

Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO₂ and land use history on the carbon dynamics of northern hardwood forests

SCOTT V. OLLINGER*, JOHN D. ABER*, PETER B. REICH† and RITA J. FREUDER*

*Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space, Morse Hall, University of New Hampshire, Durham, NH 03824, USA, †Department of Forest Resources, University of Minnesota, St. Paul MN 55108, USA

Abstract

Temperate forests are affected by a wide variety of environmental factors that stem from human industrial and agricultural activities. In the north-eastern US, important change agents include tropospheric ozone, atmospheric nitrogen deposition, elevated CO₂, and historical human land use. Although each of these has received attention for its effects on forest carbon dynamics, integrated analyses that examine their combined effects are rare. To examine the relative importance of all of these factors on current forest growth and carbon balances, we included them individually and in combination in a forest ecosystem model that was applied over the period of 1700–2000 under different scenarios of air pollution and land use history.

Results suggest that historical increases in CO₂ and N deposition have stimulated forest growth and carbon uptake, but to different degrees following agriculture and timber harvesting. These differences resulted from the effects of each land use scenario on soil C and N pools and on the resulting degree of growth limitations by carbon vs. nitrogen. Including tropospheric ozone in the simulations offset a substantial portion of the increases caused by CO₂ and N deposition. This result is particularly relevant given that ozone pollution is widespread across much of the world and because broad-scale spatial patterns of ozone are coupled with patterns of nitrogen oxide emissions. This was demonstrated across the study region by a significant correlation between ozone exposure and rates of N deposition and suggests that the reduction of N-induced carbon sinks by ozone may be a common phenomenon in other regions.

Collectively, the combined effects of all physical and chemical factors we addressed produced growth estimates that were surprisingly similar to estimates obtained in the absence of any form of disturbance. The implication of this result is that intact forests may show relatively little evidence of altered growth since preindustrial times despite substantial changes in their physical and chemical environment.

Keywords: carbon balance, climate variation, CO₂, forest productivity, land use history, nitrogen deposition, ozone

Received 22 February 2001; revised version received 23 October 2001 and accepted 30 October 2001

Introduction

Eastern US forests have been subjected to a number of environmental change agents that result from human industrial and agricultural activities. Although recent studies suggest an important role for these systems as

carbon sinks (Turner *et al.*, 1995; Fan *et al.*, 1998; Houghton *et al.*, 1999), carbon budget estimates still vary considerably and our understanding of underlying mechanisms remains incomplete. To date, attention to environmental factors that affect present-day rates of growth and carbon uptake has focused on elevated atmospheric CO₂, nitrogen deposition and land use history. Elevated CO₂ has been repeatedly shown to stimulate photosynthesis in a variety of tree seedlings (e.g. Curtis & Wang, 1998) and

Correspondence: Scott V. Ollinger, tel. US (603) 862-1792, fax US (603) 862-0188, e-mail: scott.ollinger@unh.edu

has also produced growth enhancements in mature forests subjected to open-air carbon enrichment (Ellsworth, 1999). However, the degree to which increased photosynthesis will translate to increased carbon storage over extended time periods may depend on feedbacks between altered plant C:N ratios, litter decomposition and soil N availability (Comins & McMurtrie, 1993; Lloyd, 1999). Similarly, elevated atmospheric nitrogen deposition can increase growth in N-limited systems (Vitousek & Howarth, 1991; Magill *et al.*, 1997), but its effect on whole-ecosystem carbon balances may be small if the increase occurs primarily in the form of low C:N ratio tissues (e.g. leaves) with fast turnover rates (Nadelhoffer *et al.*, 1999).

Land use history can influence forest carbon uptake in a number of ways. The first is through the relatively straightforward effects of biomass removal and forest regrowth. Between the 18th and early 20th centuries, large portions of the eastern US were cleared for agriculture and timber products, but much of that land has since regrown. The pattern of forest clearing, farm abandonment and subsequent biomass accumulation has had substantial effects on regional carbon balances, initially causing an increase in atmospheric CO₂ (as seen prior to the industrial revolution, Houghton *et al.*, 1996) and later causing an increase in forest CO₂ uptake (e.g. Houghton *et al.*, 1999; Casperson *et al.*, 2000). A less-studied role of land use history is the long-term effects that various land use practices can have on soil organic matter and nutrient availability. Although land use history effects on soil properties are complex, several studies have demonstrated altered nitrogen cycling after more than 100–200 years following agriculture, timber harvesting or fire (e.g. Compton & Boone, 2000; Goodale & Aber, 2001; Ollinger *et al.*, 2002).

An additional factor that has received relatively little attention for its role in forest carbon dynamics is tropospheric ozone. Among common air pollutants, ozone is probably the most damaging to forest vegetation and frequently occurs at high concentrations over large portions of the world (Chameides *et al.*, 1994). Ozone concentrations that are common in industrialized regions are known to cause large reductions in carbon fixation and biomass production in native plants as well as agricultural crops (Reich, 1987; Chameides *et al.*, 1994; McLaughlin & Downing, 1995; Chapelka & Samulson, 1998) and to alter patterns of plant carbon allocation (Laurence *et al.*, 1994). All of these suggest a strong potential for ozone to alter carbon balances in native ecosystems, perhaps offsetting the effects of elevated CO₂ or N deposition (Volin *et al.*, 1998). Although ozone continues to receive attention for its harmful effects on human health, food production and plant growth, it has rarely been included in analyses of broad-scale carbon fluxes.

