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

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

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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

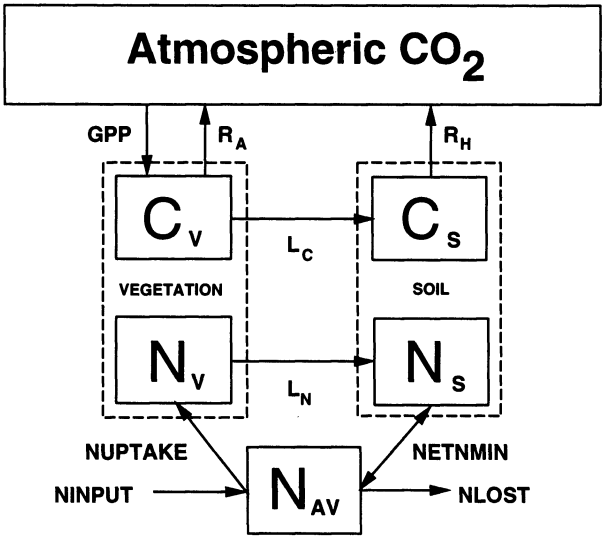

Figure 1 A generalized representation of carbon and nutrient cycles in terrestrial ecosystems. Carbon enters the vegetation pool (C_V) as gross primary production (GPP) and transfers either to the atmosphere as autotrophic (plant) respiration (R_A) or to the soil pool (C_S) as litter production (L_C); 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%	—	—	—	

Table 1 (*continued*)

Species	Baseline CO_2 (ppmv)	Elevated CO_2 (ppmv)	Growth apparatus[a]	Other details[b]	Percent change in nitrogen concentration (% gN gdm^{-1})[c] Leaf	Stem	Root	Plant	Reference
Liriodendron tulipifera	355	+300	OTC	—	–32%	—	—	—	77
	355	+150	OTC	—	–47%	—	—	—	
Liriodendron tulipifera	355	+150	OTC	—	–45%	—	—	—	131
Picea mariana	350	+350	GC	—	–25%	—	—	—	47
Pinus strobus	350	+300	GC	—	NSD	—	—	—	99
	406	+348	GC	1 year old	NSD	—	—	—	
Pinus sylvestris	406	+348	GC	current yr	–23%	—	—	—	89
	350	+150	GH	low N	–38%	—	—	—	
	350	+300	GH	low N	–29%	—	—	—	
	350	+150	GH	high N	NSD	—	—	—	
Pinus taeda	350	+300	GH	high N	NSD	—	—	—	40
	375	+335	GH	low N	–20%	–20%	NSD	NSD	
Pinus taeda	375	+335	GH	high N	NSD	NSD	NSD	NSD	54
	355	+355	GH	low P; –myc	—	—	NSD	—	
	355	+355	GH	high P; –myc	—	—	NSD	—	
	355	+355	GH	low P; +myc	—	—	NSD	—	
Pinus taeda	355	+355	GH	high P; +myc	—	—	NSD	—	55
	350	+350	GC	low water	—	—	–29%	—	
Pinus taeda	350	+350	GC	high water	—	—	–26%	—	118
	350	+150	OTC	—	–20%	—	—	—	
Pinus taeda	350	+300	OTC	—	–28%	—	—	—	123
Pinus virginiana	340	+600	OTC	—	—	—	—	+4%	60
	361	+346	OTC	45 days	–11%	—	—	—	
Populus grandidentata	361	+346	OTC	70 days	0%	—	—	—	25
	350	+400	GC	low N	–44%	—	—	—	
	350	+400	GC	medium N	–29%	—	—	—	

Populus tremuloides	350	+400	GC	high N	–21%	—	—	—	11
Populus tremuloides	350	+300	GC	—	–24%	—	—	—	56
Quercus alba	362	+328	GC	—	–19%	–27%	–17%	—	81
Quercus alba	355	+150 to +650	Natural	—	+9%	—	—	—	52
Quercus pubescens	355	+150 to +650	Natural	—	–15%	—	—	—	52
Quercus rubra	350	+300	GC	—	NSD	—	—	—	56
Robinia pseudoacacia	350	+350	GC	—	–32%	—	—	—	75
	300	+200	GH	lowest N	–29%	—	—	—	
	300	+400	GH	lowest N	–23%	—	—	—	
	300	+700	GH	lowest N	–14%	—	—	—	
	300	+200	GH	low N	–4%	—	—	—	
	300	+400	GH	low N	–17%	—	—	—	
	300	+700	GH	low N	–13%	—	—	—	
	300	+200	GH	high N	–40%	—	—	—	
	300	+400	GH	high N	–38%	—	—	—	
	300	+700	GH	high N	–35%	—	—	—	
	300	+200	GH	highest N	–4%	—	—	—	
	300	+400	GH	highest N	–31%	—	—	—	
Salix x dasyclados	300	+700	GH	highest N	–11%	—	—	—	109
Tropical vegetation	340	+270	GH	—	—	—	—	–10%	51
	350	+150	GC	—	—	—	—	NSD	
Upland species	350	+250	GC	—	—	—	—	NSD	124
Upland and Bottomland species	350	+150	GC	—	–25%	NSD	NSD	—	
	350	+250	GC	—	–25%	NSD	–20%	—	124

[a] GC—growth chamber experiments, GH—greenhouse experiments, OTC—open-top chamber experiments.
[b] Nod—nodulated, N—nitrogen, fert—fertilized, P—phosphorus, myc—mycorrhizae.
[c] Change in nitrogen concentration relative to concentration for baseline CO_2 at same fertilization level.
[d] NSD—no significant difference from nitrogen concentration at baseline CO_2.

