

THE ROLE OF NITROGEN IN THE RESPONSE OF FOREST NET PRIMARY PRODUCTION TO ELEVATED ATMOSPHERIC CARBON DIOXIDE¹

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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 CO₂. The studies in our survey report that at the tissue level, elevated CO₂ 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 CO₂, photosynthetic response depends on a linear relationship with the response of leaf nitrogen concentration and the amount of change in atmospheric CO₂ concentration. Although elevated CO₂ often results in reduced tissue respiration rate per unit biomass, the link to changes in tissue nitrogen concentration is not well studied.

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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

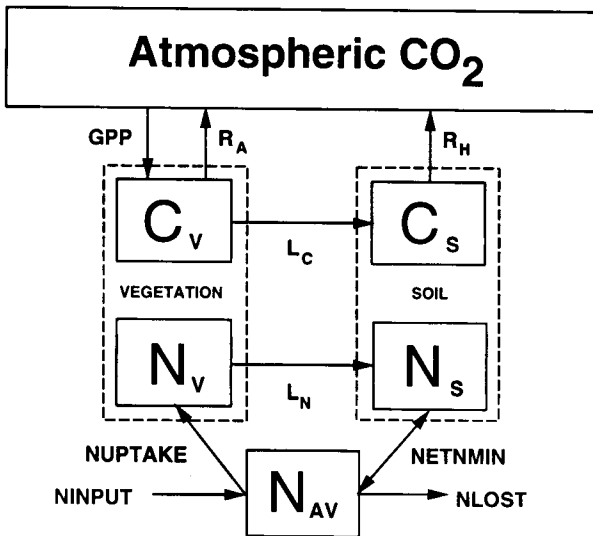


Figure 1 A generalized representation of carbon and nutrient cycles in terrestrial ecosystems. Carbon enters the vegetation pool (C_V) as gross primary production (GPP) and transfers either to the atmosphere as autotrophic (plant) respiration (R_A) or to the soil pool (C_S) as litter production (L_C); 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 CO₂ by influencing tissue, plant, and ecosystem processes.

The effects of elevated CO₂ 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 CO₂ in the context of plant and soil interactions.

TISSUE-LEVEL RESPONSES

Tissue-level processes that may be affected by elevated atmospheric CO₂ 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 CO₂ from all plant tissues. One way that the nitrogen cycle potentially interacts with elevated atmospheric CO₂ 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 CO₂, 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 CO₂. 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 CO₂ 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 CO₂ (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 CO₂ is accompanied with nitrogen fertilization. Although increased nitrogen availability and elevated CO₂ 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 CO₂ 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 CO₂, three photosynthetic acclimation responses are observed: downregulation, upregulation, and depressed photosynthesis (58). Downregulation occurs when the photosynthetic capacity of plants grown in elevated CO₂ decreases in comparison to plants grown at baseline CO₂, but the rate of photosynthesis for plants grown and measured at elevated CO₂ is still higher than the rate for plants grown and measured at baseline CO₂. For plants grown at elevated CO₂ compared to those grown at baseline CO₂, higher photosynthesis measured at both baseline and elevated CO₂ is defined as upregulation, and lower photosynthesis measured at both baseline and elevated CO₂ 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 gdm ⁻¹) ^c				Reference
					Leaf	Stem	Root	Plant	
<i>Acer pseudo-platanus</i>	390	+130	GH	—	—	—	—	-10%	86
<i>Acer saccharum</i>	390	+260	GH	—	—	—	—	-17%	56
<i>Acer saccharum</i>	350	+300	GC	—	—	—	—	—	95
<i>Acer saccharum</i>	350	+300	GC	—	NSD ^d	NSD	NSD	—	75
<i>Alnus glutinosa</i>	350	+350	GC	—	-46%	—	—	—	—
<i>Alnus rubra</i>	350	+300	GC	No nod; +N	+19%	+14%	-7%	+14%	—
<i>Artemisia tridentata</i>	350	+300	GC	Nod; No N	-11%	-5%	-2%	-6%	4
<i>Artemisia tridentata</i>	350	+300	GC	Nod; +N	-14%	-4%	+5%	-11%	48
<i>Artemisia tridentata</i>	350	+300	GC	—	-7%	—	—	—	—
<i>Artemisia tridentata</i>	350	+300	GC	low N	-17%	—	—	—	—
<i>Betula alleghaniensis</i>	350	+300	GC	high N	-28%	—	—	—	49
<i>Betula lenta</i>	350	+350	GH	—	-30%	—	—	—	97
<i>Betula papyrifera</i>	350	+350	GH	—	-25%	—	—	—	97
<i>Betula papyrifera</i>	350	+350	GH	—	-33%	—	—	—	97
<i>Betula papyrifera</i>	350	+300	GC	—	-20%	—	—	—	99
<i>Betula pendula</i>	350	+350	GC	—	-14%	-4%	+1%	—	92
<i>Betula pendula</i>	350	+350	GC	low N	—	—	—	-24%	—
<i>Betula pendula</i>	350	+350	GC	medium N	—	—	—	-20%	94
<i>Betula populifolia</i>	350	+350	GC	high N	—	—	—	-7%	97
<i>Betula populifolia</i>	350	+350	GH	—	-33%	—	—	—	—
<i>Betula populifolia</i>	350	+150	GC	—	—	—	—	-18%	—
Bottomland species	350	+250	GC	—	—	—	—	-36%	124
<i>Castanea sativa</i>	350	+350	GC	—	—	—	—	-42%	73
<i>Castanea sativa</i>	350	+350	GH	No fert	—	lower	lower	-16%	—
<i>Castanea sativa</i>	350	+350	GH	—	—	-11%	—	-13%	—