This stems in part from the inherent variability of ozone concentrations and observed plant responses (Chapelka & Samulson, 1998), but also reflects a gap between the scientific communities studying ecological ozone effects and those concerned with terrestrial carbon cycles.

A number of interactions between ozone, CO₂, nitrogen deposition and land use history can be envisioned, but the large number of possible combinations and long time periods over which they operate make it impossible to gain complete understanding through controlled experiments alone. One alternative is to incorporate information on physiological and ecosystem responses into process models and examine their combined effects on predicted carbon dynamics. Model analyses that include coupled C and N cycles have predicted that large terrestrial carbon sinks should result from the widespread occurrence of N deposition (Townsend *et al.*, 1996; Holland *et al.*, 1997; Lloyd, 1999), but the potentially antagonistic effects of ozone and land use history were not included in these assessments. Recent analysis of forest inventory data suggests that growth enhancements over the past several decades have been small relative to predictions (Casperson *et al.*, 2000), raising the question of whether other stressors such as ozone may be important.

The purpose of this study was to examine the interactive effects of tropospheric ozone, elevated CO₂ and N deposition under different scenarios of land use history in order to determine the relative importance of each mechanism on present-day forest growth and carbon storage. To accomplish this, we included response algorithms for all of these factors in a modified version of the PnET forest ecosystem model, a model of carbon, nitrogen and water balances that has previously been applied and tested across the north-east study region (Aber *et al.*, 1995, 1997; Ollinger *et al.*, 1998). Prior analyses have used the PnET-CN model to estimate N deposition and land use effects, while ozone effects have been examined with PnET-II, which does not include N cycling feedbacks (Ollinger *et al.*, 1997). Here, we add ozone response algorithms to PnET-CN, derive new algorithms describing the leaf level, physiological effects of atmospheric CO₂ and integrate all factors in a single analysis.

Methods

Model structure and response algorithms

PnET-CN is a monthly time-step forest ecosystem model that combines generalized relationships for processes such as photosynthesis, respiration, transpiration, litter production, decomposition and N mineralization along with monthly climate inputs to estimate monthly carbon, nitrogen and water fluxes (Fig. 1). The model uses a multilayered canopy submodel of photosynthesis and

