

The Decoupling of Terrestrial Carbon and Nitrogen Cycles

Human influences on land cover and nitrogen supply are altering natural biogeochemical links in the biosphere

Gregory P. Asner, Timothy R. Seastedt, and Alan R. Townsend

Global cycles of carbon (C) and nitrogen (N) are coupled through processes of terrestrial and marine biomass accumulation, decomposition, and storage. Alfred Redfield (1958) proposed that nearly constant carbon-to-nutrient ratios in marine phytoplankton and bacteria required that changes in one biogeochemical element be matched by changes in other essential elements. The "Redfield ratio" approach has proven valuable in understanding not only marine biogeochemistry (Broecker et al. 1979, Howarth 1988), but also carbon and nutrient cycles on land (Bolin and Cook 1983, Melillo and Gosz 1983, Reiners 1986, Rosswall 1981, Vitousek 1982). Both plant species diversity and their ability to produce varying amounts of structural material cause greater variation in carbon to nutrient ratios within terrestrial biomass than is found in the ocean (Vitousek et al. 1988). Yet nutrient limitation of net terrestrial

Changes in forest area, nitrogen supply, and biomass burning may decrease nitrogen-stimulated terrestrial carbon storage

primary production is still commonplace: In particular, the photosynthetic requirement for nitrogen, coupled with relatively low levels of available nitrogen in many terrestrial ecosystems, causes carbon uptake and storage on land to be tightly regulated by the nitrogen cycle (Vitousek and Howarth 1991).

Nitrogen limitation of primary production, and the consequential coupling of carbon and nitrogen, arises in large part because annual external inputs of nitrogen to most systems—through either atmospheric deposition or biological fixation—are much lower than the nutritional demand or uptake potential of plants. Nitrogen requirements must therefore be met by efficient internal recycling between live plant tissue and decomposing organic matter (Figure 1; Chapin et al. 1986, Cole and Rapp 1981, Johnson and Van Hook 1989, Seastedt and Knapp 1993, Vitousek 1982). Where nitrogen is limiting, its efficient retention within the system results in extremely low nitrogen losses to both aquatic and atmospheric environments (Bowden

et al. 1991, Howarth et al. 1995, Johnson 1992, Matson and Vitousek 1990), and any changes in the total nitrogen capital of the system are usually matched by parallel changes in total carbon (Rastetter et al. 1992).

The coupling of carbon and nitrogen cycles has attracted new focus in light of current and projected human perturbations to the environment. In particular, considerable research has been devoted to understanding how the terrestrial carbon cycle will respond to and feed back on changes in atmospheric carbon dioxide and temperature. Simple analyses based only on relationships among carbon assimilation in biomass, temperature, and carbon dioxide concentrations yield predictions that are markedly different, often even in sign, from those that account for the coupled response of carbon and nutrient cycles (Schimel et al. 1990, 1994, Townsend and Rastetter 1996). For example, the relationships among temperature, decomposition, and net primary production predict that warming will result in a net carbon loss from land to the atmosphere, producing a positive feedback to further warming (Townsend et al. 1992, Woodwell 1990). However, the increased rates of decomposition under a warmer climate that produce the carbon dioxide loss will also increase nitrogen mineralization, potentially leading to increased plant growth and a net gain—rather than loss—in overall ecosystem carbon (Rastetter et al. 1992, Schimel et al. 1994, Shaver et al. 1992). This gain occurs through a repartitioning

George P. Asner is a doctoral student in the Department of Environmental, Population, and Organismic Biology and a research assistant at the Center for the Study of Earth from Space of the Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309. Timothy R. Seastedt is an associate professor and Alan R. Townsend is an assistant professor in the Department of Environmental, Population, and Organismic Biology and the Institute for Arctic and Alpine Research, University of Colorado, Boulder, CO 80309. © 1997 American Institute for Biological Sciences.

of nitrogen pools from soils, which have low C:N ratios, to plants, which generally have much higher C:N ratios.

In the long term, however, increases in carbon storage must eventually become nitrogen limited unless a novel source brings additional nitrogen into the system (Diaz et al. 1993). Similar feedbacks leading to growth limitation are seen in the response of plants to elevated carbon dioxide: Plants grown in fertilized environments often demonstrate marked (although possibly short-term) increases in growth under elevated carbon dioxide, but when the same plants are exposed to high carbon dioxide at ambient soil nutrient levels, they tend to show much less of a response (Bazzaz 1990, Comins and McMurtrie 1993).

On a contemporary global scale, the carbon–nitrogen cycle coupling is further reflected by recent findings that part of the “missing” carbon sink¹ may be attributed to fertilization of nitrogen-limited ecosystems by anthropogenically enhanced levels of atmospheric nitrogen deposition (Galloway et al. 1995, Schimel 1995, Schindler and Bayley 1993, Townsend et al. in press). However, the developing global atmospheric perspective also reveals that perturbations to carbon and nitrogen cycles are not parallel: the net loss of carbon from land to atmosphere in recent decades has occurred concurrently with a net gain of biologically available nitrogen to terrestrial ecosystems. Although this pattern does not preclude a nitrogen-stimulated carbon sink, we believe that it is evidence of ongoing regional changes in the carbon–nitrogen cycle coupling that may ultimately eliminate such a sink.