Table 2 Effects of elevated atmospheric carbon dioxide and nitrogen fertilization on the nitrogen concentration of leaf, stem, root, and whole plant tissue of woody vegetation.[a]

Species	Baseline CO_2 (ppmv)	Elevated CO_2 (ppmv)	Growth apparatus[b]	Other details[c]	Percent change in nitrogen concentration (% gN· gdm^{-1}) Leaf	Stem	Root	Plant	Reference
	350	+300	GC	Nod; No N	−11%	−5%	−2%	−6%	
Alnus rubra	350	+300	GC	Nod; +N	−24%	−20%	+9%	−24%	4
	350	+300	GC	low N	−17%	—	—	—	
Artemisia tridentata	350	+300	GC	high N	−9%	—	—	—	49
	350	+350	GC	low N	—	—	—	−24%	
	350	+350	GC	medium N	—	—	—	+65%	
Betula pendula	350	+350	GC	high N	—	—	—	+147%	94
	350	+350	GH	no fert	—	−11%	−16%	−13%	
Castanea sativa	350	+350	GH	fert	—	−21%	−32%	−34%	32
	330	+330	GH	low N	−31%	—	—	−27%	
Eucalyptus camaldulensis	330	+330	GH	high N	−5%	—	—	0%	126
	330	+330	GH	low N	−30%	—	—	−29%	
Eucalyptus cypellocarpa	330	+330	GH	high N	−8%	—	—	−7%	126
	340	+320	GC	low N	−38%	—	—	—	
Eucalyptus grandis	340	+320	GC	highest N	−43%	—	—	—	21
	330	+330	GH	low N	−22%	—	—	−21%	
Eucalyptus pauciflora	330	+330	GH	high N	−4%	—	—	−4%	126
	330	+330	GH	low N	−18%	—	—	−17%	
Eucalyptus pulverulenta	330	+330	GH	high N	−8%	—	—	+9%	126
	350	+300	GC	no N fert	−24%	NSD[d]	NSD	−11%	

Gliricidia sepium	350	+300	GC	N fert	−14%	NSD	NSD	NSD	115
	371	+122	GC	no fert	−14%	−7%	−9%	—	
Liriodendron tulipifera	371	+122	GC	fert	−9%	−7%	−26%	—	79
	371	+416	GC	no fert	−28%	−10%	−14%	—	
Liriodendron tulipifera	371	+416	GC	fert	−28%	−19%	−45%	—	79
	350	+150	GH	low N	−38%	—	—	—	
Pinus taeda	350	+150	GH	high N	+49%	—	—	—	40
	350	+300	GH	low N	−29%	—	—	—	
Pinus taeda	350	+300	GH	high N	+49%	—	—	—	40
	375	+335	GH	low N	−20%	−20%	NSD	NSD	
Pinus taeda	375	+335	GH	high N	NSD	—	—	NSD	54
	350	+400	GC	low N	−44%	—	—	—	
	350	+400	GC	medium N	−41%	—	—	—	
Populus tremuloides	350	+400	GC	high N	+19%	—	—	—	11
	300	+200	GH	lowest N	−29%	—	—	—	
	300	+200	GH	low N	+31%	—	—	—	
	300	+200	GH	high N	+37%	—	—	—	
Salix x dasyclados	300	+200	GH	highest N	+146%	—	—	—	109
	300	+400	GH	lowest N	−23%	—	—	—	
	300	+400	GH	low N	+14%	—	—	—	
	300	+400	GH	high N	+43%	—	—	—	
Salix x dasyclados	300	+400	GH	highest N	+106%	—	—	—	109
Salix x dasyclados	300	+400	GH	highest N	+106%	—	—	—	109
	300	+700	GH	lowest N	−14%	—	—	—	
	300	+700	GH	low N	+20%	—	—	—	
	300	+700	GH	high N	+49%	—	—	—	
Salix x dasyclados	300	+700	GH	highest N	+186%	—	—	—	109

[a] relative to the nitrogen concentration for the treatment that uses baseline CO_2 and the lowest level of nitrogen fertilization.
[b] GC—growth chambers experiments, GH—greenhouse experiments.
[c] Nod—nodulated, N—nitrogen, fert—fertilized.
[d] NSD—no significant difference from nitrogen concentration at baseline CO_2.

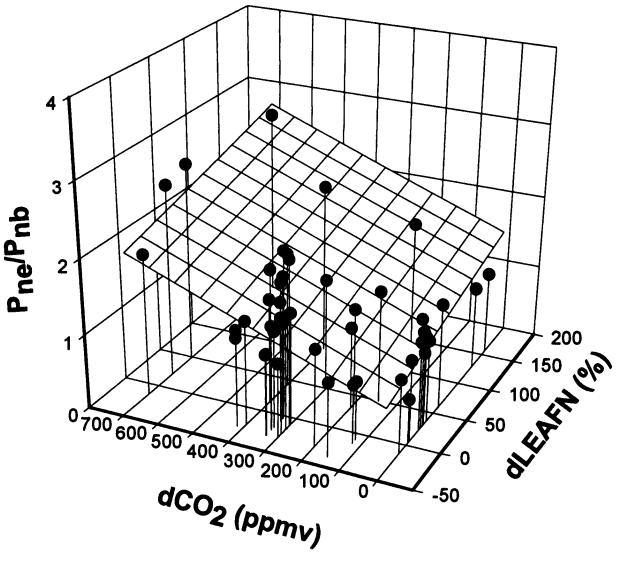

Figure 2 The relationship between photosynthetic response (P_{ne}/P_{nb}), percent change in nitrogen concentration of leaf tissue (dLEAFN), and amount of change in atmospheric CO_2 in ppmv (dCO_2), where P_{nb} is the net photosynthetic rate per unit area for plants grown and measured at both baseline CO_2 and the lowest level of nitrogen fertilization in the experiment, P_{ne} is the net photosynthetic rate for plants grown and measured at elevated CO_2 and/or higher levels of nitrogen fertilization. The plane is described by $P_{ne}/P_{nb} = 0.95924 + 0.00298$ dLEAFN $+ 0.00178$ dCO_2 ($F = 33.1$, $P < 0.0001$, df = 2,43). Data are from studies than manipulate both soil nitrogen availability and elevated CO_2 for woody species, and these are documented in Tables 2 and 3.