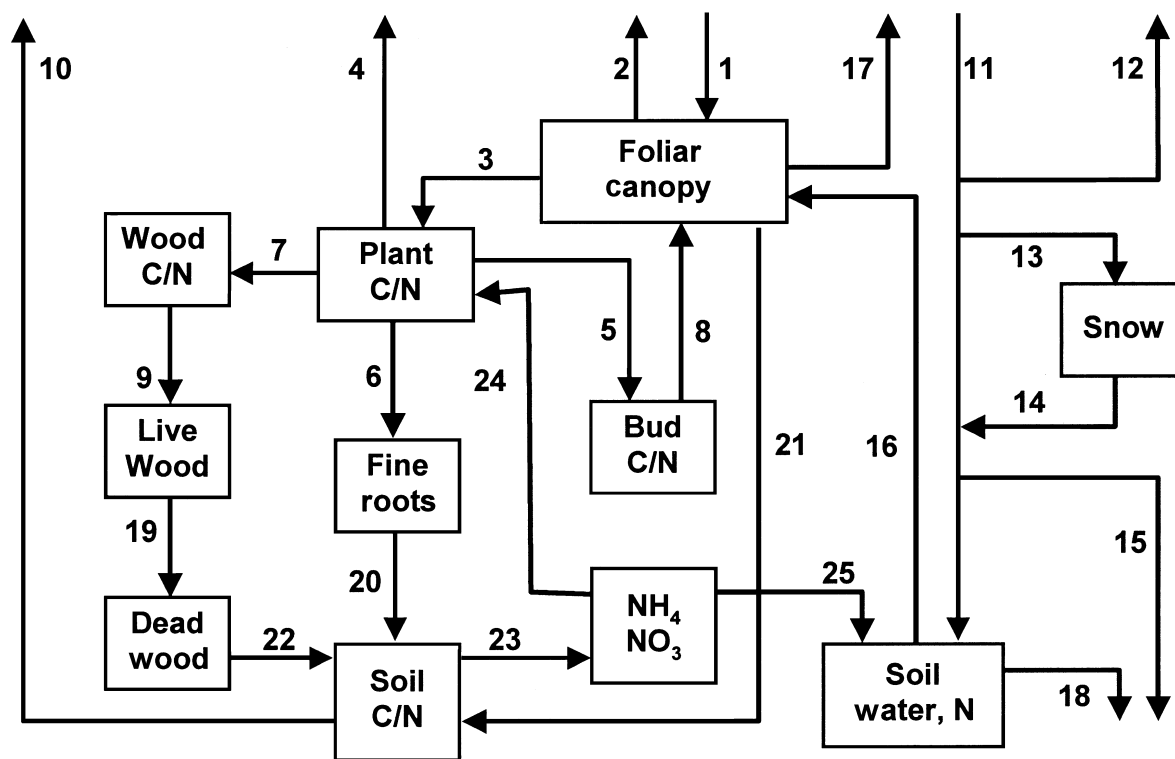


Fig. 1 Structure of the PnET-CN model. Boxes represent pools and numbered arrows represent fluxes as follows: (1) Gross photosynthesis & ozone uptake (2) Foliar respiration (3) Transfer to mobile pools (4) Growth and maintenance respiration (5) Allocation to buds (6) Allocation to fine roots (7) Allocation to wood (8) Foliar production (9) Wood production (10) Soil respiration (11) Precipitation & N Deposition (12) Canopy interception & evaporation (13) Snow-rain partitioning (14) Snowmelt (15) Macro-pore flow (16) Plant uptake (17) Transpiration (18) H₂O Drainage (19) Woody litter (20) Root litter decay (21) Foliar litterfall (22) Wood decay (23) N Mineralization & Nitrification (24) Plant N uptake (25) N transfer to soil solution.

phenology initially developed for the PnET-Day and PnET-II models by Aber *et al.* (1995, 1996). Added to this in the structure of PnET-CN are allocation and accumulation of carbon and nitrogen in live biomass, litter compartments and soil organic matter, as well as algorithms for N mineralization and nitrification, plant N uptake and leaching losses to produce complete cycles for water, carbon and nitrogen.

Carbon and nitrogen cycles interact at several points within PnET-CN. Foliar nitrogen concentrations are not fixed, but change year-to-year depending on the relative availability of C and N in plants. When plants have high internal N pools, the efficiency of N uptake from the soil is reduced and increases in N concentrations in foliage, wood and roots occur. Increased foliar N increases net photosynthesis and hence plant demand for N in the production of new tissues, completing a negative feedback. Carbon to nitrogen ratios in biomass are translated to litter and soil pools, and high C:N ratios have a negative effect on net N mineralization. PnET-CN has been validated against data on several carbon and nitrogen fluxes for forests in Germany (Postek *et al.*, 1995), and

against growth rates, water yield and nitrate concentrations at sites in the north-eastern US (Aber & Driscoll, 1997).

An important distinction between PnET-CN and PnET's canopy submodel, which lacks N cycling processes, is that PnET-CN requires inputs for disturbance history and includes dynamic interactions between soil N availability and foliar nitrogen concentrations. The simpler PnET-II and PnET-Day models trade this added complexity for the requirement of foliar nitrogen as a data input and the lack of dynamic interactions between C and N cycles.

Description of PnET-CN's canopy physiology, carbon allocation, N cycling and water balance routines have been given elsewhere (Aber *et al.*, 1996, 1997). In this study, we add algorithms for the effects of tropospheric ozone, derive new algorithms for the physiological effects of atmospheric CO₂ and integrate all factors under different scenarios of land use history. The response to each factor, as well as potential interactions among them, are briefly reviewed below. Because these stressors span a range of disciplines and have

been thoroughly reviewed elsewhere, our treatment of each will be necessarily limited.

Ozone effects Physiological ozone response algorithms were initially developed for PnET-II by Ollinger *et al.* (1997) and were derived from controlled exposure studies summarized by Reich (1987) and adding data from Tjoelker *et al.* (1995). Ozone effects on photosynthesis are based on cumulative ozone exposure and leaf stomatal conductance, which regulates ozone uptake, according to the equation:

$$dO_3 = 1 - (kgD40) \quad (1)$$

where dO_3 is the ratio of ozone-exposed to control photosynthesis, k is an empirically derived ozone response coefficient (with a value of 2.6×10^{-6} for hardwood forests), g is mean stomatal conductance (mm s^{-1}) and $D40$ is the cumulative ozone dose above a threshold concentration of 40 ppb. Vertical ozone concentration gradients are calculated as a function of canopy leaf area index, which influences resistance to vertical mixing, foliar ozone uptake and depletion on leaf surfaces (Munger *et al.*, 1996). Because ozone uptake is dependent on stomatal conductance, factors that affect conductance (e.g. water availability, foliar N concentrations) are important regulators of predicted ozone damage. An example is the interaction between soil moisture availability and predicted ozone effects, which can be reduced during periods of drought due to reduced stomatal conductance. High ozone concentrations often occur during hot, dry weather conditions, so periods of elevated ozone do not necessarily correspond to periods of maximal predicted ozone damage.

Ozone-induced declines in photosynthesis affect carbon allocation according to the model's existing carbon allocation algorithms. Although all plant compartments can be affected by ozone, the model gives higher priority to leaf and root growth than to wood growth. As a result, ozone-induced declines in carbon fixation will initially result in reduced wood growth, although leaf and root growth are also affected if wood productions fall below the level required to provide support and transport to the canopy. This response differs from some experimental results, particularly those from seedling studies, which often show reduced root growth in response to ozone (e.g. Laurence *et al.*, 1994). We have not attempted to duplicate this pattern in the model because mature trees are less allocationally plastic and because too little data are available to quantify the full cost of altered root growth in closed-canopy forests.