¹The “missing” carbon sink refers to the quantity of carbon released from fossil fuel combustion, deforestation, and cement production each year (7.1 ± 1.1 Pg C/yr; $1 \text{ Pg} = 10^{15} \text{ g}$) that is unaccounted for by measured accumulation in the atmosphere (3.2 ± 0.2 Pg C/yr) plus estimated fluxes to the ocean (2.0 ± 0.8 Pg C/yr). This missing quantity, roughly 1.5 Pg C/yr , is thought to represent a flux from the atmosphere to the terrestrial biosphere (thus the term “sink”). Potential mechanisms to account for the missing sink include fertilization of net primary production by elevated carbon dioxide or nitrogen deposition and forest regrowth in the Northern Hemisphere. For more detailed information, see Schimel (1995).

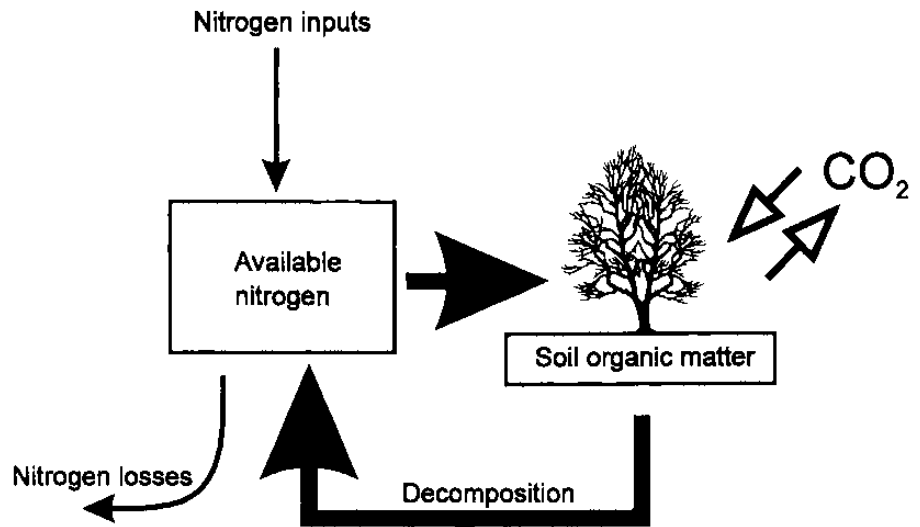


Figure 1. A simple nitrogen cycling model for forest ecosystems. Internal recycling of nitrogen through decomposition (fat arrows) provides the bulk of inorganic nitrogen for plant uptake. Nitrogen inputs and losses (thin arrows) are relatively small compared with internal fluxes, especially in nitrogen-limited ecosystems.

In this article, we emphasize three points that, when integrated to the global level, provide us with a new perspective on how human influences on the carbon and nitrogen cycles are achieving global significance. First, in the temperate zone, high levels of nitrogen deposition must eventually decrease the areal extent of nitrogen-limited ecosystems, such that further nitrogen deposition will not lead to more carbon uptake by vegetation (Figure 2a). Second, the net loss of temperate forests and woodlands and net gain in agricultural land over the past 300 years have resulted in a regional net decrease in the amount of ecosystem carbon that can be fixed and stored per unit nitrogen. Third, in tropical latitudes an increase in the extent and frequency of biomass burning—especially in tropical savannas—causes long-term losses of nitrogen from some systems, thereby reducing their potential to regain carbon lost in combustion (extreme nitrogen limitation; Figure 2a). We contend that these regional-level perturbations are altering the natural linkages between the terrestrial carbon and nitrogen cycles to an unprecedented extent, an effect that could reduce the future carbon storage potential of the biosphere. In the following sections, we provide evidence to support each of these points,

and we use a global nitrogen deposition and land-cover perturbation simulation to illustrate several of these effects. Finally, a general decoupling of terrestrial carbon and nitrogen cycles has environmental implications that go well beyond its effect on atmospheric carbon dioxide.

