intermediate model.

3.0 Results

3.1 Model response to N fertilization experiments

The clm4mod model better predicted the mean ANPP for the control simulations (i.e., no N additional fertilization added) than the clm4cn model. The mean observed ANPP across the five sites was $464 \pm 36 \text{ g C m}^{-2} \text{ yr}^{-1}$ (1 S.E. across sites), while the mean in the clm4mod and clm4cn model was 411 ± 28 and $352 \pm 50 \text{ g C m}^{-2} \text{ yr}^{-1}$ (1 S.E.), respectively (Table 4). Both models predicted lower ANPP than

Table 3: The mechanisms isolated in the analysis of the nitrogen deposition response to model structure.

Model	Multi-layer canopy	Soil buffering	Less open nitrogen cycle	Plant N buffering	All other changes	Mechanism isolated
clm4cn						Baseline
B	X					Canopy scaling and V_{cmax}
C	X	X				Soil buffering
D	X	X	X			Less open N cycle with reduced N fixation and N gas losses
E	X	X	X		X	Concentration-dependent plant N uptake, inclusion of nitrification, modifications to denitrification, inclusion of DOM dynamics
clm4mod	X	X	X	X	X	Plant N buffering

Table 4. Annual net primary productivity in the six nitrogen fertilization experiments at five temperate broadleaf deciduous forests. The field observations are compared to simulations from the clm4cn model, and clm4mod model.

	Observations	clm4cn	clm4mod
Control ANPP (n = 5)	464 ± 36	352 ± 50	411 ± 28
Fertilized ANPP (n = 6)	504 ± 40	420 ± 41	474 ± 8
Δ ANPP (n = 6) *	55 ± 8	91 ± 19	57 ± 18
Non-nitrogen limited ANPP (n = 6)	Not measured	742 ± 10	474 ± 8

*The mean fertilization responses for the observations and model simulations were different than the difference between the mean control and mean fertilization ANPP because two experiments at Harvard Forest shared the same control treatment

observed in the most productive sites (MI-B, MI-C and MI-D; Figure 1). Neither model was consistently higher or lower than observed ANPP in the two least productive sites (HF and MI-A; Figure 1).

The clm4mod also better predicted both the mean ANPP in the N fertilized simulations and the increase in ANPP over the control simulation than the clm4cn. The fertilized ANPP in the clm4mod model ($474 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$) compared better to the observed fertilized ANPP in the six experiments at the five sites ($504 \pm 40 \text{ g C m}^{-2} \text{ yr}^{-1}$) than the clm4cn model ($420 \pm 41 \text{ g C m}^{-2} \text{ yr}^{-1}$; Table 4). The mean increase in ANPP in the fertilization experiments was similar between the observations ($55 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$) and the clm4mod ($57 \pm 18 \text{ g C m}^{-2} \text{ yr}^{-1}$) with the clm4cn fertilization response 65% higher ($91 \pm 19 \text{ g C m}^{-2} \text{ yr}^{-1}$) than the observed response (note: the mean fertilization responses for the observations and model simulations were different than the difference between the mean control and mean fertilization ANPP because two experiments at Harvard Forest shared the same control treatment). On a site-by-site basis, the clm4mod corresponded substantially better to observations from the two N fertilization experiments at Harvard Forest than the clm4cn (Figure 1c). At the MI-A site, the clm4cn performed better compared to the observations than the clm4mod (Figure 1c). Both the fertilization responses in the clm4cn and clm4mod models were within the bounds of uncertainty in the observations at MI-B, MI-C, and MI-D (Figure 1).

Despite differences in ANPP response to N fertilization, both the clm4cn and clm4mod models predicted similar aboveground C increments per unit N fertilizer added ($dC_{ACI}/dN_{\text{fertilizer}}$; clm4cn: $10.7 \pm 1.3 \text{ kg C kg N}^{-1}$; clm4mod: $10.6 \pm 4.5 \text{ kg C kg}$

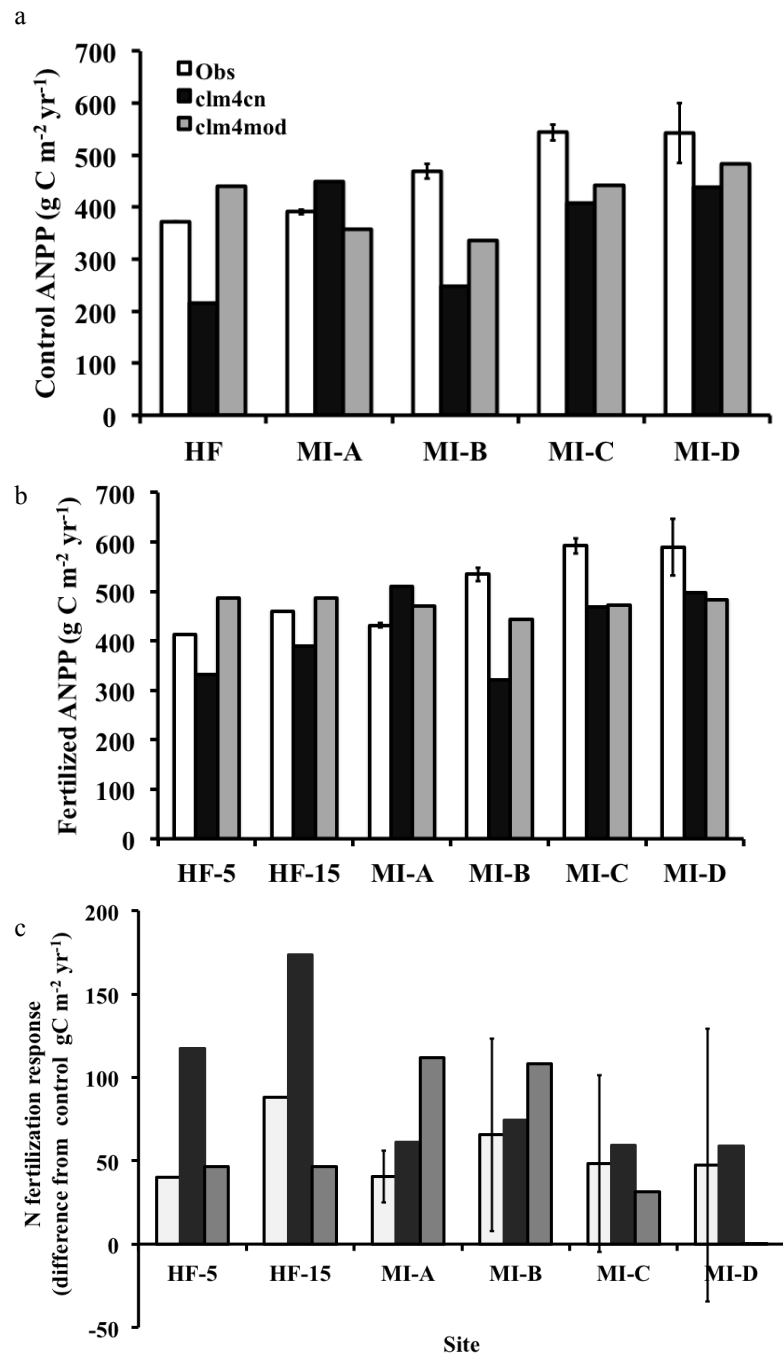


Figure 1. Mean annual aboveground net primary production (ANPP) for the five temperate deciduous forests in Table 1 from measured values, clm4cn model predictions, and clm4mod model predictions. The ANPP is shown for (a) the control (non-fertilized) plots and (b) the nitrogen fertilized plots, along with (c) the

differences between the control and fertilized treatments. The model simulations include transient nitrogen deposition, atmospheric CO₂, and land-use. Error bars represent the S. E. reported in Pregitzer et al. 2008.