woody species grown in elevated CO_2 (30, 16, 42). In a review of the photosynthetic responses of 16 woody species described in studies published in the 1980s, Eamus & Jarvis (30) observed that, for most experiments, carbon assimilation of plants grown and measured at elevated CO_2 is greater than that of plants grown and measured at baseline CO_2. Similarly, in a review of studies published in the early 1990s, Ceulemans & Mousseau (16) observed that elevated CO_2 enhances photosynthesis by an average 40% among 12 conifer species and 61% among 53 broadleaf species. Among 69 reports in Gunderson & Wullschleger (42), net photosynthesis is 44% higher on average for plants grown at elevated CO_2. However, when measured at baseline CO_2, photosynthesis for plants grown at elevated CO_2 is an average 21% lower than for plants grown at baseline CO_2. The observations of Gunderson & Wullschleger (42) indicate downregulation; only 8 of 69 reports indicate upregulation, and only 4 of 20 reports indicate depressed photosynthesis. Downregulation appears to be the predominant photosynthetic acclimation response of woody plants to elevated CO_2.

Among studies that manipulate both CO_2 and nitrogen availability, the mean enhancement of photosynthesis to elevated CO_2 at the lowest level of nitrogen availability is 40%, while the mean enhancement at higher levels of nitrogen availability is 59% (Table 3; paired-sample t-test, $t = 2.41$, $P = 0.0239$, df = 24). Relative to photosynthesis and nitrogen concentrations of the lowest fertilization treatment in each experiment, a linear relationship exists between photosynthetic enhancement, change in leaf nitrogen concentration, and the amount of CO_2 change (Figure 2):

$$P_{ne}/P_{nb} = 0.95924 + 0.00298\ \mathrm{dLEAFN} + 0.00178\ \mathrm{dCO_2}, \quad 1.$$

where P_{nb} is net photosynthesis per unit leaf area for plants grown and measured at both baseline CO_2 and the lowest level of fertilization in the experiment, P_{ne} is net photosynthesis rate for plants grown and measured at elevated CO_2 and/or higher levels of nitrogen fertilization; dLEAFN is the percent change in nitrogen concentration between leaves corresponding to the measurement of P_{nb} and those of P_{ne}; and dCO_2 is the concentration difference in ppmv between elevated and baseline CO_2. Baseline CO_2 was defined for each experiment as the CO_2 concentration that best represents contemporary atmospheric CO_2. The relationship explains 61% of the variability in P_{ne}/P_{nb} ($F = 33.1$, $P < 0.0001$, df = 2,43). Both independent variables are significant (dLEAFN: $P = 0.0154$; dCO_2: $P < 0.0001$), and each variable contributes significantly to the variance explained by the relationship. The intercept, which is significantly different from 0 ($P < 0.0001$), does not significantly differ from the expected 1.0 for no changes in leaf nitrogen and CO_2. In the absence of changes in nitrogen availability, photosynthetic response depends on how leaf nitrogen concentration responds to elevated CO_2. Severe reductions in leaf nitrogen cause depressed photosynthesis, moderate to small reductions cause downregulation, and increases cause upregulation. Because nitrogen availability affects dLEAFN, the response of photosynthesis to elevated CO_2 also depends on changes in nitrogen availability. Although other factors such as water availability would be useful to include in a relationship of photosynthetic response to elevated CO_2, the relationship indicates that nitrogen availability and nitrogen allocation play important roles in the acclimation of photosynthesis to elevated CO_2.

Acclimation to elevated CO_2 can occur by affecting one or more of three aspects of leaf-level carbon assimilation (93, 102): carboxylation, light harvest, and carbohydrate synthesis. Under saturating light conditions at low levels of intercellular CO_2, assimilation is limited by the quantity and activity of ribulose bisphosphate carboxylase (rubisco), the enzyme that is primarily responsible for capturing atmospheric carbon in the production of sugars. Rubisco may accept either CO_2 (carboxylation) or O_2 (oxygenation) as a substrate; oxygenation is responsible for photorespiration. Because CO_2 competes with O_2 for

rubisco binding sites, enhancement of photosynthesis by elevated CO_2 is possible through increased carboxylation and decreased oxygenation. Carboxylation increases with rising intercellular CO_2 to levels at which the regeneration of rubisco, and thus the ability to fix carbon, is limited by the light-harvesting machinery of photosynthesis. At high levels of intercellular CO_2, the enzymatically controlled rate of carbohydrate synthesis, which affects the phosphate regeneration that is necessary for harvesting light energy, may regulate the fixation of carbon.

Because rubisco represents a substantial proportion of leaf nitrogen (35), photosynthetic rate is generally correlated with the nitrogen content of leaves (35, 37). Reduced nitrogen availability has often been observed to decrease both leaf nitrogen content and photosynthesis (18, 34, 41, 53, 103, 104, 125). If lower nitrogen concentrations of leaves in response to elevated CO_2 primarily reflect lower rubisco concentrations, then lower assimilation over the carboxylation-limited range of intercellular CO_2 is expected in plants grown at elevated CO_2. It has been suggested that if elevated CO_2 causes intercellular CO_2 generally to rise above this region, then lower rubisco levels may be advantageous because they represent the allocation of nitrogen away from excess rubisco capacity (102) to other activities such as fine root function (33) and enzymes of the light-harvesting machinery and carbohydrate synthesis (38, 102, 105, 112, 117, 127).