Nitrogen deposition in temperate regions

Temperate northern latitudes ($25\text{--}55^\circ\text{N}$) have been subjected to elevated atmospheric nitrogen deposition for several decades, with some areas now receiving an order of magnitude more nitrogen than in preindustrial times (Galloway et al. 1995). Because plant growth in much of the temperate zone is limited by nitrogen (Vitousek and Howarth 1991), high nitrogen deposition may contribute to a significant carbon sink in these regions (Galloway et al. 1995, Townsend et al. 1996). Compared with grassland ecosystems, this sink should be amplified in forests, where a combination of high C:N ratios and long lifetimes of woody plants allows for relatively large amounts of carbon to be fixed and stored for decades per unit nitrogen (Rastetter et al. 1992). However, a negative effect of chronically high nitrogen deposition has been observed in some forested areas of

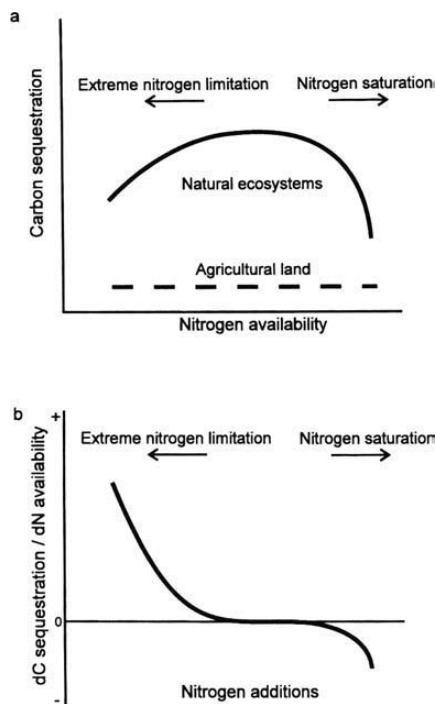
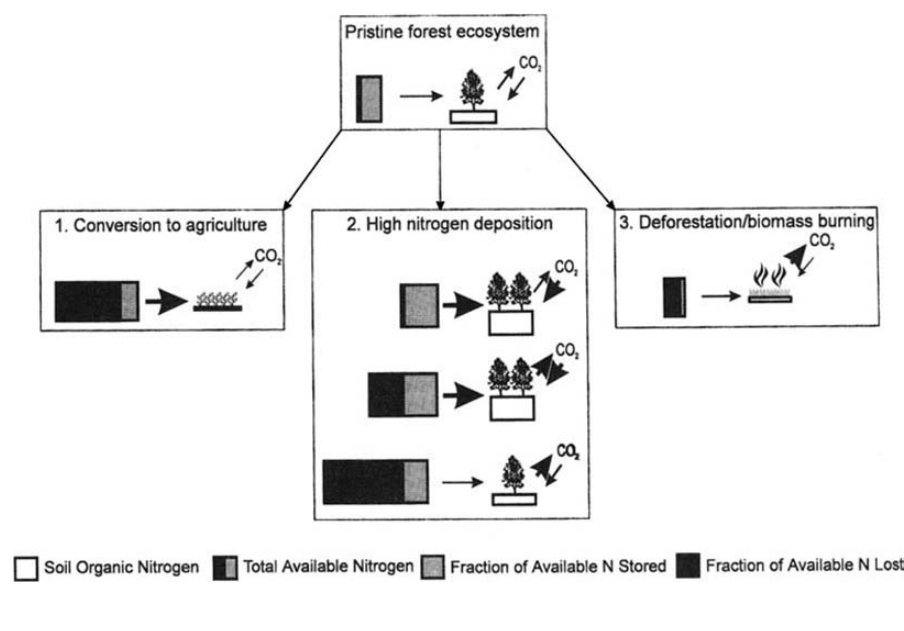


Figure 2. (a) A conceptual model showing that nitrogen enrichment affects carbon sequestration in plants and soils in a curvilinear fashion. Too much nitrogen (saturation) plays a role in ecosystem decline as micronutrient impoverishment and soil acidification increase. Too little nitrogen (e.g., as a result of high fire frequencies on land previously occupied by forest or in savannas) reduces carbon sequestration capacity because extreme nitrogen limitation may be induced through pyrodenitrification. Nitrogen levels of agroecosystems, by contrast, have little to no influence on long-term carbon storage due to soil management practices and the fast turnover time of crops. (b) Hypothetical response of vegetation carbon pool in a nitrogen-limited system to additions of anthropogenic nitrogen. Initially, there will be significant increases in carbon for every increase in nitrogen, but as nitrogen becomes less limiting, this response will approach zero, and it may even become negative in systems that chronically receive extremely high nitrogen additions.

North America and Europe, in which nitrogen enrichment results in soil acidification and micronutrient impoverishment, leading to ecosystem decline and a reduction in net carbon uptake. Aber et al. (1989) and Schulze (1989) refer to this process as *nitrogen saturation*. These saturation effects may not currently be

Figure 3. Three extreme carbon-to-nitrogen cycle perturbation phenomena: (1) conversion of forest to cropland, (2) nitrogen deposition in temperate forests, and (3) deforestation or increased savanna biomass burning in the tropics. All phenomena share the same starting point (top center), a pristine forest containing a relatively small amount of total available nitrogen, from which nitrogen losses are small. Arrow thickness indicates the relative fluxes of nitrogen and carbon dioxide in each nitrogen perturbation scenario. Boxes within each section depict the relative nitrogen pool sizes for each scenario; see key at bottom. (1) Conversion of forests to croplands creates large regions that cannot store carbon in the long term (decades to centuries). Nitrogen inputs via fertilizer are enormous, and losses are typically high due to fertilizer application inefficiencies and crop harvesting. (2) In temperate regions, increased nitrogen deposition from fossil fuel burning supports a transient increase in carbon storage or carbon dioxide assimilation. However, as nitrogen deposition rates exceed biological demand, nitrogen losses by denitrification and leaching increase. Extreme nitrogen loading (saturation) can lead to large nitrogen losses, forest decline, and carbon release to the atmosphere. (3) Tropical biomass burning causes nitrogen losses by pyrodenitrification. Deforestation in these regions and increased fire frequency in some savannas create nitrogen deficits that impede carbon sequestration. Under extremely frequent fire regimes, carbon lost through combustion is not replaced in subsequent regrowth.