N^{-1}), that was on average 1.5 times larger than the observed $dC_{\text{ACI}}/dN_{\text{fertilizer}}$ (4.0 ± 2.7 kg C kg N^{-1} ; Table 2). However, the site-to-site variability in the clm4mod $dC_{\text{ACI}}/dN_{\text{fertilizer}}$ was larger than the variability in clm4cn, leading to overlapping uncertainty with the observations. The mean annual net ecosystem production response to N fertilization ($dC_{\text{NEP}}/dN_{\text{fertilizer}}$) across all five sites was 27.9 ± 2.8 and 23.2 ± 9.4 kg C kg N^{-1} for the clm4cn and clm4mod models, respectively (Table 2). The clm4cn compared better to the observed $dC_{\text{NEP}}/dN_{\text{fertilizer}}$ at the six fertilization experiments (30 ± 10 kg C kg N^{-1} ; Table 2), although both models were contained in the observational uncertainty. Additionally, both net ecosystem production responses were within the uncertainty (24 ± 8.7 kg C kg N^{-1}) reported by Lui and Greaver (2009) in a meta-analysis of forest C response to N fertilization (Table 2).

3.2 Model response to historical N deposition

The clm4mod model had a 144% larger response of aboveground C increment ($dC_{\text{ACI}}/dN_{\text{deposition}}$) to N deposition than the clm4cn model (Table 2). The $dC_{\text{ACI}}/dN_{\text{deposition}}$ was 14.0 and 34.2 in the clm4cn and clm4mod models, respectively (Table 2). Both models predicted lower responses than reported for aboveground C increment across the Northeastern U.S. (Thomas et al. 2010; 50 kg C kg N^{-1}); however, the bias was substantially reduced in the clm4mod model (Table 2). Adding the belowground vegetation and soil response increased average $dC_{\text{NEP}}/dN_{\text{deposition}}$ across the five sites to 74.1 and 30.0 kg C kg N^{-1} in the clm4mod and clm4cn models, respectively.

In the simulations with higher rates of N deposition (1995-2004 mean = 2.2 g N m⁻² yr⁻¹), the aboveground C increment response to N deposition ($dC_{ACI}/dN_{deposition}$) decreased in both models (Table 2). The simulations with a large increase in N deposition were designed to test model sensitivity to N deposition levels larger than typically found in the U.S. but similar to levels found in parts of Western Europe. Comparing the model results to observations from Western Europe, the mean $dC_{ACI}/dN_{deposition}$ across all sites in the clm4mod model (26 kg C kg N⁻¹) was contained within the range reported from inventory measurements of European forests across a N deposition gradient (15-40 kg C kg N⁻¹, Table 3; DeVries et al. 2009), while the mean clm4cn model result was lower than the reported range (11.8 kg C kg N⁻¹). For the NEP response to N, the $dC_{NEP}/dN_{deposition}$ for the clm4mod model (49.5 kg C kg N⁻¹) was within the range of values recalculated for European forest by Sutton et al. (2008; 50-75 kg C kg N⁻¹) using eddy flux observations reported by Magnani et al. (2007). The mean $dC_{NEP}/dN_{deposition}$ from the clm4cn model (24.5 kg C kg N⁻¹) was 50% less than the lower bound reported in Sutton et al. (2008).

3.3 Mechanisms explaining the increased responsiveness of the modified model to N deposition and fertilization

Mean retention of N deposition within the ecosystem was strongly associated with the larger $dC_{ACI}/dN_{deposition}$ in the clm4mod than clm4cn. Across all five sites, the mean retention of N deposition was higher in the clm4mod model than the clm4cn model (Figure 2). Ecosystem N retention decreased over time in both models (Figure 2; sum of N recovery in vegetation and soil), as the four-year retention (2000-2004:

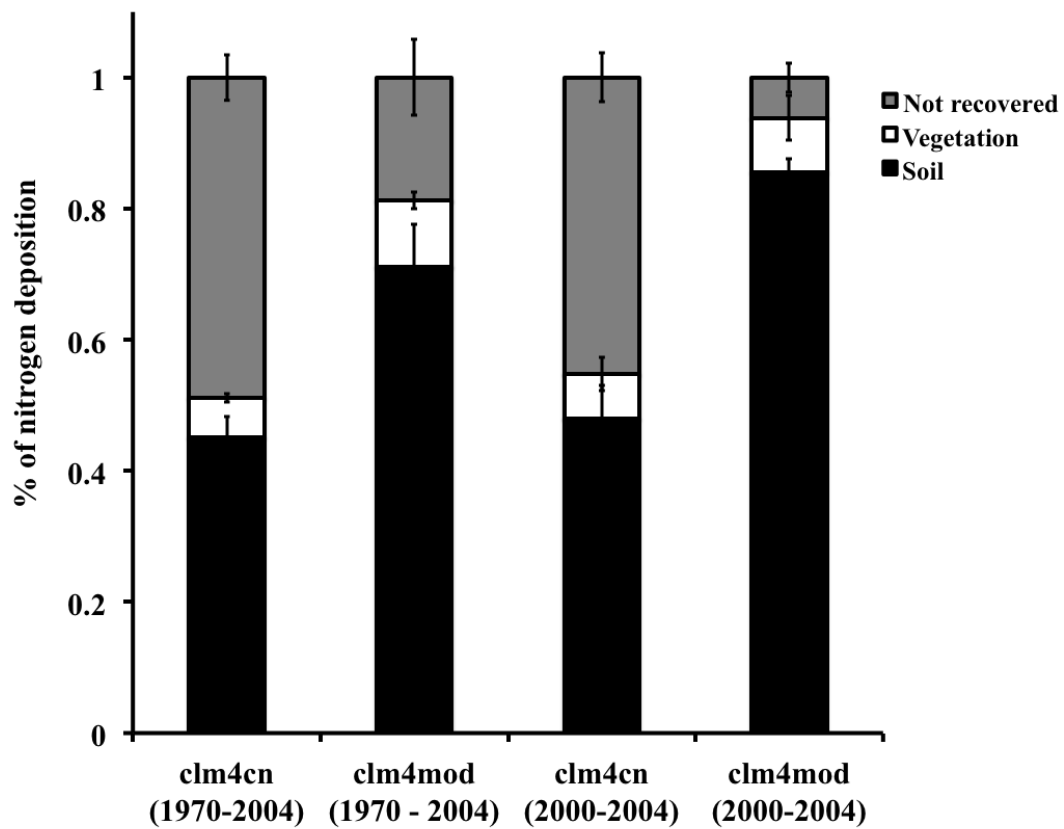


Figure 2. Model predictions of ecosystem retention of nitrogen deposition, partitioned among soil organic matter and vegetation averaged across all five sites for two time periods: 1970 – 2004 and 2000-2004. Error bars represent variation among sites (1 S.E.).