Nitrogen deposition N deposition and land use history act through their effects on soil carbon and nitrogen pools,

plant and soil C:N ratios, rates of N supply to vegetation and losses to drainage water (Aber *et al.*, 1997). Nitrogen fluxes are determined for all plant pools based on rates of N supply vs. plant demand. The C:N ratio of plant tissues are reflected in litter which decomposes into a single soil organic matter pool. Nitrogen mineralization is affected by soil C:N ratios, with high C:N ratio material increasing immobilization and decreasing N supply to vegetation. Prior analyses of these interactions indicate that historical disturbance effects on soil C and N dynamics can persist for several hundred years, depending on disturbance severity and rates of atmospheric N deposition (Aber & Driscoll, 1997).

CO₂ Response Previous versions of PnET have not included explicit CO₂ effects on photosynthesis, so the present study required development of a CO₂ response that was consistent with the model's structure and allowed for interactions with ecosystem nitrogen dynamics. Existing CO₂ response models range in complexity from simple dose-response multipliers to detailed biochemistry submodules. Recently, several findings suggest that canopy response to CO₂ can be adequately captured using a hybrid approach. The first is the observation that plants maintain relatively constant ratios of internal to ambient CO₂ concentrations (C_i/C_a ratios) in response to varying atmospheric CO₂ (e.g. Beerling, 1996; Drake & Gonzalez-Meler, 1996). The second is the tendency for leaf photosynthetic rates at varying CO₂ to scale along relatively stable A-C_i curves, suggesting a lack of photosynthetic down-regulation (Ellsworth, 1999). Collectively, these suggest that CO₂ effects on carbon assimilation can be approximated using response functions that retain the basic properties of the A-C_i curve (Katul *et al.*, 2000).

Building on these findings, we derived a CO₂ response algorithm that uses a Michaelis-Menton equation, fit to normalized A-C_i curves (scaled from 0 to 1, where 1 is CO₂-saturated carbon fixation) taken from a number of eastern tree species grown in CO₂ exposure studies (Pettersson & McDonald, 1992; Curtis *et al.*, 1995; Ellsworth *et al.*, 1995; Lewis *et al.*, 1996). Although the absolute A-C_i responses varied considerably between species (due to factors that affect photosynthetic potential such as leaf nitrogen), the relative responses were quite uniform (Fig. 2). We included this response in the model using the equation:

$$R_{C_a} = 1.22 * (C_i - 68)/(C_i + 136) \quad (2)$$

where R_{C_a} is the rate of photosynthesis at a given atmospheric CO₂ concentration (C_a) relative to that which occurs at CO₂ saturation. C_i is the internal leaf CO₂ concentration that occurs at the ambient concentration (C_a)

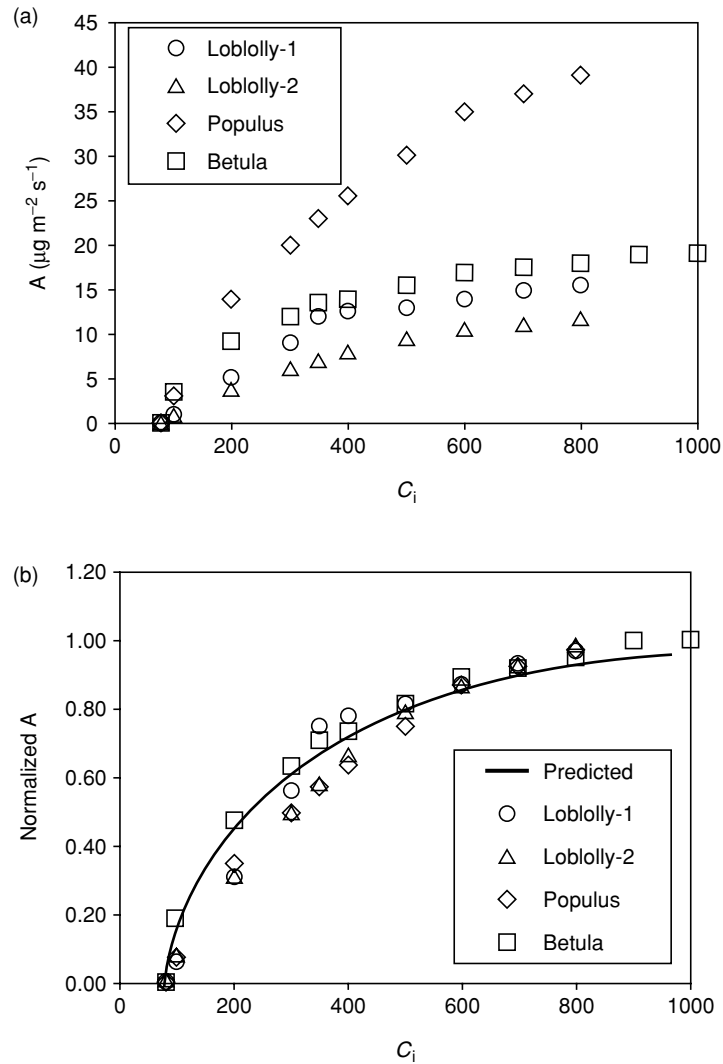


Fig. 2 (a) Photosynthesis in relation to internal leaf CO_2 concentrations (C_i) for conifer and hardwood (*Pinus taeda*, *Betula pendula* and *Populus euroamericana*) species taken from the literature (Pettersson & McDonald, 1992; Curtis *et al.*, 1995; Ellsworth *et al.*, 1995; Lewis *et al.*, 1996). (b) Data from Fig. 2(a) with photosynthesis normalized to CO_2 -saturated rates. The line represents the function given in Equation 2.