observed in some regions where nitrogen deposition is high; nevertheless, the amount of carbon stored per nitrogen deposited must eventually decrease as other factors that limit net primary production (e.g., other nutrients) increase in relative importance. In a sense, nitrogen saturation can be considered a process that begins when nitrogen no longer limits production due to human activities, and that may ultimately result in ecosystem decline.

Global nitrogen deposition is expected to double in the next 25 years (Galloway et al. 1994), but carbon storage is unlikely to rise at a similar rate. In the northern temperate zone, continued high levels of nitrogen

deposition will eventually increase the areal extent of ecosystems that are no longer limited by nitrogen, leading to a decrease in annual carbon storage that results from nitrogen fertilization in this region. Southern latitude forests (20–50°S) are expected to experience increases in nitrogen deposition as nations continue to industrialize (Galloway et al. 1994), which will likely result in effects similar to those seen in northern forests: a short-term rise in carbon sequestration followed by a long-term leveling or decline in carbon uptake as the amount of deposited nitrogen exceeds that which is usable by vegetation. Even if southern latitude forests do continue to ac-

cumulate carbon for decades to centuries, their total area is not sufficient to produce a significant global carbon dioxide sink (Townsend et al. 1996).

Pronounced increases in nitrogen deposition to moist tropical forests are also expected in the coming century, but nitrogen limitation is less pervasive in these forests (Vitousek and Howarth 1991). Tropical forest soils tend to be highly weathered. Plant growth in these ecosystems is often limited by phosphorus, by other rock-derived elements (Crews et al. 1995), or perhaps even by light; thus, tropical forests are unlikely to store significant excess carbon in response to increases in available nitrogen.

In sum, where nitrogen is in short supply, increases in nitrogen should be matched by significant increases in carbon, but as nitrogen inputs continue to rise, the response of the carbon cycle must eventually approach zero and may even become negative in some regions (Figure 2b). Thus, at best, a nitrogen-stimulated carbon sink can last only until nitrogen limitation of growth is alleviated; at worst, any net storage of carbon in the early years of elevated deposition may be offset by later carbon loss as the system degrades (Figure 3).

Shifting land use and land cover

The link between the carbon and nitrogen cycles is highly dependent on the global distribution of land cover, which has changed dramatically in the last 300 years (Table 1). The world has experienced a large decrease in forest and woodland cover and a concomitant increase in agricultural land. Global cropland and pasture area has more than doubled in the last 140 years, to 32% of the earth's terrestrial surface (Houghton 1994). Much of this agricultural land was converted from forests; aside from dense urban centers, such transformations represent the most dramatic shift in the carbon and nitrogen storage and flux characteristics of the earth's surface. An additional 21% to 37% of the global land surface may be convertible to crop land, and much of this land will

Table 1. Regional and total global percentage change in forest/woodland, grassland/pasture, and agricultural land from 1700 to 1980 (Houghton et al. 1983, Richards 1990). The first group of entries includes regions or countries that are currently experiencing, or will experience, significant levels of nitrogen deposition in the next 25 years (Galloway et al. 1994, Townsend et al. 1996). The second group includes regions that are likely to experience extreme nitrogen limitation via deforestation and biomass burning (Crutzen and Andreae 1990, Robertson and Rosswall 1986). Numbers in parentheses indicate the actual areal extent of change in 10^6 ha.

Region	Forest/woodland	Grassland/pasture	Cropland
Subject to N deposition			
Europe	-7.8% (-18)	-27.4% (-52)	+104.5% (+70)
North America	-7.3% (-74)	-13.7% (-125)	+666.7% (+200)
Russia/North Asia	-17.3% (-197)	-0.3% (-3)	+606.1% (+200)
China	-57.0% (-77)	-2.9% (-28)	+362.1% (+105)
Southeast Asia	-7.1% (-18)	-26.4% (-33)	+1275.0% (+41)
South Asia	-46.3% (-155)	-1.1% (-2)	+296.2% (+157)
Northern Africa/ Middle East	-63.2% (-24)	-5.6% (-63)	+435.0% (+87)
Subject to N depletion			
Tropical Africa	-20.9% (-284)	+10.1% (+106)	+404.5% (+178)
Latin America	-20.3% (-294)	+26.2% (+159)	+1928.6% (+135)
Pacific developed countries	-7.9% (-21)	-4.9% (-31)	+1060.0% (+53)
Global total	-18.7% (-1162)	-1.0% (-72)	+466.4% (+1236)

likely be transformed in the future (Houghton 1994).