clm4cn = 55%, clm4mod = 94%) was larger than the 34-year retention (1970-2004: clm4cn = 51%; clm4mod = 81%). The fate of N retained in the ecosystem was predominately in soil organic matter in both models and at both time scales (Figure 2). However, the proportion of N deposition retained in both vegetation and soil was higher in the clm4mod than the clm4cn model (Figure 2) with particularly large increases in N retained in soil.

The larger $dC_{ACI}/dN_{deposition}$ in the clm4mod than the clm4cn was also strongly associated with the implementation of a less open N cycle with lower N inputs and outputs. As a result of implementing a less open N cycle, $dC_{ACI}/dN_{deposition}$ increased by 66% ($10.4 \text{ kg C kg N}^{-1}$) between Model C (more open N cycle) and Model D (less open N cycle) in Table 4 and Figure 3. The model modifications that included switching the plant N uptake to a buffered kinetic-based approach, introducing nitrification processes, and modifying the denitrification routine also increased the N deposition response by 11 $dC_{ACI}/dN_{deposition}$ (Models D and Model E; Figure 4; Table 3). Adding multi-layer canopy scaling along with modifying the maximum photosynthetic capacity (V_{cmax} ; clm4cn model to Model B; Figure 3; Table 3), adding soil buffering (Model B to Model C), and adding plant N buffering (Model E to clm4mod model) had a small impact on the N deposition response (range of $\Delta dC_{ACI}/dN_{deposition}$: -0.2 to 1.4; Figure 3; Table 3).

The sensitivity of N fertilization response to model modifications differed from the response to N deposition. In contrast to the sensitivity to N deposition, the model modifications (Model E) that changed the plant N uptake to a buffered kinetic-based approach to plant uptake, added nitrification processes, and introduced a modified

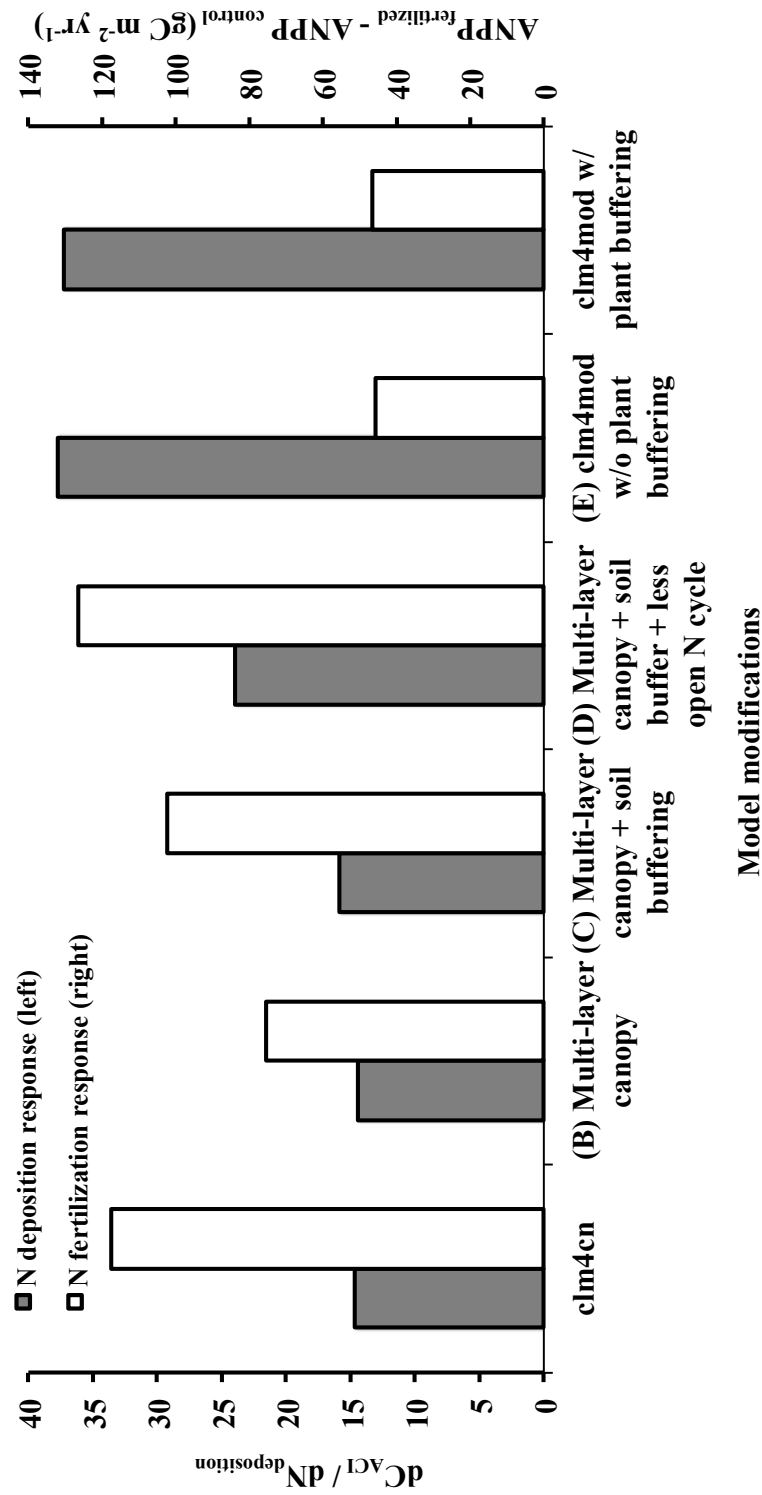


Figure 3. The sensitivity of the nitrogen deposition response to key changes in model structure for a single site (Harvard Forest). The figure shows the nitrogen deposition response, expressed as an annual aboveground carbon increment ($dC_{AC1}/dN_{deposition}$), for the clm4cn model, clm4mod, and intermediary models (B, C, D, and E). See Table 3 for a description of the mechanisms isolated in each model.

denitrification routine resulted in the most substantial decrease in the ANPP response to N fertilization (Figure 3). This set of model modifications was central to both reducing the response to N fertilization and increasing the response to N deposition, both improving the correspondence to the observational data (Table 2; Figure 1). However, the introduction of a less open nitrogen cycle resulted in a larger response to N fertilization and poorer comparison to observations from fertilization experiments.