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

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					Reference
					Leaf	Stem	Root	Plant		
<i>Liriodendron tulipifera</i>	355	+300	OTC	—	-32%	—	—	—	—	77
	355	+150	OTC	—	-47%	—	—	—	—	
<i>Liriodendron tulipifera</i>	355	+150	OTC	—	-45%	—	—	—	—	131
<i>Picea mariana</i>	350	+350	GC	—	-25%	—	—	—	—	47
<i>Pinus strobus</i>	350	+300	GC	—	NSD	—	—	—	—	99
	406	+348	GC	1 year old	NSD	—	—	—	—	
<i>Pinus sylvestris</i>	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	—	—	—	—	40
<i>Pinus taeda</i>	350	+300	GH	high N	NSD	—	—	—	—	
	375	+335	GH	low N	-20%	NSD	NSD	NSD	NSD	54
<i>Pinus taeda</i>	375	+335	GH	high N	NSD	NSD	NSD	NSD	NSD	
	355	+355	GH	low P; -myc	—	—	—	—	—	
	355	+355	GH	high P; -myc	—	—	—	—	—	
	355	+355	GH	low P; +myc	—	—	—	—	—	
<i>Pinus taeda</i>	355	+355	GH	high P; +myc	—	—	—	—	—	55
	350	+350	GC	low water	—	—	—	-29%	—	
<i>Pinus taeda</i>	350	+350	GC	high water	—	—	—	-26%	—	118
	350	+150	OTC	—	-20%	—	—	—	—	
<i>Pinus taeda</i>	350	+300	OTC	—	-28%	—	—	—	—	123
<i>Pinus virginiana</i>	340	+600	OTC	—	—	—	—	+4%	—	60
	361	+346	OTC	45 days	-11%	—	—	—	—	
	361	+346	OTC	70 days	0%	—	—	—	—	25
<i>Populus grandidentata</i>	350	+400	GC	low N	-44%	—	—	—	—	
	350	+400	GC	medium N	-29%	—	—	—	—	

<i>Populus tremuloides</i>	350	+400	GC	high N	-21%	—	—	—	11
<i>Populus tremuloides</i>	350	+300	GC	—	-24%	—	—	—	56
<i>Quercus alba</i>	362	+328	GC	—	-19%	-17%	—	—	81
<i>Quercus alba</i>	355	+150 to +650	Natural	—	+9%	—	—	—	52
<i>Quercus pubescens</i>	355	+150 to +650	Natural	—	-15%	—	—	—	52
<i>Quercus rubra</i>	350	+300	GC	—	NSD	—	—	—	56
<i>Robinia pseudoacacia</i>	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%	—	—	—	109
<i>Salix x dasyclados</i>	300	+700	GH	highest N	-11%	—	—	—	51
Tropical vegetation	340	+270	GH	—	—	—	-10%	—	—
	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	NSD	—	124

^a GC—growth chamber experiments, GH—greenhouse experiments, OTC—open-top chamber experiments.

^b Nod—modulated, N—nitrogen, fert—fertilized, P—phosphorus, myc—mycorrhizae.

^c Change in nitrogen concentration relative to concentration for baseline CO₂ at same fertilization level.

^d NSD—no significant difference from nitrogen concentration at baseline CO₂.