One explanation for acclimation to elevated CO_2 is that restricted rooting volume in small pots causes photosynthesis to be regulated by sink activity (5). A mechanism proposed to explain this phenomenon is that the accumulation of carbohydrates in leaves induces feedback to reduce phosphate regeneration (10, 105), a phenomenon labeled "end-product inhibition." This explanation is consistent with the observed accumulation of photosynthate in leaves of some plants that have received long-term exposure to elevated CO_2 (15, 26, 28, 31, 43, 87, 111, 129). Most of the evidence concerning end-product inhibition is from studies of herbaceous plants, and the hypothesis does not explain acclimation in trees when rooting volume is not restricted (42). Because end-product inhibition may represent an artifact of inappropriate pot size (5, 10, 116; but see 8, 50, 61, 62), true photosynthetic acclimation in response to elevated CO_2 may be best understood in terms of the allocation of nitrogen and other components to leaf function, i.e. carbon capture, and root function, i.e. the acquisition of nutrients and water (see 58).

Effects on Respiration

The study of respiration responses to elevated CO_2, a rapidly expanding field, has recently been reviewed by Amthor (3), Bunce (14), and Wullschleger et al (134). Emerging evidence indicates that the long-term acclimation of woody plants to elevated CO_2 often results in reduced leaf respiration rates (6, 45, 46,

95, 130, 131, 133) and perhaps in reduced respiration rates for whole seedlings (13, 72, 95). When the leaf respiration response has been partitioned into growth and maintenance components, the reduction is dominated by maintenance respiration (131). Although growth respiration per unit leaf biomass may decrease (130, 131), larger leaves in elevated CO_2 may compensate for the reduced rate (131; see also 95). Similarly, Norby (76) reports that although the respiration rate per unit fine root biomass was decreased in *Quercus alba* grown at elevated CO_2, increased fine root density probably results in higher total fine root respiration. Reid & Strain (95) observed decreased respiration per belowground biomass for *Acer saccharum,* but not for *Fagus grandifolia;* total belowground respiration was not affected by elevated CO_2 in either species. In contrast, both maintenance respiration per stem volume and growth respiration per stem increment in *Q. alba* are unaffected by long-term acclimation to elevated CO_2 (132), but higher rates of stem growth cause higher total stem respiration.

Changes in tissue nitrogen concentrations may have effects on both growth and maintenance respiration. The energy required to construct tissues with reduced nitrogen/protein concentrations may be less at elevated CO_2 (131, 134; but see 57). Maintenance respiration involves the energy cost of many cell functions, which include numerous biochemical pathways, cell repair, membrane function, and protein synthesis and maintenance. Protein synthesis and maintenance represent a substantial proportion of maintenance respiration (88), and a linear relationship often exists between tissue maintenance respiration and tissue nitrogen concentrations (101). Wullschleger et al (131) documented a linear relationship between leaf respiration rates and leaf nitrogen concentrations among *Liriodendron tulipifera* plants grown at ambient and elevated levels of atmospheric CO_2, but Azcon-Bieto et al (6) observed that respiration per unit leaf nitrogen declined for *Lindera benzoin* plants grown in elevated CO_2. To our knowledge, these are the only reported relationships among tissue respiration, nitrogen concentration, and elevated CO_2 for woody species. Additional research is required to elucidate the role that changes in tissue nitrogen concentration play in the acclimation response of tissue respiration to elevated CO_2 (134).

PLANT-LEVEL RESPONSES

Studies of tissue-level responses to elevated CO_2 and nitrogen availability help us to understand how these two variables interact to affect the exchange of carbon between the plant and the atmosphere on a per unit biomass or per unit leaf area basis. For us to understand how whole-plant carbon exchange is affected, we need to know how growth and biomass allocation are influenced. The responses of growth and allocation are important to consider because

Table 3 Effects of elevated atmospheric carbon dioxide and nitrogen fertilization on net photosynthesis (P_n), growth, and root to shoot ration (R/S)

Species	Baseline CO_2 (ppmv)	Elevated CO_2 (ppmv)	Growth apparatus[a]	Other details[b]	Change[c]			Reference
					P_n	Growth	R/S	
	350	+350	GH	low PAR; low N	—	1.3/1.3	+20/+20	
Acer pennsylvanicum	350	+350	GH	low PAR; high N	—	1.6/6.4	+1/+4	7
	350	+350	GH	high PAR; low N	—	1.2/1.2	+33/+33	
Acer pennsylvanicum	350	+350	GH	high PAR; high N	—	1.2/11.3	+11/–5	7
	350	+350	GH	low PAR; low N	—	1.3/1.3	–6/–6	
Acer rubrum	350	+350	GH	low PAR; high N	—	1.6/8.9	–6/–22	7
	350	+350	GH	high PAR; low N	—	1.1/1.1	+3/+3	
Acer rubrum	350	+350	GH	high PAR; high N	—	1.4/28.0	+0/–22	7
	350	+300	GC	Nod; No N	2.2/2.2	1.2/1.2	–19/–19	
Alnus rubra	350	+300	GC	Nod; +N	2.0/2.0	1.7/3.0	+16/+24	4
	350	+300	GC	low N	1.5/1.5	1.0/1.0	–19/–19	
Artemisia tridentata	350	+300	GC	high N	1.1/1.5	1.7/2.3	–49/–56	49
	350	+350	GH	low PAR; low N	—	1.2/1.2	+8/+8	
Betula allegheniensis	350	+350	GH	low PAR; high N	—	1.6/9.0	–13/–32	7
	350	+350	GH	high PAR; low N	—	1.2/1.2	–3/–3	
Betula allegheniensis	350	+350	GH	high PAR; high N	—	1.1/10.6	–1/–15	7
	350	+350	GC	low N	1.4/1.4	—	+4/+4	
	350	+350	GC	medium N	1.0/1.5	—	+9/–48	
Betula pendula	350	+350	GC	high N	1.3/2.1	—	–5/–60	94
	350	+350	GH	low PAR; low N	—	1.1/1.1	+5/+5	
Betula populifolia	350	+350	GH	low PAR; high N	—	1.4/6.8	+8/–29	7
	350	+350	GH	high PAR; low N	—	1.0/1.0	+9/+9	
Betula populifolia	350	+350	GH	high PAR; high N	—	1.2/11.4	+5/–9	7
	350	+350	GH	no fert	—	1.2/1.2	+8/+8	
Castanea sativa	350	+350	GH	fert	—	1.2/2.9	–11/–34	32
	330	+330	GH	low N	1.1/1.1	1.8/1.8	+6/+6	

