Annu. Rev. Ecol. Syst. 1995. 26:473–503

THE ROLE OF NITROGEN IN THE RESPONSE OF FOREST NET PRIMARY PRODUCTION TO ELEVATED ATMOSPHERIC CARBON DIOXIDE[1]

A. David McGuire and Jerry M. Melillo
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

Linda A. Joyce
Rocky Mountain Forest and Range Experiment Station, US Department of Agriculture Forest Service, Fort Collins, Colorado 80526

KEY WORDS: carbon dioxide, net primary production, nitrogen cycle, photosynthesis, respiration

---

ABSTRACT

We review experimental studies to evaluate how the nitrogen cycle influences the response of forest net primary production (NPP) to elevated CO_2. The studies in our survey report that at the tissue level, elevated CO_2 reduces leaf nitrogen concentration an average 21%, but that it has a smaller effect on nitrogen concentrations in stems and fine roots. In contrast, higher soil nitrogen availability generally increases leaf nitrogen concentration. Among studies that manipulate both soil nitrogen availability and atmospheric CO_2, photosynthetic response depends on a linear relationship with the response of leaf nitrogen concentration and the amount of change in atmospheric CO_2 concentration. Although elevated CO_2 often results in reduced tissue respiration rate per unit biomass, the link to changes in tissue nitrogen concentration is not well studied.

At the plant level, soil nitrogen availability is an important factor that often constrains the response of woody plant growth to elevated CO_2. Also, increased nitrogen availability and elevated CO_2 have opposite effects on the relative allocation of carbon to aboveground and belowground biomass. At the ecosystem level, the effects of elevated CO_2 on tissue nitrogen concentration, plant growth, and biomass allocation have the potential to alter soil nitrogen availability indirectly by influencing decomposition, nitrogen mineralization, and nitrogen fixation. Our analyses in this review indicate that the nitrogen cycle plays an important role in the response of forest NPP to elevated CO_2. Because interactions between the nitrogen cycle and elevated CO_2 are complex and our understanding is incomplete, additional research is required to elucidate how such interactions affect forest NPP.

INTRODUCTION

Net primary production (NPP) is the net rate at which the vegetation in an ecosystem captures carbon from the atmosphere. Forests, which cover 43% of the terrestrial biosphere, are potentially responsible for 72% of annual global terrestrial NPP (69). Humans rely on a portion of this production for fiber, fuel, and food. During the past 250 years the combustion of fossil fuels and deforestation have increased atmospheric carbon dioxide from preindustrial levels of approximately 280 ppmv to 353 ppmv in 1990 (128). The projection is that CO_2 concentrations will reach 500 ppmv by the year 2040, and 800 ppmv by the year 2100, if no steps are taken to limit CO_2 emissions (128). This projection necessitates that the scientific community advance its understanding concerning the sensitivity of forest NPP to elevated CO_2.

The availability of inorganic nitrogen often limits production in terrestrial ecosystems, and increased forest production in response to nitrogen fertilization has been observed in numerous studies (63–65, 122). A number of studies have recently reviewed various aspects of NPP response to elevated CO_2 (3, 14, 16, 38, 42, 44, 76, 83, 93, 98, 102, 127, 134). Many of the reviews identify uncertainties that represent gaps in our knowledge about the role of nitrogen in the response of forest ecosystems to elevated CO_2. Knowledge about the influence of nitrogen on forest carbon dynamics is a major issue that limits, in part, the ability of ecologists to model the response of terrestrial ecosystems to global change (121a). In this study we discuss the potential role of nitrogen in the response of forest NPP to elevated CO_2.