Agricultural lands dramatically alter the natural linkages between carbon and nitrogen cycles. They typically receive large amounts of excess nitrogen from fertilizer (Matthews 1994), but a combination of management practices, low C:N ratios of most crops, and rapid turnover time of crops prevents the nitrogen inputs from resulting in long-term carbon storage (Burke et al. 1989). Thus, the global-scale expansion of cropland is decreasing the available surface area on which the natural carbon-nitrogen cycle coupling can function and is increasing fluxes of excess reactive nitrogen from the terrestrial landscape to aquatic systems and to the atmosphere (Figure 3; Howarth et al. 1996).

Many areas that might have the potential to store carbon in response to elevated nitrogen are experiencing concurrent losses in forests and woodlands and gains in croplands. For example, by the year 2020, anthropogenic nitrogen enrichment mediated by fossil fuel combustion and fertilizer use in Asia alone is expected to increase the global anthropogenic input of nitrogen to the biosphere by 40% (Galloway et al.

1995); moreover, Asia continues to have one of the highest deforestation and cropland expansion rates in the world (Houghton 1994, Richards 1990). Forest and woodland extent is also decreasing due to urban and rural development, producing artificial or degraded landscapes that contribute little, if at all, to carbon storage. From a regional standpoint, the rate at which an area's carbon cycle becomes less sensitive to nitrogen additions increases successively as forests are converted to croplands, towns, and cities.

Some temperate regions, including parts of North America, Europe, and the former Soviet Union, have undergone reforestation of abandoned agricultural land since the turn of the century (Dixon et al. 1994, Richards 1990), and these changes may partially offset the general decrease in carbon storage hypothesized here. However, current carbon sink estimates for Northern hemisphere forest regrowth are highly variable, ranging from 0–1 Pg C/yr (1 Pg = 10^{15} g; Dixon et al. 1994, Houghton 1993, Schimel 1995). The uncertainty in this estimate reflects the difficulty in quantifying such things as the geographic extent of recovering forests, the decay of logging debris for decades after the ini-

tial and repeated cutting of forests, the oxidation of removed wood products and in situ soil carbon, and the immediate burning of forest materials at the logging sites (Houghton 1993).

Part of the uncertainty in the “regrowth sink” also arises from the difficulty in discerning how much additional regrowth is being stimulated by elevated carbon dioxide and nitrogen. However, the effects of regrowth on the overall regional coupling of carbon and nitrogen cycles are somewhat independent of this debate. A given secondary forest may or may not be a significant carbon sink, but conversion of agricultural land back to forests does represent the best way to restore some of the natural carbon–nitrogen cycle linkages of a region. Even if forest recovery in the Northern Hemisphere is currently a significant carbon sink, it is surely a temporary one because net annual carbon uptake declines with increasing stand age (Houghton 1993). Moreover, increases in demand for agricultural land could result in the felling of these secondary forests again in the future.

Combined land cover and nitrogen deposition effects

To better demonstrate the effect of land-cover change on potential terrestrial carbon storage, we used a nitrogen deposition perturbation model to estimate 1990 global terrestrial carbon uptake due to fossil fuel–derived nitrogen deposition. The model is described in detail by Townsend et al. (1996); briefly, it uses a global nitrogen deposition map linked to spatially explicit ecosystem response algorithms that vary based on land-cover and land-use category. These algorithms, adapted from the CENTURY model (Parton et al. 1993, Schimel et al. 1994), control carbon and nitrogen fluxes between vegetation and soil compartments based on biome-specific C:N stoichiometries. The model operates on a global 1×1 degree grid to capture the spatially heterogeneous response of the world’s biomes to nitrogen enrichment. Nitrogen deposition is estimated for each grid cell based on a three-dimensional atmospheric chemical transport model (Penner et al. 1991).

Our carbon storage calculation was based on a global data set of probable pristine biome distribution, with no human influence (e.g., agriculture) on land cover (Matthews 1983). We compared this result with two previous simulations by Townsend et al. (1996), in which carbon storage was assumed to be negligible in agricultural areas. Of their two simulations, one included a gradual decrease in ecosystem nitrogen retention with time in regions of high nitrogen deposition (e.g., North America, Europe, Asia), thereby simulating the likely effects of nitrogen saturation. Our no-agriculture/no–nitrogen saturation simulation estimated global carbon uptake at 1.04 Pg/yr. Townsend et al.’s estimates with agriculture/no-saturation and agriculture/saturation were 0.74 and 0.44 Pg/yr, respectively. This comparison clearly demonstrates that agricultural expansion has decreased the global capacity for carbon sequestration in the biosphere, and this decline in carbon storage has likely been further affected by nitrogen saturation.