which varies over time. The constant 68 is the photosynthetic CO_2 compensation point, 136 is the half saturation concentration and 1.22 is an empirically derived constant. The equation has a similar form to that used in other models of photosynthesis (e.g. McMurtrie & Wang, 1993), but here is fit to data for eastern US tree species. Changes in photosynthesis over time are given by applying Equation 2 to varying CO_2 concentrations and determining the resulting change in R_{C_a} such that

$$\Delta A = (R_{C_{a2}} - R_{C_{a1}}) / R_{C_{a1}} \quad (3)$$

where ΔA is a proportional change in photosynthesis and C_{a1} and C_{a2} are CO_2 concentrations at time 1 and time 2, respectively.

Internal leaf CO_2 concentrations (C_i) are estimated from C_i/C_a ratios, which remain relatively constant, but vary slightly as a function of foliar nitrogen concentrations

(after Farquhar & Wong, 1984). This reflects greater internal CO_2 assimilation, and greater draw-down of C_i in foliage with higher N concentrations. In the model, C_i/C_a ratios vary linearly from 0.8 to 0.65 as foliar N increases from 1 to 3%. Photosynthetic capacity at present-day CO_2 levels and response to variation in foliar nitrogen concentrations are described by equations from Reich *et al.* (1995) and are unchanged from previous versions of PnET.

To check the model's photosynthetic CO_2 response against observed responses reported in the literature, we used the equations to estimate the relative change in photosynthesis between ambient and twice ambient CO_2 as well as between ambient and historical CO_2 . When foliar N was varied from 1 to 3%, the predicted change in photosynthesis between CO_2 concentrations of 350 and 700 ppm varied from +36 to +43%, which is within the range of measured responses for woody tree species (Curtis & Wang, 1998). The predicted change in

photosynthesis between CO₂ concentrations of 280 and 350 ppm – representing the change that has taken place over the past several centuries – varied from +17 to +21% which is in accordance with measurements over this CO₂ range (Polley *et al.*, 1992) and is close to the value of +23% estimated for woody plants from δ¹³C concentrations in leaf samples that have been preserved since preindustrial times (Beerling, 1996).

Although there has been considerable discussion regarding CO₂ effects on stomatal conductance, consensus on the likelihood of a long-term, sustained response has been slow to emerge. Field *et al.* (1995) suggested that reduced conductance would be a major component of ecosystem response to elevated CO₂, but subsequent evidence from a comprehensive meta-analysis (Curtis & Wang, 1998) and a mature-forest CO₂ exposure experiment (Ellsworth, 1999) showed little or no effect. However, a more recent synthesis by Medlyn *et al.* (2001) using data from experiments on European tree species found a significant (21%) reduction in conductance in response to doubled CO₂ concentrations and saw no evidence of acclimation. The contrast between this result and the Curtis & Wang (1998) findings was attributed to the duration of treatments in the experiments examined. Medlyn *et al.* (2001) limited their analysis to longer-term (> 1 year) studies and showed that stomatal response became more evident and less variable as the length of exposure to elevated CO₂ increased.

Conceptually, stomatal response to CO₂ can be characterized using the following approach: if conductance and photosynthesis are treated as coupled processes (e.g. Jarvis & Davies, 1998) then conductance can be related to the ratio of CO₂ flux across the leaf surface and the absolute CO₂ concentration gradient from the ambient air to the leaf interior. Assuming that canopy resistance is negligible and that CO₂ flux and photosynthesis are essentially equivalent, conductance can be represented by

$$g_s = A / (C_a - C_i) \quad (4)$$

where A is photosynthesis and (C_a - C_i) is the CO₂ concentration gradient, which drives diffusion across the stomatal boundary. Given the relative constancy of C_i/C_a ratios, the response of conductance to a change in ambient CO₂ concentrations can be described as

$$\Delta g_s = \Delta A (C_{a1} - C_{i1}) / (C_{a2} - C_{i2}) \quad (5)$$

where Δg_s and ΔA are proportional changes in conductance and photosynthesis, respectively, and (C_{a1} - C_{i1}) / (C_{a2} - C_{i2}) is the ratio of the CO₂ gradient at the initial CO₂ concentration C_{a1} and the final CO₂ concentration C_{a2}. If, for example, a change in CO₂ from 280 to 360 ppb caused a 19% increase in A (from equations 2 and 3) and C_i/C_a ratios have remained at 0.7, then Equation 5 yields

Δg_s = 0.93, implying a 7% reduction in conductance from preindustrial times. This approach has been used by other models (McMurtrie & Wang, 1993), and in the present analysis, causes a negative interaction between CO₂ concentrations and processes that are linked to stomatal conductance (e.g. transpiration, ozone uptake).