Eucalyptus camaldulensis	330	+330	GH	high N	1.2/1.3	2.7/6.9	+0/–32	126
	330	+330	GH	low N	1.1/1.1	1.9/1.9	+7/+7	
Eucalyptus cypellocarpa	330	+330	GH	high N	1.3/1.6	3.1/11.7	+0/–31	126
	340	+320	GC	lowest N	—	2.5/2.5	—	
	340	+320	GC	low N	—	3.1/3.3	—	
	340	+320	GC	high N	—	3.1/4.2	—	
Eucalyptus grandis	340	+320	GC	highest N	—	4.0/5.0	—	22
	330	+330	GH	low N	1.4/1.4	3.1/3.1	–9/–9	
Eucalyptus pauciflora	330	+330	GH	high N	1.2/1.9	2.4/10.1	–10/–45	126
	330	+330	GH	low N	1.3/1.3	2.6/2.6	–25/–25	
Eucalyptus pulverulenta	330	+330	GH	high N	1.3/1.4	3.2/9.2	–40/–34	126
	350	+350	GH	low PAR; low N	—	1.1/1.1	+2/+2	
Fraxinus americana	350	+350	GH	low PAR; high N	—	1.6/18.5	+20/–21	7
	350	+350	GH	high PAR; low N	—	0.7/0.7	–27/–27	
Fraxinus americana	350	+350	GH	high PAR; high N	—	1.3/8.1	+3/–33	7
	350	+300	GC	no N	—	1.1/1.1	–35/–35	
Gliricidia sepium	350	+300	GC	+N	—	1.3/2.4	–1/–34	115
	371	+122	GC	no fert	0.8/0.8	1.2/1.2	+25/+25	
Liriodendron tulipifera	371	+122	GC	fert	1.5/0.8	1.1/11.6	–12/+11	79
	371	+416	GC	no fert	1.2/1.2	1.2/1.2	+46/+46	
Liriodendron tulipifera	371	+416	GC	fert	2.2/1.3	1.2/13.0	+16/+34	79
	350	+400	GC	low N	—	1.3/1.3	+8/+8	
	350	+400	GC	medium N	—	1.2/9.1	+31/–32	
Picea glauca	350	+400	GC	high N	—	1.5/15.1	–8/–61	12
	362	+349	GH	low fert	—	1.8/1.8	–13/–13	
Picea rubens	362	+349	GH	high fert	—	1.8/1.8	–13/–13	106
	374	+339	GH	low fert	1.9/1.9	—	—	
Picea rubens	374	+339	GH	high fert	1.9/1.9	—	—	107
	350	+150	OTC	high P; low N	—	1.3/1.3	—	
Pinus taeda	350	+150	OTC	high P; low N	—	1.2/5.1	—	113
	350	+300	OTC	high P; low N	—	1.1/1.1	—	

Table 3 (*continued*)

Species	Baseline CO_2 (ppmv)	Elevated CO_2 (ppmv)	Growth apparatus[a]	Other details[b]	Change[c]			Reference
					P_n	Growth	R/S	
Pinus taeda	350	+300	OTC	high P; low N	—	1.3/5.4	—	113
	350	+150	GH	low N	1.0/1.0	1.0/1.0	—	
Pinus taeda	350	+150	GH	high N	1.1/1.5	1.4/4.0	—	40
	350	+300	GH	low N	1.0/1.0	1.0/1.0	—	
Pinus taeda	350	+300	GH	high N	1.1/1.5	1.6/5.8	—	40
	375	+335	GH	low N	2.1/2.1	1.6/1.6	+6/+6	
Pinus taeda	375	+335	GH	high N	2.0/2.2	1.8/1.8	–3/+0	54
	350	+300	OTC	low N	0.9/09	—	—	
Pinus taeda	350	+300	OTC	high N	1.6/2.1	—	—	117
	350	+300	GH	high P; low N	1.0/1.0	—	—	
Pinus taeda	350	+300	GH	high P; high N	1.6/2.2	—	—	114
	350	+400	GC	low N	—	1.3/1.3	+3/+3	
	350	+400	GC	medium N	—	1.0/8.0	+1/+8	
Populus tremuloides	350	+400	GC	high N	—	1.0/17.8	–17/+21	12
	389	+107	GC	high P; no N	—	1.1/1.1	–16/–16	
Quercus alba	389	+107	GC	high P; +N	—	1.2/1.3	–12/–35	78
	389	+404	GC	high P; no N	—	1.1/1.1	–28/–28	
Quercus alba	389	+404	GC	high P; +N	—	1.2/1.3	–12/–35	78
	350	+350	GH	low PAR; low N	—	1.8/1.8	+23/+23	
Quercus rubra	350	+350	GH	low PAR; high N	—	3.0/8.4	–17/–32	7
	350	+350	GH	high PAR; low N	—	1.4/1.4	–9/–9	
Quercus rubra	350	+350	GH	high PAR; high N	—	1.2/9.0	+39/–19	7
	300	+200	GH	lowest N	1.3/1.3	1.1/1.1	—	
	300	+200	GH	low N	1.1/1.1	1.1/1.7	—	
	300	+200	GH	high N	1.2/1.3	1.5/3.2	—	