3.4. Synergy between N deposition and atmospheric CO₂

Averaged across all five sites, the clm4mod and clm4cn models predicted similar increases in NPP over pre-industrial NPP, attributed to the increase in both N deposition and atmospheric CO₂ over the period from 1850 to 2004 (clm4cn = 84.1 g C m⁻² yr⁻¹; clm4mod = 87.2 g C m⁻² yr⁻¹; 1994-2004; Figure 4a). However, the relative contribution of N deposition and CO₂ fertilization differed strongly between the two models (Figure 4b). The increase in NPP predicted by the clm4cn model was comprised of a pure N deposition response (46%) and a pure CO₂ fertilization response (57%) that were largely independent of each other, as the synergy only explained 7% of the NPP change (Figure 4b). In contrast, the pure CO₂ fertilization response in the clm4mod model was small (12%) while the majority of the NPP increase was explained by a pure N deposition response (58%) and a synergy between N deposition and rising CO₂ (30%; Figure 4b).

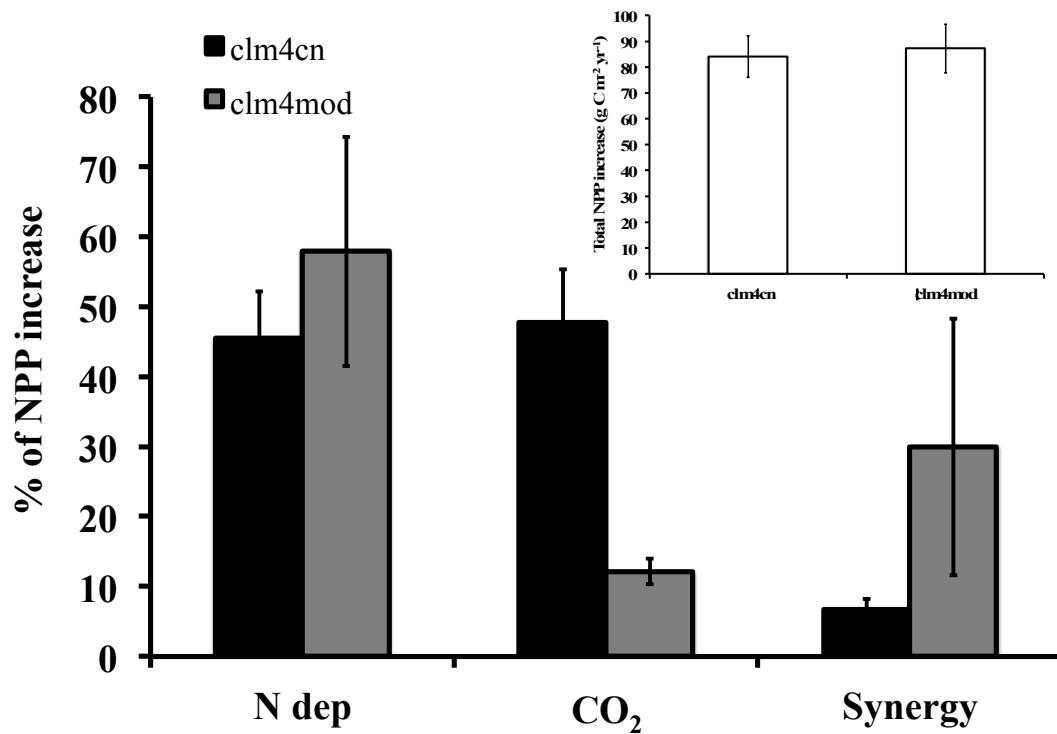


Figure 4. Model predictions of net primary production (NPP) response to rising nitrogen deposition and atmospheric CO₂ averaged across all five sites. The total NPP increase between 1850 and 2004 (inset) is partitioned into the increase due only to nitrogen deposition, only to CO₂ fertilization, and the synergy between nitrogen deposition and CO₂ fertilization. Error bars represent variation among sites (1 S.E.).

4.0 Discussion

Overall, our modifications to the CLM-CN 4.0 substantially improved predictions of C storage in response to historical N deposition. The modifications in the clm4mod model increased the aboveground C increment response to historical N deposition in the clm4cn model and compared more closely with observations across N deposition gradients in the northeastern U.S. and Western Europe. Two broad mechanisms are responsible for the increased aboveground C increment response to N deposition in the clm4mod model: 1) increased ecosystem retention of N deposition, and 2) increased synergy between N deposition and fertilization from elevated atmospheric CO₂.

4.1 Response to historical N deposition

The increased response to N deposition was dependent on the retention of N deposition within the ecosystem, as greater long-term N retention increased the availability of N to plants and allowed them to respond to rising atmospheric CO₂. Retention of N deposition within the five simulated forests at the 4 to 30 year time horizon in the clm4mod model was between 81 and 95%, and only 51 to 55% in the clm4cn model. The higher N retention rate in the clm4mod model than the clm4cn model better matches observations from field tracer experiments in which isotopically labeled N (¹⁵N) was added to forests and total isotope recovery was used to measure N retention (Nadelhoffer et al. 1999, 2004, Templer et al. 2012). At the Harvard Forest site, retention of added ¹⁵N in two experiments after 7 years ranged from 88 to 100%, which compares well to clm4mod (Nadelhoffer et al. 2004; treatments with no additional N fertilization added). In contrast, a ¹⁵N tracer experiment at one of the

Michigan sites (MI-B) only recovered 17.5% of added ^{15}N , which is substantially lower than both the clm4cn and clm4mod models (Zak et al. 2004). This tracer study differed markedly from most others. That is, a meta-analysis of ^{15}N experiments found that approximately 78% of added N was recovered in 11 temperate deciduous broadleaf forest ecosystems, and 75% was recovered across all forests (Templer et al. 2012). A similar analysis on nine sites, many of which were included in the meta-analysis conducted by Templer et al. (2012), found 90% recovery of ^{15}N after 1-3 years of addition (Nadelhoffer et al. 1999). Overall, on the balance of evidence, the increased N retention in the clm4mod better reflects the ^{15}N retention observed in most temperate forest tracer studies.

The most important change to the CLM-CN that was responsible for increasing N retention in the clm4mod model was the implementation of a less open N cycle. N cycles range from being open to closed depending on the importance of the inputs and outputs of N relative to the internal N cycling fluxes. For example, at steady state in global biogeochemical models, all N fixation inputs are balanced by N losses from the ecosystem. As such, models with larger N inputs will have larger outputs at steady state, resulting in faster and a more open N cycle. The degree of openness of the N cycle in an ecosystem is not explicitly specified in ecosystem models; rather, it is controlled by the balance of N inputs to outputs. Here, we show that model structure and parameterizations that led to a less open N cycle, through reduced inputs from N fixation and reduced losses from N gas loss, increased N retention and plant growth response to N deposition (Figure 3: Model C to D), which compared better to observations.