Study sites and model simulations

Addition of the above responses to PnET-CN allows multiple-factor interactions to occur through a series of feedbacks involving leaf physiology, soil moisture availability, foliar N concentrations, carbon allocation, biomass production, litterfall content and litter C:N ratios, decomposition, soil N supply and plant N demand. Acclimation to any environmental change can occur through source-sink interactions between soil nitrogen availability and plant demand. For instance, an increase in canopy photosynthesis due to elevated CO₂ creates increased plant demand for N and reduced foliar N concentrations, which affects photosynthesis and alters litter C:N ratios and subsequent rates of decomposition.

Regional model runs To examine the potential importance of multiple-factor interactions on present-day forest carbon gain, we applied the modified PnET-CN model to a series of sites that span the range of climatic conditions, ozone concentrations and N deposition levels experienced across the north-eastern US region. Of the required climatic and atmospheric data inputs, ozone was the only variable that was not available from an existing regional data set. Hence, model simulations were performed for locations where ground-level ozone concentration data were available directly from US EPA monitoring stations (Fig. 3). Methods for data quality screening and monthly ozone D40 calculations were described by Ollinger *et al.* (1997) and resulted in a total of 64 sites. Ozone data used in the model were mean monthly D40 values, calculated from hourly measurements at each site over the period from 1987 to 1992.

For nitrogen deposition, annual wet + dry N deposition rates were estimated for each site from a regional deposition model that was derived by combining concentration gradients for NH₄⁺, NO₃⁻ and HNO₃ in precipitation and ambient air masses with precipitation data layers and deposition velocity estimates (Ollinger *et al.*, 1993). The resulting deposition patterns indicated that within the north-east region, total N deposition declines along a south-west to north-east gradient from a high of approximately 12 kg ha⁻¹ year⁻¹ to a low of around 3 kg ha⁻¹ year⁻¹. Because we had no means of accounting for fine-scale variation due to factors such as local N emissions and elevation effects on dry deposition, N deposition estimates for the 64 sites probably differ to

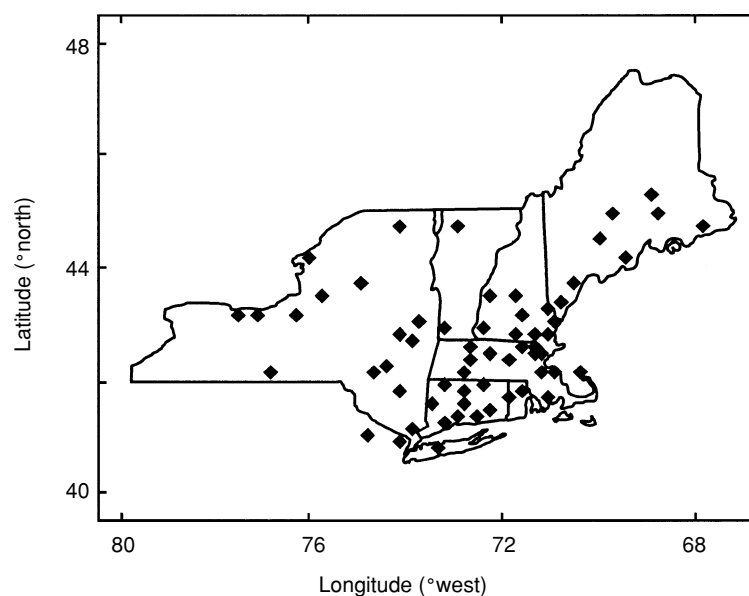


Fig. 3 Locations of 64 ozone monitoring sites in north-eastern US where model simulations were performed.

some degree from actual rates, although the overall magnitude and relative spatial patterns should be reasonably well captured.

Monthly climate data (maximum and minimum temperature, precipitation and solar radiation) were obtained from a statistical climate model, derived from 30-year means at over 300 weather stations (Ollinger *et al.*, 1995). We used mean rather than historical climate in order to identify more clearly the effects of the environmental factors this study was intended to examine. Soil water holding capacity for the 0–50 cm soil layer was estimated for each site using data from Kittel *et al.* (1996). Table 1 gives the range of site variables and climatic conditions encountered across the simulation sites.

The model was parameterized for northern hardwood forest vegetation (Table 2) and run for each site under historical scenarios of agricultural and timber harvesting (Table 3) as well as a control scenario with no land use. We ran all sites with each disturbance regime to allow clear identification of site history effects and because site history information were not available for each location. The timber harvest scenario was based on the history of the Hubbard Brook Experimental Forest in New Hampshire, USA as described by Whittaker *et al.* (1974). We included the following treatments: a 50% harvest in 1850, a 20% thinning in 1909, and an 80% harvest in 1917. In each case, 80% of harvested biomass was removed and 20% was assumed to remain on the ground as slash. We also included a 20% mortality event in 1938, with 40% of dead biomass removed. This mirrors damage caused by a major hurricane and a subsequent salvage logging operation.