Salix x dasyclados	300	+200	GH	highest N	1.6/1.7	1.5/3.7	—	109
	300	+400	GH	lowest N	1.4/1.4	1.2/1.2	—	
	300	+400	GH	low N	1.3/1.4	1.1/1.7	—	
	300	+400	GH	high N	1.7/1.8	1.5/3.2	—	
Salix x dasyclados	300	+400	GH	highest N	2.1/2.3	1.5/3.6	—	109
	300	+700	GH	lowest N	1.9/1.9	1.0/1.0	—	
	300	+700	GH	low N	2.5/2.6	1.0/1.5	—	
	300	+700	GH	high N	2.5/2.7	1.8/3.9	—	
Salix x dasyclados	300	+700	GH	highest N	2.4/2.6	1.4/3.5	—	109
	300	+200	GH	lowest N	—	1.5/1.5	—	
	300	+200	GH	low N	—	0.9/1.1	—	
	300	+200	GH	high N	—	1.1/2.2	—	
Salix phylicifolia	300	+200	GH	highest N	—	3.8/6.8	—	110
	300	+400	GH	lowest N	—	1.0/1.0	—	
	300	+400	GH	low N	—	1.7/2.0	—	
	300	+400	GH	high N	—	1.8/3.5	—	
Salix phylicifolia	300	+400	GH	highest N	—	1.3/6.0	—	110
	300	+700	GH	lowest N	—	1.0/1.0	—	
	300	+700	GH	low N	—	1.7/2.0	—	
	300	+700	GH	high N	—	2.5/5.0	—	
Salix phylicifolia	300	+700	GH	highest N	—	2.7/4.8	—	110

[a] GC—growth chamber experiments, GH—greenhouse experiments.

[b] PAR—photosynthetically active radiation, N—nitrogen, Nod—nodulated, fert—fertilized, P—phosphorus.

[c] Change is indicated as the ratio of the quantities at elevated and baseline CO_2 for P_n and growth, and as percent change from the quantity at baseline CO_2 for R/S. P_n values are from measurements made at growth CO_2. Quantity on the left is relative to the treatment that uses baseline CO_2 and the same level of fertilization, and the quantity on the right is relative to the treatment that uses baseline CO_2 and the lowest level of nitrogen fertilization.

resources may be allocated so that growth becomes equally limited by all resources, i.e. carbon, nutrients, and water (2, 9, 17, 96). In this section we examine how changes in nitrogen availability and atmospheric CO_2 interact to influence growth and allocation.

Effects on Growth

Among the studies reviewed by Eamus & Jarvis (30), a doubling of CO_2 reportedly increased biomass approximately 40%. Ceulemans & Mousseau (16) observed that biomass increased 38% for conifer species and 63% for broadleaf species in response to elevated CO_2. In studies in which both CO_2 and nitrogen availability were manipulated, the mean increase in biomass to elevated CO_2 at the lowest level of availability is 35%, while at higher levels of nitrogen availability, the mean increase is 71% (Table 3; Wilcoxin Signed Rank Test, $W = 883.0$, $P < 0.0001$, $N = 55$). In comparison to the biomass accumulation at baseline CO_2 and the lowest level of nitrogen availability, elevated CO_2 accompanied by increased nitrogen availability enhanced biomass an average 6.5 times the baseline biomass among the 55 reports in our survey. These analyses indicate that low nitrogen availability constrains the response of growth to elevated CO_2; they contrast with the conclusion of Idso & Idso (44) that "the percentage increase in plant growth produced by raising the air's CO_2 content is generally not reduced by less than optimal levels of ... soil nutrients."

Effects on Allocation

Eamus & Jarvis (30) observed that, under conditions of low nutrient availability, trees increase the proportion of root biomass in response to elevated CO_2, but under conditions of high nutrient availability, root proportion may decrease, remain unaltered, or increase. Citing unpublished work (by SD Wullschleger), Norby (76) indicates that the mean response of root/shoot ratio to elevated CO_2 is an increase of 6% among 224 observations for woody species, and that there is no effect of nutrient status on the response. Reports in the review by Ceulemans & Mousseau (16) are dominated by increases in root/shoot ratio, which the authors interpreted as investment to ensure better acquisition of mineral nutrients in poor forest soils. They also observed that, at higher levels of nutrients, the change in root/shoot ratio is less. For studies that manipulate nitrogen availability, we observe trends for these patterns, but they are not statistically significant. At the lowest levels of nitrogen availability, the mean increase in root/shoot ratio is 1%, and at higher levels the mean change is –2% (Table 3). These observations are not statistically distinguishable from each other (Paired-sample t-test, $t = 0.764$, $P = 0.4508$, df = 32) and are not different

from no change in root/shoot ratio. Because the power of the test for differences is low (0.05 vs. desired 0.80), the conclusion from Table 3 that elevated CO_2 has no effect on root/shoot ratio among studies that manipulate nitrogen availability is probably an artifact of inadequate sample size. Studies that manipulate nitrogen availability in woody species clearly identify an effect of increased nitrogen availability in reducing root/shoot ratio. In comparison to root/shoot ratios at baseline CO_2 and the lowest level of nitrogen availability, the mean decrease in root/shoot ratios for elevated CO_2 accompanied with higher nitrogen availability is 21% (Table 3), which is significantly lower than changes in root/shoot ratio at the lowest level of nitrogen availability (Paired-sample t-test, $t = 5.30$, $P < 0.0001$, df = 31). Thus, elevated CO_2 and increased soil nitrogen availability have opposite effects on relative allocation of aboveground and belowground biomass.