MAJOR LINKAGES BETWEEN THE CARBON AND NITROGEN CYCLES

The carbon and nitrogen cycles are closely coupled in terrestrial ecosystems (Figure 1). Nitrogen exerts control over the rates of several carbon cycling

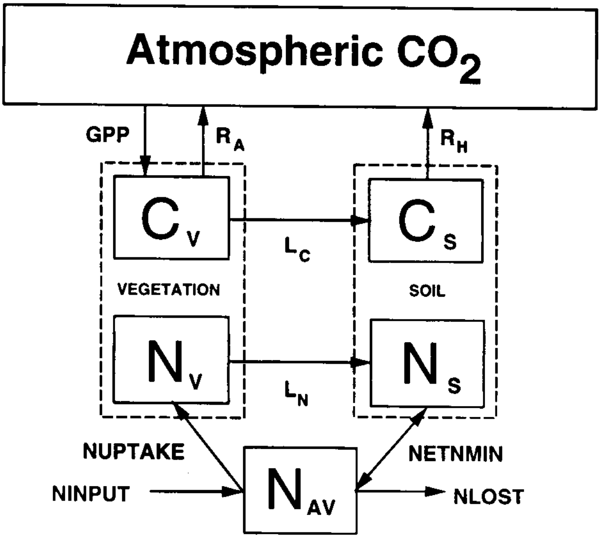

Figure 1 A generalized representation of carbon and nutrient cycles in terrestrial ecosystems. Carbon enters the vegetation pool (C_V) as gross primary production (GPP) and transfers either to the atmosphere as autotrophic (plant) respiration (R_A) or to the soil pool (C_S) as litter production (L_C); it leaves the soil pool as heterotrophic respiration (R_H). Nitrogen enters the vegetation pool (N_S) from the inorganic nitrogen pool of the soil (N_{AV}) as NUPTAKE. It transfers from the vegetation to the organic soil pool (N_S) in litter production as the flux L_N. Net nitrogen mineralization (NETNMIN) accounts for nitrogen exchanged between the organic and inorganic nitrogen pools of the soil. Nitrogen inputs from outside the ecosystem (NINPUT) enter the inorganic nitrogen pool; losses leave this pool as the flux NLOST.

processes including net primary production (NPP). Net primary production is the difference between gross primary production (GPP; i.e. gross assimilation of carbon captured through photosynthesis), and plant respiration (R_A; the energy cost of metabolic activity). Because both gross primary production and plant respiration represent biochemical processes that are catalyzed by nitrogen-rich enzymes, the rate of these processes depends, in part, on the nitrogen content of tissue. Also, because the construction of new tissue requires nitrogen in addition to carbon, gross primary production may depend on the nitrogen status of the plant. Nitrogen status is influenced by both the amount of nitrogen stored in vegetation (N_V) and the supply of nitrogen to vegetation (NUPTAKE). The supply to vegetation depends on effort expended by the plant to obtain nitrogen from the soil and the amount of nitrogen available in the soil solution (N_{AV}). Soil nitrogen availability is influenced by plant uptake (NUPTAKE), the net amount of nitrogen mineralized during the decomposition of soil organic matter (NETNMIN), inputs from the atmosphere (NINPUT) that include nitrogen fixation and deposition of atmospheric nitrogen, and nitrogen losses both to the atmosphere and to groundwater (NLOST). Thus, nitrogen may play a role in the response of forest NPP to elevated CO_2 by influencing tissue, plant, and ecosystem processes.

The effects of elevated CO_2 on NPP have been investigated at the tissue, plant, and ecosystem levels. Studies at the tissue level have focused primarily on the response of net photosynthesis and tissue respiration. Net photosynthesis is the net amount of carbon assimilated during photosynthesis and is the difference between gross assimilation and the leaf respiration that occurs simultaneously with photosynthesis (36). In contrast to studies at the tissue level, those at the level of the individual plant have focused primarily on the response of growth, which is NPP minus biomass losses such as herbivory and litter production (L_C in Figure 1). Because growth is essentially equivalent to NPP if biomass losses are negligible, growth is generally a better integrative measure of NPP than are net photosynthesis and respiration because of the difficulties in continually measuring both of these processes for entire plants. For practical reasons, studies at the plant level generally focus on the response of "potted" seedlings in growth chambers, greenhouses, and field chambers. Although these studies integrate the response of photosynthesis and respiration for individual organisms, they do not necessarily capture the feedback between plant and soil processes that operates in ecosystems. Studies at the ecosystem level focus primarily on how growth responds to elevated CO_2 in the context of plant and soil interactions.