The magnitude and mechanisms governing N fixation and N losses vary widely among global biogeochemical models, likely indicating that the degree of openness of the N cycle also varies among models. For example, in comparison to two other global biogeochemical models, the clm4cn model uses a relationship between NPP and N fixation derived from Cleveland et al. (1999) while O-CN model (Zaehle and Friend 2010) uses a relationship between N fixation and evapotranspiration based on an alternative relationship presented in Cleveland et al. (1999), and the LM3V model (Gerber et al. 2010) uses a demand-driven approach to N fixation that recognizes that N fixation is limited in closed-canopy temperate and boreal forests (Crews 1999). Given the range of approaches to modeling N inputs and outputs, we suggest that a metric of the openness of the N cycle in global biogeochemical models, such as the ratio of outputs to net mineralization at steady state, can help diagnose differences in how the modeled ecosystems respond to N deposition.

Altering the internal cycling of N also increased N retention and improved the prediction of the response of aboveground C increment to N deposition. By adding the kinetic uptake of N by plant roots, nitrification, and an alternative denitrification routine, we increased the N deposition response by 25% (Figure 4, Model D to E). Allowing plant N uptake at night likely caused the greatest increase in N retention. In the clm4cn model, N uptake only occurred when plants were photosynthesizing but the loss processes occurred throughout the day. In the clm4mod model, the plant roots took up N throughout day and night, leading to buffered N uptake over time and continuous competition for N between plants and N loss processes. This indicates that

N retention in models can depend on the time scale that the model resolves the N cycle. For example, having N uptake as a direct function of photosynthesis may be suitable for models that resolve N dynamics at a daily to monthly time scale, such as the Biome-BGC (Thornton et al. 2002), while models that resolve N dynamics at sub-daily scales may need mechanisms through which N uptake is directly related to root biomass allocation and only indirectly related to photosynthesis.

Increased synergy between N deposition and atmospheric CO₂ also contributed to the larger response of C storage to N deposition in the clm4mod model than in the clm4cn model. Surprisingly, when averaged across all five sites, the increase in NPP resulting from N deposition was similar between the two models in the simulations when rising atmospheric CO₂ was not included (Figure 4a). However, when rising atmospheric CO₂ was included, the synergy between N deposition and CO₂ led to a larger total response to N deposition in the clm4mod model than clm4cn model. This increase in synergy was due to the greater retention of N deposition in the clm4mod than the clm4cn model. The reduction of N limitation resulting from the additional ecosystem N allowed an enhancement of photosynthesis by the next most limiting resource in the model, CO₂, whereas the clm4cn model remained N limited.

Consequently, the clm4mod model exhibited CO₂ fertilization in the simulation with both rising CO₂ and N deposition, enabled in part by rising N deposition. Overall, the increased enhancement of NPP due to synergy between N deposition and CO₂ from 7% in clm4cn to 30 % in clm4mod led to better correspondence with other studies: a 25% synergistic effect measured in field-based CO₂ fertilization experiment of needle

leaf pine forest (Oren et al. 2001) and a 28% synergistic effect reported by a global modeling analysis using BIOME-BGC model (Churkina et al. 2009).

4.2 Response to N fertilization

Overall, the clm4mod either improved or had no impact on the comparison to observations from N fertilization experiment, depending on the metric used in the model evaluation. In this study, we used three metrics to compare model predictions from clm4cn and clm4mod to N fertilization experiments, with each metric testing different aspects of model representation of N limitation. The first metric, the increase of ANPP in response to N fertilization, tested the productivity response, particularly wood and leaf production, to N fertilization. The ANPP response metric showed that, on average, the clm4mod corresponded better to observations than the clm4cn, with particular improvements at the Harvard Forest site. The improved correspondence at the Harvard Forest site was attributable to both a decrease in potential ANPP when N was not limiting (see discussion below) and an increase in the ANPP of the control treatment when buffered kinetic-based plant N uptake (along with the associated modifications to nitrification and denitrification) and soil buffering was included.

However, the ANPP increase metric did not include changes in mortality that were included in the second metric, $dC_{ACI}/dN_{\text{fertilization}}$ (i.e., the change in standing stock of aboveground C between years). The model modifications did not have an impact on the mean $dC_{ACI}/dN_{\text{fertilization}}$ response to N fertilization and both the clm4mod and clm4cn predicted larger $dC_{ACI}/dN_{\text{fertilization}}$ than observed. The two key differences between the ANPP responses and $dC_{ACI}/dN_{\text{fertilization}}$ to fertilization were:

one, increased mortality from N fertilization in the field studies may not decrease ANPP but will decrease dC/dN , and two, increased foliar production in the models increases ANPP without directly increasing dC/dN . It is likely that both of these mechanisms contributed to why the ANPP response in the clm4mod compared better to observations than the dC/dN response. Neither model included mechanisms through which elevated N inputs could increase tree mortality and tissue turnover, and both models predicted an increase in foliar productivity not found in the fertilization experiments (Magill et al. 2004, Pregitzer et al. 2008).

The productivity of the N fertilized treatment alone is the third metric describing how productivity responded to N fertilization. The ANPP in the field fertilized plots can be viewed as an approximation of the N unlimited productivity, assuming the fertilization level was high enough to meet plant demand and low enough to prevent negative effects of soil acidification. If so, the measure of N unlimited productivity is a metric that does not test the model response to N *per se*; rather, it tests the representation of the next most limiting resource in the models. Averaged across all six fertilization experiments, the clm4mod model did improve predictions of ANPP in the fertilized treatment. Higher ANPP in the fertilization treatments in the clm4mod model than the clm4cn model was surprising because the clm4mod model included changes to the CLM-CN 4.0, described in Bonan et al. (2012), that decreased canopy level photosynthesis. Therefore, including the modifications that lowered photosynthesis should have decreased the simulated productivity when N limitation was relieved. However, a key difference between the clm4cn and clm4mod models was that the simulated N fertilization experiments

relieved N limitation in the clm4mod simulations while it did not in the clm4cn simulations, potentially due to the high ecosystem retention of N in the clm4mod. Table 2 shows that the N unlimited ANPP in the clm4mod did not differ from the ANPP in the fertilization simulations, while the N unlimited ANPP in the clm4cn was 77% greater than the ANPP in the fertilization simulations. In contrast, the low ecosystem retention of N in the clm4cn maintained N limitation even at fertilization levels over double net N mineralization rates.