The agriculture scenario was based on site history records for the Harvard Forest in Central Massachusetts,

Table 1 Summary statistics for site variables and climatic conditions across the 64 simulation sites. Lat. and Lon. are latitude and longitude in decimal degrees, elevation is in meters, WHC is soil water holding capacity (cm), Prec. is estimated annual precipitation (cm), Ndep. is estimated annual wet plus dry nitrogen deposition ($\text{kg ha}^{-1} \text{ year}^{-1}$) and ozone is the mean dose (in ppm-h) of hourly concentrations above a threshold of 40 ppb. Ozone dose values shown here are summed over the growing season (May through October)

	Lat.	Lon.	Elev.	WHC	Prec.	Ndep.	Ozone
Max.	45.04	76.81	942	23.00	129	10.30	32.56
Min.	40.68	68.28	7	14.80	80	4.10	5.47
Mean	42.56	72.39	143	20.27	112	7.90	16.48

USA. Although precise carbon and nitrogen removal rates are unknown, the land within Harvard Forest was cultivated from approximately 1750–1850 and so a significant fraction of production would have been removed annually. Following forest regrowth, a large portion of the area was severely damaged in 1938 by the same hurricane that affected Hubbard Brook and subjected to a salvage harvest around 1945. We simulated these patterns in the model with the following treatments: forest clearing in 1750 followed by continuous removal of 5% of biomass production through 1850, and an 80% timber harvest in 1945, 20% of which was left as slash. We will refer to this as the agriculture scenario for simplicity, but the posthurricane salvage harvest should also be remembered.

The model was run at monthly intervals from 1700 to 2000 with and without transient increases in CO_2 , O_3 and

Table 2 Input parameters required to run PnET-CN and values used

Parameter	Description	Value
<i>Site variables</i>		
Lat	Latitude	varies, see Table 1
WHC	Soil water holding capacity (cm)	varies, see Table 1
<i>Canopy variables</i>		
k	Canopy light attenuation constant	0.58
FolReten	Foliage retention time (years)	1
SLWMax	Top canopy specific leaf weight (g m^{-2})	100
SLWDel	Change in SLW with increasing foliar mass above ($\text{g m}^{-2} \text{g}^{-1}$)	0.2
FolRelGroMax	Maximum relative growth rate for foliage (year^{-1})	0.95
GDDFolStart	Growing degree days of foliage production onset	100
GDDFolEnd	Growing degree days of at which foliage production ends	900
GDDWoodStart	Growing degree days of wood production onset	100
GDDWoodEnd	Growing degree days of at which wood production ends	900
<i>Photosynthesis variables</i>		
AmaxA	Intercept (A) and Slope (B) for relationship between Foliar N and max. photosynthesis $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$	- 0.46
AmaxB		71.5
BaseFolRespFrac	Respiration as a fraction of max. photosynthesis	0.1
HalfSat	Half saturation light level $\mu\text{mol m}^{-2} \text{ s}^{-1}$	200
AmaxFrac	Daily Amax as a fraction of early morning instantaneous rate	0.75
PsnTOpt	Optimum temperature for photosynthesis $^{\circ}\text{C}$	24
PSNTMin	Minimum temperature for photosynthesis $^{\circ}\text{C}$	4
RespQ10	Q10 value for respiration	2
<i>Water balance variables</i>		
DVPD1	Coefficients for power function converting VPD to fractional loss in photosynthesis	0.05
DVPD2		2
PreIntFrac	Fraction of precipitation intercepted and evaporated	0.11
WUEConst	Constant in equation for WUE as a function of VPD	10.9
FastFlowFrac	Fraction of water inputs lost directly to drainage	0.1
f	Soil water release parameter	0.04
<i>Carbon allocation variables</i>		
CFracBiomass	Carbon fraction of biomass	0.45
RootAllocA	Intercept (A) and Slope (B) of relationship between foliar and root allocation	0
RootAllocB		2
GRespFrac	Growth respiration, as a fraction of allocation	0.25
RootMRespFrac	Ratio of fine root maintenance respiration to biomass production	1
WoodMRespA	Wood maintenance respiration as a fraction of photosynthesis	0.07
PlantCReserveFrac	Fraction of Plant C held in reserve after allocation to bud carbon	0.75
MinWoodFolRatio	Minimum ratio of carbon allocation to wood and foliage	
<i>Biomass Turnover and N Concentration Variables</i>		1.5
WoodTurnover	Fractional mortality of live wood per year	0.02
WoodLitTrans	Fractional transfer from dead wood to SOM per year	0.1
WoodLitCLoss	Fractional loss of mass in wood decomposition	0.8
RootTurnoverA	Coefficients for fine root turnover (fraction year^{-1}) as a function of annual N mineralization	0.789
RootTurnoverC		0.191
RootTurnoverB	(quadratic equation)	0.0211

MaxNStore	Maximum N content in mobile plant pool (g m ⁻²)	20
Ksom	Decomposition constant for soil organic matter pool (year ⁻¹)	0.075
NImmobA	Coefficients for fraction of mineralized N	151
NImmobB	reimmobilized as a function of SOM C:N ratio	-35
RLPctN	Min N concentration in root litter (%)	1.2
FLPctN	Min N concentration in foliar litter (%)	0.9
WLPctN	Min N concentration in wood litter (%)	0.2
FolNConRange	Maximum fractional increase in N concentration	0.6

Aber *et al.*, 1997 for details and complete equations.