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)				Reference
					Leaf	Stem	Root	Plant	
<i>Alnus rubra</i>	350	+300	GC	Nod; No N	-11%	-5%	-2%	-6%	4
	350	+300	GC	Nod; +N	-24%	-20%	+9%	-24%	
<i>Artemisia tridentata</i>	350	+300	GC	low N	-17%	—	—	—	49
	350	+300	GC	high N	-9%	—	—	-24%	
	350	+350	GC	low N	—	—	—	+65%	
	350	+350	GC	medium N	—	—	—	+147%	
<i>Betula pendula</i>	350	+350	GC	high N	—	—	—	-13%	94
	350	+350	GC	no fert	—	-11%	-16%	-13%	
<i>Castanea sativa</i>	350	+350	GH	fert	—	-21%	-32%	-34%	32
	330	+330	GH	low N	-31%	—	—	-27%	
<i>Eucalyptus camaldulensis</i>	330	+330	GH	high N	-5%	—	—	0%	126
	330	+330	GH	low N	-30%	—	—	-29%	
<i>Eucalyptus cypellocarpa</i>	330	+330	GH	high N	-8%	—	—	-7%	126
	340	+320	GC	low N	-38%	—	—	—	
<i>Eucalyptus grandis</i>	340	+320	GC	highest N	-43%	—	—	—	21
	330	+330	GH	low N	-22%	—	—	-21%	
<i>Eucalyptus pauciflora</i>	330	+330	GH	high N	-4%	—	—	-4%	126
	330	+330	GH	low N	-18%	—	—	-17%	
<i>Eucalyptus pulverulenta</i>	330	+330	GH	high N	-8%	—	—	+9%	126
	350	+300	GC	no N fert	-24%	NSD ^d	NSD	-11%	

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

^a relative to the nitrogen concentration for the treatment that uses baseline CO₂ and the lowest level of nitrogen fertilization.

^b GC—growth chambers experiments, GH—greenhouse experiments.

^c Nod—modulated, N—nitrogen, fert—fertilized.

^d NSD—no significant difference from nitrogen concentration at baseline CO₂.

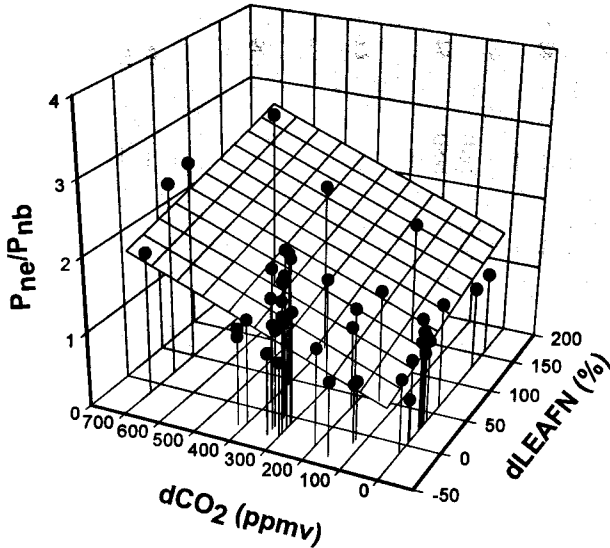


Figure 2 The relationship between photosynthetic response (P_{ne}/P_{nb}), percent change in nitrogen concentration of leaf tissue (dLEAFN), and amount of change in atmospheric CO_2 in ppmv (d CO_2), where P_{nb} is the net photosynthetic rate per unit area for plants grown and measured at both baseline 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 $P_{ne}/P_{nb} = 0.95924 + 0.00298 \text{ dLEAFN} + 0.00178 \text{ d}CO_2$ ($F = 33.1$, $P < 0.0001$, $df = 2,43$). Data are from studies that 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 & Wullschlegel (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 & Wullschlegel (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 CO₂ and nitrogen availability, the mean enhancement of photosynthesis to elevated CO₂ 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 CO₂ change (Figure 2):

$$P_{ne}/P_{nb} = 0.95924 + 0.00298 \text{ dLEAFN} + 0.00178 \text{ dCO}_2, \quad 1.$$

where P_{nb} is net photosynthesis per unit leaf area for plants grown and measured at both baseline CO₂ and the lowest level of fertilization in the experiment, P_{ne} is net photosynthesis rate for plants grown and measured at elevated CO₂ 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 dCO₂ is the concentration difference in ppmv between elevated and baseline CO₂. Baseline CO₂ was defined for each experiment as the CO₂ concentration that best represents contemporary atmospheric CO₂. 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: $P = 0.0154$; dCO₂: $P < 0.0001$), 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 CO₂. In the absence of changes in nitrogen availability, photosynthetic response depends on how leaf nitrogen concentration responds to elevated CO₂. 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 CO₂ 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 CO₂, the relationship indicates that nitrogen availability and nitrogen allocation play important roles in the acclimation of photosynthesis to elevated CO₂.

Acclimation to elevated CO₂ 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 CO₂, assimilation is limited by the quantity and activity of ribulose biphosphate carboxylase (rubisco), the enzyme that is primarily responsible for capturing atmospheric carbon in the production of sugars. Rubisco may accept either CO₂ (carboxylation) or O₂ (oxygenation) as a substrate; oxygenation is responsible for photorespiration. Because CO₂ competes with O₂ 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 Wullschlegel 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,