4.3 Implications

The set of model simulations presented in this study also provide insight into the observational data. The reported dC/dN is lower for the fertilization experiments than for the dC/dN from N deposition gradients (Table 2). Furthermore, there is a lower reported dC/dN in gradient studies in Europe than in the U.S (Table 2). Despite these disparities, we show that the reported dC/dN data are largely consistent with each other, if the differences in the magnitude and time-scale of N additions are taken into account. The clm4mod model simulations overlapped or were near the uncertainty bounds in the observations across the different times scales and magnitudes of N additions. The N deposition gradient studies measured the response to lower N inputs over a longer period of time (decades to a century), while the N fertilization experiments measured the response to higher inputs over a shorter time scale (years to decades). This indicates that the differences in N use efficiencies reported for different fertilization studies and N deposition gradients can be explained by differences in the magnitude and time scale of N addition.

Overall, the substantial increase in C storage response to N deposition that occurred as a result of modifications to the CLM-CN 4.0 model resulted in a better comparison to observations of forest growth across N deposition gradients and to N fertilization experiments. The improved sensitivity to N inputs was driven primarily by the introduction of a less open N cycle through reduced rates of N fixation and N gas loss and greater buffering of plant N uptake over time. At the global scale, the modifications to CLM-CN presented are likely to improve the model correspondence to the globally distributed set of nitrogen fertilization experiments, ^{15}N tracer studies, and small catchment N budgets that have been previously used to benchmark global biogeochemical models (see Chapter 2). Furthermore, we show that due to non-linearity in ecosystem response to N addition, testing models with both the response to gradual increases in N inputs over decades (N deposition) and N pulse additions of N over multiple years (nitrogen fertilization) allows for greater understanding of the mechanisms governing C-N coupling.

5.0 Acknowledgements

We would like to thank Cayelan Carey, Timothy Fahey, and Natalie Mahowald for helpful comments on the manuscript. Eric Kluzek, Dan Ricutto, and Peter Thornton provided assistance with the CLM-CN simulations. National Science Foundation (NSF) awards to Peter Hess et al. (NSF-ETBC award #1021613), the NSF IGERT in Cross-Scale Biogeochemistry and Climate, and the Cornell Biogeochemistry and Environmental Biocomplexity Small Grant Program financially supported the project.

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SUPPLEMENTAL INFORMATION

SI.1 clm4mod model description

The clm4mod model includes changes to the canopy scaling of photosynthesis, maximum photosynthetic rates, radiative transfer, leaf photosynthesis, and stomatal conductance described in Bonan et al. (2012) and (2011). Additional modifications are described below.

SI.1.1 Nitrogen uptake by plants

Plant uptake of mineral nitrogen (N) in CLM-CN 4.0 (“clm4cn”) is based on the N required to match the demand set by N unlimited photosynthesis (i.e. potential gross primary productivity) and plant tissue C:N stoichiometric constraints. In the clm4cn model, N uptake is independent of allocation to fine root mass. The clm4mod model represents N uptake as a function of fine root carbon (C) mass (C_{root}), soil mineral N availability ($\text{NH}_{4,\text{av}} + \text{NO}_{3,\text{av}}$), soil temperature ($f(T)$), and plant demand for N ($f(N_{\text{labile}})$).

$$U_{N,\text{plant}} = V_{n,\text{max}} \frac{\text{NH}_{4,\text{av}} - \text{NO}_{3,\text{av}}}{(\text{NH}_{4,\text{av}} + \text{NO}_{3,\text{av}}) + K_{\text{min}}} C_{\text{root}} f(N_{\text{labile}}) f(T)$$

where $f(N_{\text{labile}})$ down regulates the uptake capacity based on the stock of labile N in the plant. As N_{labile} approached one year's worth of N turnover of live tissue (x ; leaves,

fine roots, and live wood), the maximum uptake capacity decreases. The down regulation function is based on Aber et al. (1997).

$$f(N_{labile}) = \sqrt{1 - \frac{N_{labile}}{x}}$$

The temperature function $f(T)$, is the same function governing soil decomposition, nitrification (see below), and denitrification (see below). $NH_{4,av} + NO_{3,av}$ are the concentrations of ammonium and nitrate that are available for plant uptake (see below). V_{nmax} is the maximum uptake capacity at 25°C when N demand was large (i.e. $f(N_{labile}) = 1$). K_{min} is the half saturation constant for plant uptake.

The availability of N within the plant for growth is buffered so that a proportion (2%) of the labile N pool is available to build plant tissue.

SI.1.2 Fine root turnover

In the clm4cn model, the turnover of fine root C is linked to the turnover of leaf C. In the clm4mod version, the root turnover is an explicit parameter and is decoupled from leaf turnover. Root turnover occurs throughout the year, rather than only when leaves senesce. Root turnover is maintained at the same rate as the clm4cn model for all species (1.0 yr^{-1}), except boreal and temperate needleleaf species, which has a turnover of 0.3 yr^{-1} based on White et al. (2000). Decoupling fine root turnover from leaf turnover allows fine roots to be present throughout the year and permits a fast response of plant N uptake in the spring.

SI.1.3 Soil N dynamics

The clm4mod version of the model includes soil inorganic pools of NH_4 and NO_3 , rather than a single inorganic mineral N pool, as implemented in the clm4cn model. The NH_4 pool is buffered to represent an exchangeable pool and a pool in solution that is available for plants, immobilization, nitrification, and leaching.

$$\text{NH}_{4,av} = b_{\text{NH}_4} \text{NH}_4$$

where b_{NH_4} is assumed to be 10% of total soil NH_4 (Gerber et al. 2010). Constant buffering capacity is a first approximation for a more complex process of resorption/desorption. Future model development could parameterize non-linearity into the buffering capacity that is a function of the total soil organic matter and the bulk density of the soil. NO_3 is assumed to have no buffering capacity in the soil therefore $\text{NO}_{3,av} = \text{NO}_3$.

SI.1.4 Internal N cycling

The clm4mod model assumes that microbes have priority for soil mineral N to meet the immobilization demand. Plant uptake and immobilization of N is divided between NH_4 and NO_3 in proportion to the availability of each N species ($\text{NH}_{4,av}$; $\text{NO}_{3,av}$). The conversion of NH_4 to NO_3 (nitrification) is represented as function of net N mineralization, NH_4 availability, temperature, and water availability based on Parton

et al. (2001). Nitrifiers are assumed to be less competitive for NH_4 than plants and immobilization into soil organic matter

$$N_{\text{nitr}} = K_{\text{nitr1}} N_{\text{mineralization}} + K_{\text{nitr2}} \text{NH}_{4,\text{av,nitr}} f(T) f(W)$$

where the $\text{NH}_{4,\text{av,nitr}}$ is the NH_4 available for nitrification

$$\text{NH}_{4,\text{av,nitr}} = \text{NH}_{4,\text{av}} - U_{\text{NH}_4,\text{plant}} - U_{\text{NH}_4,\text{soil}}$$

K_{nitr1} , K_{nitr2} , $f(T)$, and $f(W)$ are the proportion of net mineralization that is nitrified, maximum nitrification rate (sec^{-1}) based on available $\text{NH}_{4,\text{av,nitr}}$, temperature modifier, and water availability modifier, respectively. $f(T)$ and $f(W)$ are the same temperature and water functions that modified decomposition and plant N uptake (Thornton et al. 2007, 2009). The clm4mod model ignores the effect of pH on nitrification (Parton et al. 1996). A proportion (0.02) of the nitrification is lost to N_2O and not converted to NO_3 (Parton et al. 2001)

SI.1.5 Inorganic N loss

In the clm4mod model, the leaching of NH_4 is a function of the soil water drainage and $\text{NH}_{4,\text{av}}$, minus the NH_4 uptake by plants, immobilization, and nitrifiers during the model time step. Likewise, the leaching of NO_3 is a function of the soil water drainage and NO_3 , minus the NO_3 taken up by plants and immobilization during the model time step.