The spatial patterns of estimated 1990 carbon storage for the no-agriculture/no-saturation simulation are shown in Figure 4a and for the agriculture/saturation simulation are shown in Figure 4b. A comparison of these two maps illustrates the loss of carbon storage potential in regions of North America, Europe, and Southeast Asia due to land-cover and land-use change and extreme nitrogen loading. The development of two nitrogen saturation “holes,” one in central Europe and one in the northeastern United States, is also evident (Figure 4b). These regions receive the greatest quantities of deposited nitrogen, yet the decrease in nitrogen limitation and the spatial distribution of agricultural lands combine to prevent carbon storage relative to pristine conditions. These negative effects of nitrogen enrichment and agricultural expansion will likely increase as croplands continue to expand globally and as nitrogen saturation increases from a regional to a global phenomenon.

In these atmospheric transport and deposition simulations, only NO_y (NO , NO_2 , and NHNO_3) produced from fossil fuel use is simulated. Because NO_y constitutes ap-

proximately 25% (approximately 21×10^{12} g N) of all known anthropogenic sources of nitrogen, the nitrogen saturation effects shown here are greatly understated. A comprehensive analysis that includes all known nitrogen compounds has recently been provided by Holland et al. (in press), and their results strongly support our argument—nitrogen saturation and land-cover change are significantly altering global carbon storage potential.

Frequency and extent of biomass burning in the tropics

Changing fire regimes in the tropics represent another important anthropogenic perturbation to the carbon–nitrogen cycle coupling. Current increases in the extent and frequency of tropical biomass burning cause nitrogen losses, which may lead to a reduction in the capacity of the tropics to store carbon. Although these increases do not literally decouple the nitrogen and carbon cycles—in fact, they may strengthen the coupling under certain fire regimes—the effects of unnaturally high fire frequencies and the permanent conversion of forests to fire-prone grasslands result in a breakdown of established biogeochemical links in the tropics. These human activities effectively cause a decoupling of the carbon and nitrogen cycles.

Some tropical burning occurs as forests are converted to croplands and pastures; however, many fires take place yearly or even biennially in savannas (Cook 1994, Lacey et al. 1982). Savannas cover roughly 55%, 50%, and 40% of the African, Australian, and South American continents, respectively (Hao and Liu 1994). Savannas are burned for many purposes, including pest control, litter removal, nutrient mobilization, and cultural tradition. Whereas a portion of emitted nitrogen is released as NO_x ($2.1\text{--}5.5 \times 10^{12}$ g N/yr), more than 50% of the total nitrogen released can be lost as N_2 ($11\text{--}19 \times 10^{12}$ g N/yr; Crutzen and Andreae 1990, Kuhlbusch et al. 1991). Although emitted NO_x may be deposited downwind of a burning site and reincorporated into vegetation, nitrogen lost as N_2 cannot be incorporated back into the vegetation through deposi-