ECOSYSTEM-LEVEL RESPONSES

The CO_2 responses of tissue nitrogen concentration, growth, and relative allocation of biomass to root function appear to be functionally linked (58). Our analyses in this review indicate that tissue nitrogen concentration, growth, and root/shoot ratio in woody species are affected by changes in atmospheric CO_2 and soil nitrogen availability. Because most experiments with woody plants involve seedlings or saplings, the possibility exists that reduced tissue nitrogen concentration and root/shoot ratio may, in part, represent the indirect effect of elevated CO_2 in accelerating development (1, 20, 76, 20). If the responses of nitrogen concentration, growth, and biomass allocation persist throughout development, they have the potential to alter soil nitrogen availability indirectly. In this section we examine how elevated CO_2 may influence soil nitrogen availability through effects on plant nitrogen concentration and on plant growth and allocation.

Effects of Changes in Plant Nitrogen Concentration

The effect of elevated CO_2 in reducing nitrogen concentration of plant tissue may alter soil nitrogen availability by influencing decomposition. Rates of leaf decomposition are often correlated with several indices of nitrogen litter quality, which include nitrogen concentration, carbon/nitrogen ratio, and lignin/nitrogen ratio (67). Nitrogen concentration generally is positively correlated with decomposition, whereas the other two indices generally are negatively correlated. Compared to leaf litter of woody plants grown at baseline CO_2, decreased nitrogen concentration for leaf litter of plants grown at elevated CO_2 has been observed for *Liquidambar styraciflua* (sweetgum; 66), *Quercus alba* (white oak;

82), *Castanea sativa* (sweet chestnut; 24), *Fraxinus excelsior* (ash; 23), *Betula pubescens* (birch; 23), *Acer pseudoplantanus* (sycamore; 23), *Picea sitchensis* (sitka spruce; 23), *Liriodendron tulipifera* (yellow poplar; 83), *Acer rubrum* (red maple; 68), and *Acer pennsylvanicum* (striped maple; 68). Increased carbon/nitrogen ratio has been observed for all these species except sitka spruce and yellow poplar, where carbon/nitrogen ratio was the same. Increased lignin/nitrogen ratio was observed for all species except white oak, in which it decreased from 5.7 to 4.8, and yellow poplar, in which it was the same.

The predicted decay rates for white oak, which were determined from lignin/nitrogen and lignin/phosphorus ratios of leaf litter, suggest there would be no difference between litter derived from plants grown in baseline and those in elevated CO_2 (82). In contrast, rates of decay for maple species, also determined from lignin/nitrogen ratios, suggest decay rates per unit of litter would be slower for elevated-CO_2 material (68). For sweet chestnut leaf litter incubated with only microflora and protozoa, mass loss was 60% less for litter derived from elevated CO_2 plants than that from baseline CO_2 plants (24). However, mass loss was similar between the CO_2 treatments for litter incubated with nematodes and collembola in addition to microflora and protozoa; the addition of isopods increased mass loss by 30% in the elevated CO_2 treatment. The enhanced decomposition was attributed to a change in the microflora community, which became dominated by white-rot fungus. Among decomposition experiments with leaf litter of ash, birch, sycamore, and sitka spruce, cumulative respiration rates were lower for litter derived from elevated CO_2 plants among the three deciduous species, but rates were similar for spruce (23). Significantly lower mass loss was observed for both birch and spruce, but there was also a nonsignificant trend for lower mass loss in ash. Cumulative nitrogen mineralization did not differ between CO_2 treatments for any of the four species. No difference in mass loss rates were observed for yellow poplar after two years of decomposition in litter bags (83).

If decomposition and nitrogen mineralization are depressed because of CO_2-induced changes in litter quality, soil nitrogen availability may be reduced in ecosystems. Our earlier analyses suggest that reduced nitrogen availability has the potential to limit both photosynthetic and growth responses to elevated CO_2. Thus, reduced litter quality resulting from elevated CO_2 has the potential to cause long-term negative feedback to constrain the response of NPP. Reductions in leaf litter quality seem to be common among woody species, but these may not be universal. If nitrogen is not resorbed from fine roots prior to senescence, as suggested by Nambiar (74), then the response of fine root nitrogen concentration may be a good indicator of changes in fine root litter quality (76). Small reductions in the nitrogen concentrations of fine roots and stems may contribute to lower total litter quality, but to our knowledge no published studies examine how elevated

CO_2 affects decomposition of fine root and stem litter in woody plants. One study of fine root decomposition in a grass reports lower decomposition rates for root residue from plants grown in elevated CO_2; a lower decomposition rate is associated with an increase in carbon/nitrogen ratio from 18 in baseline plants to 32 in elevated-CO_2 plants (39). At present, the available data suggest that CO_2-induced reductions in litter quality may depress decomposition rates, but the data are ambiguous. Effects on nitrogen mineralization of CO_2-induced reductions in litter quality are less well documented. Also, there is no information on how nitrogen mineralization might be affected by the combination of CO_2-induced reductions in decay rate and enhancements in litter production. Clearly, more research is needed on the potential for CO_2-induced reductions in litter quality to decrease soil nitrogen availability and cause long-term feedback that constrains the response of forest NPP to elevated CO_2.