TISSUE-LEVEL RESPONSES

Tissue-level processes that may be affected by elevated atmospheric CO_2 include photosynthesis and respiration. Net photosynthesis in plant leaves represents both carbon gain and loss during the process of photosynthesis; carbon loss is caused by aerobic respiration occurring simultaneously with gross assimilation. Aerobic respiration, which represents the oxidative energy cost of numerous enzyme-catalyzed biochemical pathways, results in carbon loss in the form of CO_2 from all plant tissues. One way that the nitrogen cycle potentially interacts with elevated atmospheric CO_2 to influence tissue metabolism is through effects on enzyme concentrations in tissue.

Nitrogen is a major constituent of enzymes, and changes in nitrogen concentration of tissue generally reflect changes in enzyme concentration. Although nitrogen concentration of woody plant tissues is commonly observed to decline in response to long-term exposure to elevated atmospheric CO_2, much more information is available for leaf tissue (77 reports in Table 1) than for stems (18 reports) and fine roots (26 reports). Among the reports in our survey, the mean decrease of leaf nitrogen concentration is 21% in response to elevated CO_2. In 10 reports no change in nitrogen concentration occurs, and in 2 it increases. Decreases in leaf nitrogen concentration are greater than decreases in other tissues (Kruskal-Wallis Test, $H = 24.1$, $P < 0.0001$, df = 2); decreases in stems (7%) and fine roots (7%) are not statistically distinguishable. It is not clear whether decreases in stem and fine root nitrogen concentration are different from no change; tests for differences are not significant but have low power to detect differences (0.22 for stems and 0.33 for roots vs. desired 0.80). Among 33 reports in our survey, the mean decrease in plant nitrogen concentration is 15%, which is statistically different from no change.

Although elevated CO_2 generally reduces leaf nitrogen concentration when the nitrogen fertilization regime is held constant, a different pattern emerges if changes in nitrogen concentration are examined across fertilization treatments. When compared to the nitrogen concentration at the lowest level of nitrogen availability, higher levels of nitrogen availability generally lessen the reduction or increase the nitrogen concentration of leaves in woody plants grown at elevated CO_2 (Table 2; Paired-sample t-test, $t = 4.31$, $P = 0.0003$, df = 23). Of the 24 comparisons in Table 2, a further reduction in leaf nitrogen concentration is observed under conditions of higher nitrogen availability only for *Eucalyptus grandis* and the nitrogen-fixing species *Alnus rubra.* Leaf nitrogen concentrations increase for *Pinus taeda, Populus tremuloides,* and *Salix* × *dasyclados* when elevated CO_2 is accompanied with nitrogen fertilization. Although increased nitrogen availability and elevated CO_2 have opposite effects on leaf nitrogen concentration, the extant data are too few to determine whether nitrogen concentrations in stems, fine roots, and whole plants of woody vegetation are similarly affected. Clearly, more information is needed on how elevated CO_2 interacts with nitrogen availability to affect nitrogen concentrations in stems, fine roots, and whole plants in woody vegetation.

Effects on Net Photosynthesis

For plants grown in elevated CO_2, three photosynthetic acclimation responses are observed: downregulation, upregulation, and depressed photosynthesis (58). Downregulation occurs when the photosynthetic capacity of plants grown in elevated CO_2 decreases in comparison to plants grown at baseline CO_2, but the rate of photosynthesis for plants grown and measured at elevated CO_2 is still higher than the rate for plants grown and measured at baseline CO_2. For plants grown at elevated CO_2 compared to those grown at baseline CO_2, higher photosynthesis measured at both baseline and elevated CO_2 is defined as upregulation, and lower photosynthesis measured at both baseline and elevated CO_2 is defined as depressed photosynthesis.

The long-term responses of net photosynthesis have been reviewed for

Table 1 Effects of elevated atmospheric carbon dioxide on the nitrogen concentration of leaf, stem, root, and whole plant tissue of woody vegetation.