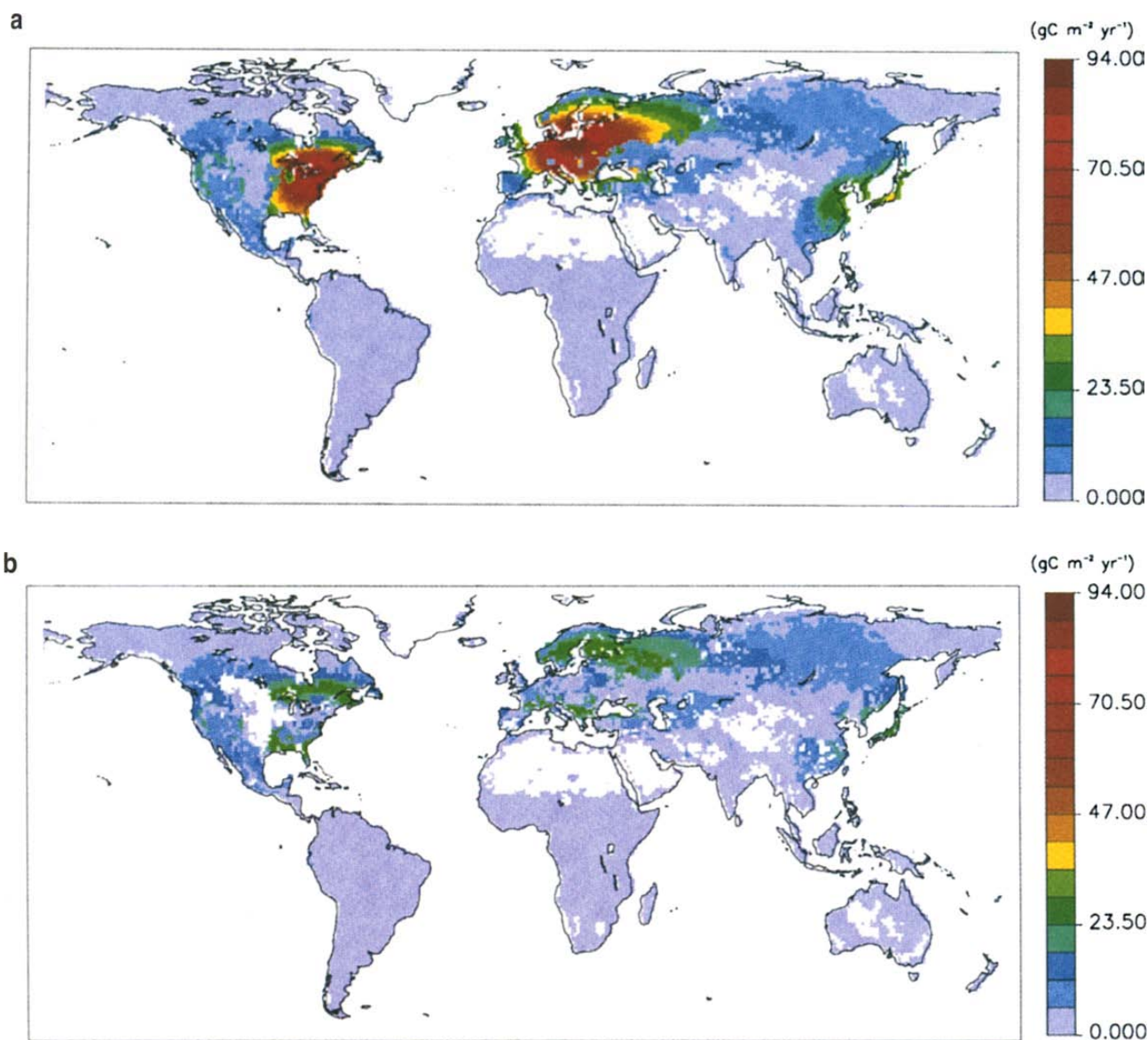


Figure 4. Global distribution of carbon storage ($\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) due to nitrogen deposition in 1990, calculated from the nitrogen deposition perturbation model. (a) Scenario with a pristine biome distribution and with no nitrogen saturation. Regions with greatest carbon storage are forested areas with the high rates of nitrogen deposition. (b) Scenario with current global distribution of agricultural lands and potential nitrogen saturation effects. Regions of high carbon storage shown in part (a) are decreased significantly in part (b) due to both changing land cover and nitrogen losses resulting from saturation. Observed areas of forest decline in the northeastern United States and Eastern Europe can be seen as two “holes” in part (b), each with carbon storage approaching $0 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

tion. Changes in biological nitrogen fixation following burning appear insufficient to recover the emitted N_2 (Cook 1994, Lacey et al. 1982); thus, the losses are essentially permanent in the short term (annual to decadal time scales; Robertson and Rosswall 1986). Eventually, such fire-driven losses of N_2 (known as *pyrodenitrification*; Cook 1994, Crutzen and Andreae 1990) from these typically nitrogen-limited savannas must be matched by losses of

carbon as productivity declines (Figures 2 and 3; Ojima et al. 1994, Robertson and Rosswall 1986).

Increases in tropical fire frequency are not limited to savanna regions. Many areas of both seasonally dry and moist tropical forests are experiencing a dramatic increase in grassland cover (Table 1) as a result of deforestation and the widespread invasion of grasses (D’Antonio and Vitousek 1992). Forested areas that are converted to croplands or pas-

tures are prone to invasion by fire-promoting C_4 grass species (Parsons 1972). These derived fire-enhanced ecosystems tend to self-maintain and spread even without human involvement (Fosberg et al. 1990), altering the carbon and nitrogen biogeochemistry drastically (D’Antonio and Vitousek 1992, Raison 1979). Once initiated, such grass/fire cycles prevent the establishment of woody biomass (Wright and Bailey 1982), thus serving as another form of carbon

storage limitation. These areas do not readily return to forests and woodlands without significant restoration effort, and even then, full recovery is unlikely because biotic and abiotic controls have been altered extensively (Hughes and Vitousek 1993).

These changes in burning practices and land cover make projections of changes in carbon–nitrogen cycle linkages especially difficult in the tropics. In the temperate zone, the primary change is one of increasing nitrogen loading. In the tropics, deforestation and increases in grassland area and burning frequency are causing nitrogen losses, whereas increases in fertilizer use and industrial development are causing nitrogen gains. Thus, although the temperate zone appears to be limited primarily by nitrogen, the tropics represent a matrix of nitrogen-limited and relatively nitrogen-rich ecosystems.

Despite this complexity, the tropics as a whole are unlikely to store excess carbon in response to excess nitrogen. First, nitrogen-limited savannas cannot store carbon in response to nitrogen deposition at the same levels as forests (Rastetter et al. 1992, Townsend et al. 1996), and burning losses of nitrogen will counteract any carbon gain. Second, much of the forested area of the tropics is not nitrogen limited (Walker and Syers 1976, Vitousek and Howarth 1991), so adding nitrogen to these systems would not cause increased carbon storage. Third, those tropical forests that are limited by nitrogen are often at least seasonally dry and therefore highly subject to deforestation and grass invasion (D'Antonio and Vitousek 1992, Houghton 1991).