Effects of Changes in Growth and Allocation

Increased growth and root/shoot ratio in response to elevated CO_2 have the potential to increase production of belowground biomass in forest ecosystems. Belowground biomass represents both storage in coarse roots and investment for the acquisition of nutrients and water by fine roots. To the extent that increased belowground inputs are manifested in enhanced fine root growth, nitrogen uptake to plants might increase because of additional or more efficient exploration of soil volume by rooting systems. However, in mature ecosystems it is not clear whether the soil exploration by rooting systems is saturated under present CO_2 conditions. Increased production in response to elevated CO_2 may also enhance the transfer of carbon to microbes by means of increased fine root turnover or by the exudation of soluble organic carbon from roots into the soil. If elevated CO_2 causes greater inputs of root-derived carbon into the soil, it may increase nitrogen availability by enhancing nitrogen fixation (59) or nitrogen mineralization (135).

Symbiotic nitrogen fixers acquire carbon from their host plants and provide inorganic nitrogen to their hosts. Elevated CO_2 enhances nitrogen fixation per plant for symbiotic associations involving woody species by increasing nodule mass (4, 75, 115), nodule number (4), or nitrogenase activity per nodule (4). In addition to carbon availability, nitrogen fixation may be limited by phosphorus availability (27). Elevated CO_2 enhances colonization of ectomycorrhizae in woody plants (55, 83, 85), presumably because of enhanced root exudation of soluble carbon (80). Because mycorrhizae are important for supplying phosphorus to plants, increased inputs of root carbon into the soil may indirectly affect nitrogen availability by helping to supply phosphorus to symbiotic nitrogen fixers. Effects of elevated CO_2 on nitrogen fixation may

have important consequences for NPP of tropical forests, where symbiotic nitrogen fixation is more important than in extratropical regions (83). The consequences may be especially relevant for tropical forests that occur on extremely weathered soils, which are often deficient in phosphorus (108). Whereas the effects of elevated CO_2 on symbiotic nitrogen fixation have received some attention, the effects on asymbiotic nitrogen fixation have not been addressed by the scientific community. Because asymbiotic nitrogen fixation may be important for most of the atmospheric nitrogen fixed in some ecosystems (83), progress is needed to understand how elevated CO_2 may affect this potentially important process.

It has also been hypothesized that if elevated CO_2 results in a greater flow of carbon from roots to soil, then nitrogen mineralization may be enhanced (135). This hypothesis makes the prediction that: 1. microbial growth in the vicinity of the root will be enhanced by increased root turnover or exudation, and 2. that nitrogen mineralization will be increased by higher rates of protozoan grazing on microbial populations (19) or by increased rates of organic matter decomposition (135). Enhanced decomposition of organic matter could increase nitrogen availability through greater mineralization of microbial nitrogen derived from either root residues or native soil organic matter (135). Zak et al (135) tested the hypothesis for *Populus grandidentata* grown in open top chambers. For elevated CO_2 treatments, they observed root and microbial biomass increased, net nitrogen mineralization increased in short-term laboratory incubations of the bulk soil, respiration rates were higher in the rhizosphere, and there were nonsignificant trends for higher rates of respiration and nitrogen mineralization in the bulk soil.

Although the results of the experiment are consistent with the hypothesis of Zak et al (135), an alternative explanation for the results may be related to the fact that they added inorganic nitrogen to all treatments (4.5 g N m^{-2} over a 47-day period). If microbial growth were simultaneously limited by both carbon and nitrogen availability, then this inorganic nitrogen addition may have stimulated microbial growth in the elevated-CO_2 treatments because of increased root-derived carbon inputs into the soil (see 121). The enhanced microbial growth, if it causes increased grazing by protozoa or increased microbial turnover, could result in higher mineralization rates. This interpretation of the Zak et al (135) results, if correct, has important implications for the effects of elevated CO_2 on forest growth in regions of the world where soils receive substantial inputs of anthropogenic nitrogen from the atmosphere (see 70). Clearly, the link between nitrogen availability and CO_2-induced inputs of carbon into the soil is complex, and additional research is required to elucidate how elevated CO_2 and nitrogen availability interact to influence nitrogen cycling in forest ecosystems.

CONCLUSION

The interaction between soil nitrogen availability and elevated CO_2 is important to consider because: 1. nitrogen availability is spatially variable (65), and 2. elevated temperature, which might accompany elevated CO_2 (71), has the potential to affect soil nitrogen availability by influencing decomposition (63, 65, 69, 90, 91, 119, 120). To make progress in modeling the response of forest ecosystems to global change, the scientific community needs to improve its understanding of how nitrogen availability and elevated CO_2 interact to affect forest NPP. In this study we identified important influences of the nitrogen cycle in the potential response of forest NPP to elevated CO_2. At the tissue level, effects appear to be related to changes in tissue nitrogen concentration, and they may influence photosynthetic and respiration responses to elevated CO_2. However, it is important to recognize that increased nitrogen availability and elevated CO_2 have opposite effects on nitrogen concentration of leaf tissue. Although more research is needed to understand how changes in nitrogen concentration affect biochemical and physiological processes, an important challenge will be to understand the mechanisms responsible for changes in tissue nitrogen concentration. Research to address this issue requires attention at the levels of both tissue and plant. 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. Thus, changes in nitrogen availability in response to climatic changes influence the ability of vegetation to incorporate elevated CO_2 into production. Effects of elevated CO_2 at the tissue and plant levels may have important consequences for nitrogen cycling at the ecosystem level, but our knowledge of how CO_2-induced changes in litter quality and in root-derived soil carbon influence nitrogen availability is based on a small number of studies. Additional research is required at the ecosystem level to understand how interactions of the nitrogen cycle and elevated CO_2 affect forest NPP. Factorial studies that manipulate both atmospheric CO_2 and soil nitrogen availability for whole ecosystems would advance understanding.

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