The loss of NO_3 through denitrification is modeled as a function of the available nitrate $\text{NO}_{3,av}$ (minus nitrate uptake by plants, immobilization, and leaching), the ratio of soil water to saturated soil water, and total respiration from soil organic matter decomposition (a proxy for microbial activity and oxygen composition; $\text{CO}_{2,soil}$). The representation is described in Bradbury et al. (1993) and Yang et al. (2010).

$$N_{denit} = D \text{CO}_{2,soil} \text{NO}_{3,av} \frac{W}{W_s}$$

where D is the denitrification rate per g of CO_2 respiration of soil organic matter, the W is soil water in the top five soil layers and W_s is water holding capacity at saturation.

SI.1.6 Biological N fixation

The biological N fixation in temperate and boreal forests is modified to better represent observations that N fixing tree species are largely absent from mid- to late-successional forests, but can be present in earlier successional forests (Crews 1999). Based on biome specific data on N fixation and evapotranspiration in Cleveland et al. (1999), annual non-symbiotic fixation is a function of annual evapotranspiration and occurs in all ecosystems:

$$N_{fix,nonsym} = 0.0006AAET + 0.0117$$

where $AAET$ is annual evapotranspiration of the previous year. Non-symbiotic N fixation is added to the soil NH_4 pool.

Symbiotic N fixation is function of the plant functional type, proportion of grid cell occupied by the plant function type, leaf area index, and annual evapotranspiration. Symbolic N fixed is determined by subtracting the non-symbiotic relationship described above from the relationship between total N fixation and evapotranspiration in Cleveland et al. (1999: central relationship; Figure 3.SI.1). In grasslands and tropical ecosystems, symbolic N fixation is added to the plant labile N pool. In temperate and boreal forests with leaf area index < 1 , symbiotic N fixation is also added to the plant labile N pool, as they are assumed to be early successional and contain some N fixing plants. No symbiotic N fixation is added to the plant labile N pool in temperate and boreal forest with leaf area index ≥ 1 . The overall relationship describing symbiotic N fixation is

$$N_{fix,sym} = \begin{cases} w_{pft}(0.0018AAET - 0.289) & \text{temperate or boreal trees and LAI} < 1 \\ 0 & \text{temperate or boreal trees and LAI} \geq 1 \\ w_{pft}(0.0018AAET - 0.0289) & \text{all other pfts} \end{cases}$$

where w_{pft} is the proportion of the grid cell occupied by the plant functional type. N fixation is constrained to be $\geq 0 \text{ g N m}^{-2} \text{ yr}^{-1}$

SI.1.6 Dissolved organic matter dynamics

Dissolved organic N losses can be important for maintaining N limitation (Menge 2011, especially in ecosystems with low anthropogenic N inputs (Hedin et al.

1995). A simple representation of the production and leaching of dissolved organic matter is added to the CLM-CN. As presented in Gerber et al. (2010), DOM production is assumed to be a fraction of the turnover of the structural litter pool. In the clm4mod model, DOM production is parameterized to be 1.5% (p_{dom}) of the transfer from the lignin-based litter pool (Litter 3) to its receiving soil organic matter pool (SOM 3). So that DOM production does not alter the decomposition rate of the litter pool, the C:N ratio of DOM must equal that of receiving SOM pool. Therefore, the C:N of DOM is set to be 10:1 (CN_{DOM}). Future research should focus on improving the representation of DOM production so that the C:N better match observations (i.e. more C produced for the same N production). However, increasing the C:N ratio of the DOM while maintaining the same production of DON will likely have little effect on N cycle. All DOM produced is assumed to be unavailable for plant uptake and immobilization. The leaching of DOM is based on the water drainage and the total soil water.

SI.2 Model descriptions for intermediary models used in sensitivity analysis

The series of intermediary models using to the sensitivity analysis are described below:

Model A (clm4cn): described in the main text and (Thornton and Rosenbloom 2005, Thornton et al. 2007, 2009)

Model B (Multi-layer canopy): Model B adds to model A modifications to the canopy scaling of photosynthesis using a multi-layer approach, maximum photosynthetic rates, radiative transfer, leaf photosynthesis, stomatal conductance described in Bonan et al. (2012) and (2011). Model B used Kattge et al. 2009 values for V_{cmax} (see main text).

Model C (Multi-layer + soil buffering): Model C adds a soil buffering parameter to Model B. The soil buffering assumes that 19% of the generic soil mineral N pool is available for plant uptake, immobilization in to soil organic matter, leaching, and denitrification. The parameter (19%) is chosen to represent a distribution of the generic soil mineral N pool into 90% NH_4 and 10% NO_3 with the same buffering parameters used in the clm4mod model. By assuming 10% of N is NO_3 , the model is consistent with the preexisting parameterization in of N available for leeching losses in Models A and B.

Models D (Multi-layer canopy + soil buffer + less open N cycle): Model D creates a less open N cycle by adding to Model C the lower N fixation parameterization described in the main text and Supplemental Information. To isolate the impact of a less open N cycle rather than the sensitivity to N reduced N inputs, we adjusted two parameters to decrease the N loss and maintain the same pre-industrial productivity as Model C. In Model C has two primary N loss pathways: 1) 1% of net mineralization is lost through denitrification and 2) 50% per day of N that exceeds plant and microbial demand is lost through denitrification. N loss from the former depends on

the turnover of soil organic matter and requires increased net mineralization to increase N loss. In contrast, N loss from the latter does not directly depend on N mineralization and responses to changed in N availability at short-time scales. Model D decreases the proportion of net mineralization that is denitrified from 1% to 0.75% and excludes loss pathway #2 by setting the excess denitrification rate to 0. We also investigated an alternative parameterization of N loss by decreasing proportion excess N loss through denitrification from 50% to 3.5% day⁻¹ and excluded loss pathway #1 by setting proportion of net mineralization lost through denitrification to 0. Both approaches gave similar results.