Beyond the carbon sink

Human activities are causing a significant perturbation to terrestrial carbon and nitrogen cycles at the global scale. A combination of decreasing nitrogen limitation of plant growth, increasing extent of agricultural land use, and increasing biomass burning will make any current nitrogen-stimulated sink for anthropogenic carbon dioxide only temporary. Interest in solving an unbalanced global carbon budget has motivated more than two decades of

research aimed at identifying the missing carbon sink (Broecker et al. 1979, Schimel 1995). We believe that most of the current candidates for this sink are unlikely to be long-term mechanisms for carbon storage.

In addition to elevated nitrogen deposition, such factors as forest regrowth, climate variability, and the direct effects of elevated carbon dioxide may all contribute to current terrestrial carbon uptake (Schimel 1995). However, regrowth can be a net sink for only a limited time, until forests mature. Moreover, climate variability can produce either sources or sinks on decadal time scales (Dai and Fung 1993), and most studies of carbon dioxide effects show that the initially elevated rates of photosynthesis that follow prolonged exposure to high carbon dioxide atmospheres are ultimately down-regulated. Thus, although these processes of carbon dioxide and nitrogen fertilization and forest regrowth may well have slowed rates of atmospheric carbon dioxide accumulation in this century, our hopes for similar effects in future centuries may have to rest on other mechanisms for terrestrial carbon storage, such as direct negative feedbacks to warmer temperatures (Rastetter et al. 1992) or increases in carbon stocks due to shifting distributions of natural biomes (Friedlingstein et al. 1995, Prentice and Sykes 1995).

The rapidly changing global nitrogen cycle may well have more pressing implications than its effect on atmospheric carbon dioxide. From a purely climatic perspective, increasing nitrogen deposition can not only decrease carbon dioxide levels, it can also lead to increases in methane, nitrous oxide, and tropospheric ozone (Bowden et al. 1991, Logan et al. 1981, Mosier et al. 1991). The overall effects of nitrogen deposition on the radiative balance of the atmosphere must therefore account for all of these other factors as well. Furthermore, increases in reactive nitrogen throughout much of the world have already caused a litany of other environmental impacts (Vitousek 1994), including photochemical smog and tropospheric ozone formation (Logan et al. 1981), freshwater nitrogen loading and coastal eutrophication

(Howarth et al. 1996), acid rain and forest decline (Schulze 1989), decreased water quality (Gabric and Bell 1993, Murdoch and Stoddard 1992), and shifts in community structure (Bobbink 1991, Bowman et al. 1995) and ecosystem function (Aber et al. 1989, McNulty et al. 1991, Neff et al. 1994). As natural linkages between terrestrial carbon and nitrogen cycles continue to deteriorate in the coming decades, such changes are likely to become even more pronounced.

Acknowledgments

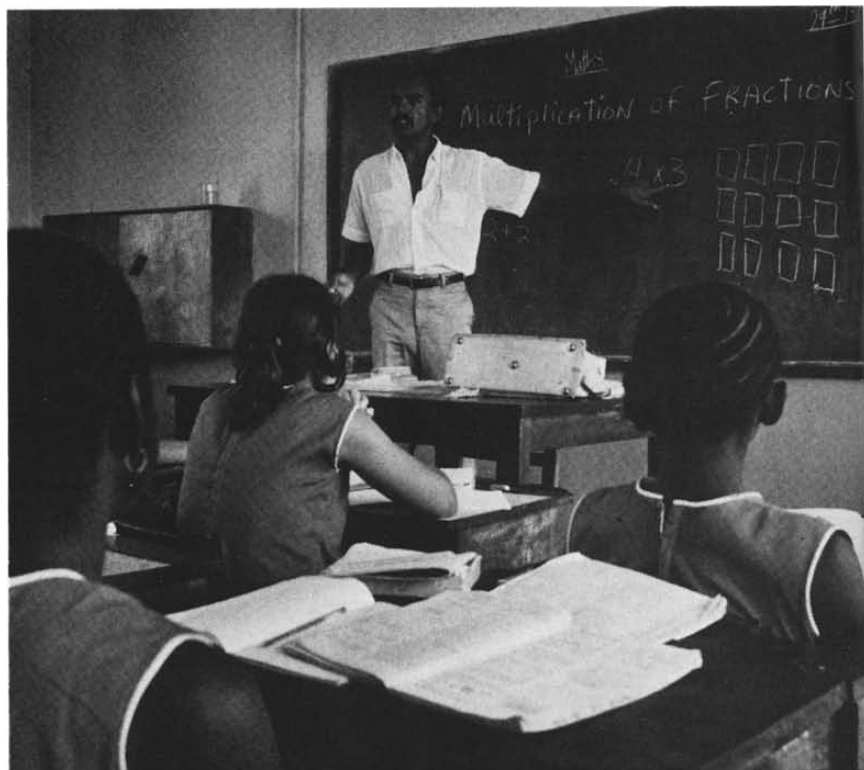
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