Species	Baseline CO_2 (ppmv)	Elevated CO_2 (ppmv)	Growth apparatus[a]	Other details[b]	Percent change in nitrogen concentration (% $gN^{\cdot}\ gdm^{-1}$)[c]				Reference
					Leaf	Stem	Root	Plant	
	390	+130	GH	—	—	—	—	−10%	
Acer pseudo-plantanus	390	+260	GH	—	—	—	—	−17%	86
Acer saccharum	350	+300	GC	—	−17%	—	—	—	56
Acer saccharum	350	+300	GC	—	NSD[d]	—	NSD	—	95
Alnus glutinosa	350	+350	GC	—	−46%	—	—	—	75
	350	+300	GC	No nod; +N	+19%	+14%	−7%	+14%	
	350	+300	GC	Nod; No N	−11%	−5%	−2%	−6%	
Alnus rubra	350	+300	GC	Nod; +N	−14%	−4%	+5%	−11%	4
Artemisia tridentata	350	+300	GC	—	−7%	—	—	—	48
	350	+300	GC	low N	−17%	—	—	—	
Artemisia tridentata	350	+300	GC	high N	−28%	—	—	—	49
Betula alleghaniensis	350	+350	GH	—	−30%	—	—	—	97
Betula lenta	350	+350	GH	—	−25%	—	—	—	97
Betula papyrifera	350	+350	GH	—	−33%	—	—	—	97
Betula papyrifera	350	+300	GC	—	−20%	—	—	—	99
Betula pendula	350	+350	GC	—	−14%	−4%	+1%	—	92
	350	+350	GC	low N	—	—	—	−24%	
	350	+350	GC	medium N	—	—	—	−20%	
Betula pendula	350	+350	GC	high N	—	—	—	−7%	94
Betula populifolia	350	+350	GH	—	−33%	—	—	—	97
	350	+150	GC	—	—	—	—	−18%	
Bottomland species	350	+250	GC	—	—	—	—	−36%	124
Castanea sativa	350	+350	GC	—	—	lower	lower	−42%	73
	350	+350	GH	No fert	—	−11%	−16%	−13%	

Castanea sativa	350	+350	GH	fert	—	–19%	–28%	–23%	32
Castanea sativa	350	+350	GH	18 months	–36%	–26%	NSD	—	100
Elaeagnus angustifolia	350	+350	GC	—	—	—	—	–29%	75
	330	+330	GH	low N	–31%	—	—	–27%	
Eucalyptus camaldulensis	330	+330	GH	high N	–26%	—	—	–21%	126
	330	+330	GH	low N	–30%	—	—	–29%	
Eucalyptus cypellocarpa	330	+330	GH	high N	–25%	—	—	–22%	126
	340	+320	GC	low N	–38%	—	—	—	
Eucalyptus grandis	340	+320	GC	highest N	–60%	—	—	—	21
Eucalyptus miniata	355	+345	GH	—	NSD	—	—	—	29
	330	+330	GH	low N	–22%	—	—	–21%	
Eucalyptus pauciflora	330	+330	GH	high N	–21%	—	—	–16%	126
	330	+330	GH	low N	–18%	—	—	–17%	
Eucalyptus pulverulenta	330	+330	GH	high N	–17%	—	—	–15%	126
Eucalyptus tetrodonta	355	+345	GH	—	–33%	—	—	—	29
Fagus grandifolia	350	+300	GC	—	NSD	—	+13%	—	95
	390	+130	GH	—	—	—	—	–9%	
Fagus sylvatica	390	+260	GH	—	—	—	—	–10%	86
	350	+300	GC	no N	–24%	NSD	NSD	–11%	
Gliricidia sepium	350	+300	GC	+N	–14%	NSD	NSD	NSD	115
Lindera benzoin	350	+340	OTC	—	–11%	—	—	—	6
Liriodendron tulipifera	367	+325	GC	low N	—	—	—	–33%	84
	371	+122	GC	no fert	–14%	–7%	–9%	—	
	371	+416	GC	no fert	–28%	–10%	–14%	—	
	371	+122	GC	fert	–12%	–5%	–4%	—	
Liriodendron tulipifera	371	+416	GC	fert	–30%	–18%	–28%	—	79
	355	+150	OTC	—	–24%	—	—	—	