Model E (clm4mod w/o plant buffering): Model E includes all the changed described for the clm4mod model (main text and Supplemental Information), but set plant buffering capacity (b_{nlabile}) to 0 (i.e. 100% of plant labile N is available to fix with C in a time step).

Model F (clm4mod w/ plant buffering): Model F includes all the changed described for the clm4mod model (main text and Supplemental Information).

Supplemental Information References

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Supplemental Information Table 1. New parameters introduced to the CLM-CN 4.0.

Parameter	Value	Units	Description	Reference
V_{nmax}	$2.7 \cdot 10^{-8}$	$\frac{g\ N}{g\ C} sec^{-1}$	Maximum N uptake per unit fine root C at 25C	none
K_{min}	1	$gN\ m^{-2}$	Half saturation constant for plant nitrogen uptake	Yang et al. 2010
x	1	proportion	Proportion of 1 years worth of live tissue nitrogen turnover	Gerber et al. 2010
b_{NH_4}	0.10	proportion	Proportion of soil NH_4 available for plant uptake, immobilization and loss processed	Gerber et al. 2010
b_{NO_3}	1	proportion	Proportion of soil NO_3 available for plant uptake, immobilization and loss processed	Gerber et al. 2010
$b_{nlabile}$	0.02	proportion	Proportion of plant labile nitrogen available to build tissue per 30 minute time step	none
K_{nitr1}	0.2	proportion	Proportion of net mineralization that is nitrified	Parton et al. 2000
K_{nitr2}	0.1	day^{-1}	Maximum proportion of available NH_4 nitrified	Parton et al. 2000
K_{n2o}	0.02	proportion	Proportion of nitrification lost as N_2O	Parton et al. 2000
D		gC^{-1}	Maximum denitrification rate per g of soil respiration	Bradberry et al. 1993
p_{DOM}	0.015	proportion	Proportion of litter mass transferred from litter 3 pool to soil 3 pool that produces dissolved organic carbon and nitrogen	Gerber et al. 2010

Supplemental Information Table 2. Mean simulated pre-industrial nitrogen fluxes ($\text{g N m}^{-2} \text{yr}^{-1}$) average across all five sites in Table 1 (± 1 S. E.).

Flux	clm4cn	clm4mod
Nitrogen fixation	1.3 ± 0.1	0.26 ± 0.01
Nitrogen deposition	0.15 ± 0.01	0.15 ± 0.01
Nitrogen gas loss	1.4 ± 0.1	0.26 ± 0.01
Mineral nitrogen leaching	0 ± 0	0.07 ± 0.01
DON leaching	NA	0.1 ± 0.004
Plant nitrogen uptake	6.2 ± 0.67	6.9 ± 0.29
Net nitrogen mineralization	6.1 ± 0.66	6.5 ± 0.25
Nitrification	NA	3.6 ± 0.06

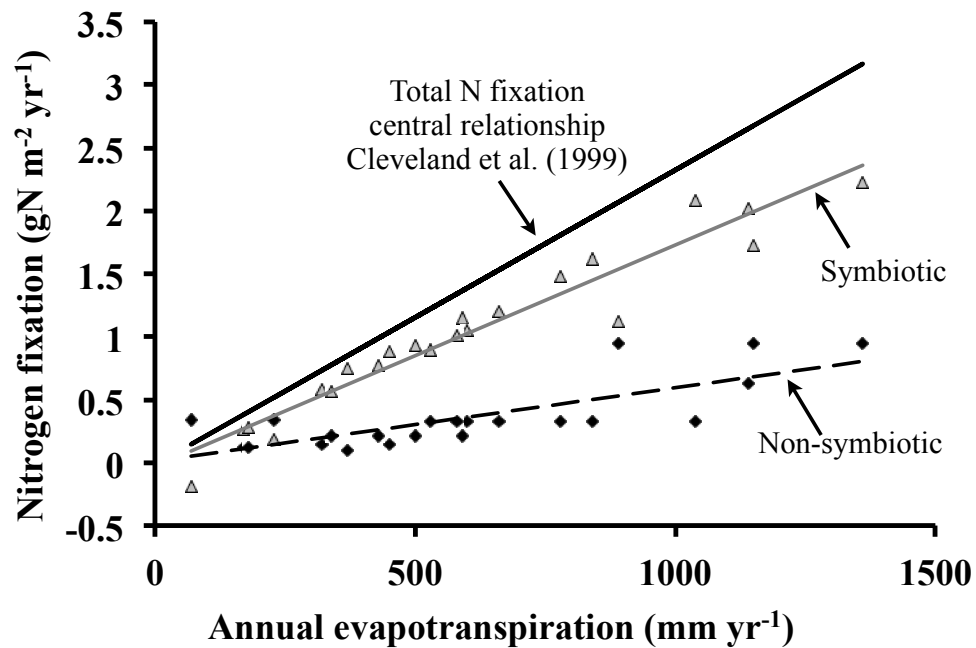


Figure 3.SI.1. The relationship between total, symbiotic and non-symbiotic nitrogen fixation and annual evapotranspiration. Data are from Cleveland et al. (1999). The relationship for total fixation is from the central N fixation line in Figure 1 of Cleveland et al. (1999).

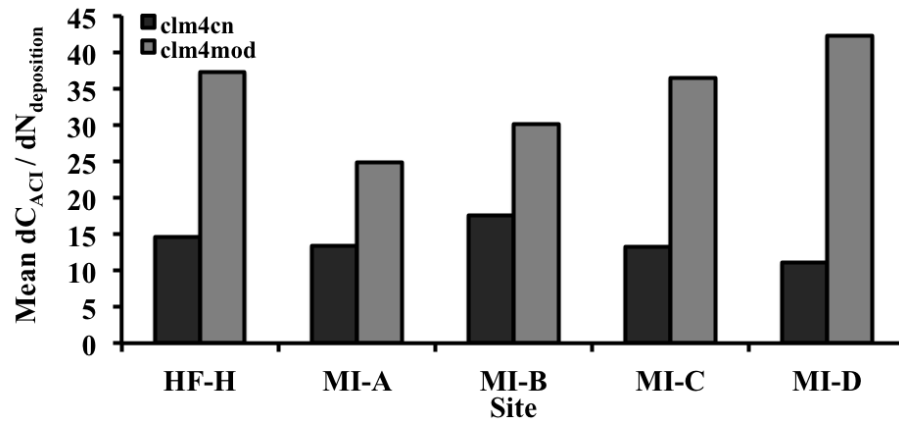


Figure 3.SI.2. Aboveground carbon increment (ACI) response to nitrogen deposition for the five different temperate deciduous forests in Table 1. The response is expressed as the additional net stem increment per additional nitrogen deposition input ($dC_{ACI}/dN_{deposition}$). The mean for the period (1994-2004) is shown.