Table 3 Disturbance history parameters used to simulate the effects of agriculture and timber harvesting

Year	Treatment	Mortality (proportion of biomass)	Biomass removed (proportion of mortality)
<i>Agriculture (From Harvard Forest, MA)</i>			
1750	Vegetation removal	0.9	0.6
1750–1850	Agriculture period	0.05 year ⁻¹	1
1945	Timber Harvest	0.8	0.8
<i>Timber Harvest (From Hubbard Brook, NH)</i>			
1850	Timber harvest	0.5	0.8
1909	Selective cut	0.2	0.8
1917	Timber harvest	0.8	0.8
1938	Hurricane salvage	0.2	0.4

N deposition. Atmospheric CO₂ concentrations were determined from an algorithm that was derived fit to ice core CO₂ data and the Mauna Loa CO₂ record. CO₂ concentrations were held at 280 ppb prior to 1800 and then increased nonlinearly to 363 ppb by year 2000 (Houghton *et al.*, 1996). The CO₂ ramp is described by:

$$\text{CO}_2 = 280 + [0.0188 * (\text{year} - 1800)]^{3.35} \quad (6)$$

where CO₂ concentrations are in ppm and *year* refers to the simulation year beyond 1800. The equation also projects increases in CO₂ concentrations into the future, reaching a level of 600 ppb by 2100. After Aber & Driscoll (1997), we held N deposition at 20% of its current level prior to 1930 and increased deposition inputs linearly to their present values. Because ozone formation in the atmosphere results from similar forms of industrial activity as N deposition, a similar ramp was used for changes in ozone exposure.

Transient dynamics at Hubbard Brook and Harvard Forest. To examine the transient effects of land use, CO₂, O₃ and N deposition, we conducted an additional set of simulations for the Hubbard Brook Experimental Forest and the Harvard Forest. These simulations were performed under the same conditions described above with a few minor exceptions. First, for Harvard forest, we

included a mild ground fire that occurred at that site in 1950 by removing 10% of the soil organic matter. Second, we used climate data collected at each site and added historical climate variability as an additional treatment. This was done by first compiling existing monthly climate records for all years where data were available (beginning in 1955 at Hubbard Brook and in 1964 at Harvard Forest). Next, data for maximum and minimum temperature, precipitation and solar radiation were extended back to 1895 using climate reconstructions available through the VEMAP program data set (Vegetation/Ecosystem Modelling and Kittel *et al.*, 1996, www.cgd.ucar.edu/vemap/). These reconstructions were scaled to match the Hubbard Brook and Harvard Forest sites by developing regression equations between the two data sets for the period where measured data were available (VEMAP values were taken from the grid locations that best matched Harvard Forest and Hubbard Brook). All equations were highly significant, with *R*² values of 0.97–0.99 for maximum and minimum temperatures, 0.74 for precipitation and 0.85 for radiation (*n* = 396–516). This demonstrated that temporal patterns in the VEMAP data matched those in the measured records and allowed us to extend those records back to 1895 by scaling the VEMAP data to equivalent values for the two simulation sites.

Finally, simulations at Hubbard Brook were conducted with measured wet plus dry N deposition data obtained from nearby sites operated by the National Atmospheric Deposition Program (NADP 2001) and the US EPA CASTNET program (Clean Air Status and Trends Network). N deposition at Harvard Forest, which does not have an on-site monitoring station, was estimated from the Ollinger *et al.* (1993) deposition model.

Results and discussion

Effects of CO₂, O₃ and N deposition under agriculture site history

Running all sites with an agricultural site history and preindustrial atmospheric conditions (background CO₂, O₃ and N deposition) produced present-day net primary production (NPP) values that ranged from 841 to 1003 g m⁻² year⁻¹ (dry biomass) with a mean of 933 g m⁻² year⁻¹ (Fig. 4a). Predictions for total annual carbon accumulation, or net carbon exchange (NCE) ranged from 87 to 124 gC m⁻² year⁻¹ with a mean of 106 gC m⁻² year⁻¹ (Fig. 4b). This positive carbon balance (net accumulation of carbon in the ecosystem) reflects the long-term effects of agriculture and biomass removal on soil carbon, soil respiration and biomass accumulation. Simulating the historical increase in atmospheric CO₂ caused a 17.4% increase in NPP and a 53.6% increase in NCE (Fig. 4a,b). The greater increase in NCE than NPP occurred because of the slow turnover rates for woody biomass and soil organic matter, which create long lag times between increased growth and soil respiration. Including the historical increase in ozone offset a substantial portion of the growth increase has been caused by elevated CO₂ and resulted in a regional mean NPP of 1045 g m⁻² year⁻¹. NCE remained elevated with respect to the control run, but was 12% lower than when ozone was not included.

The combination of rising N deposition and CO₂ (but no ozone) caused large gains in NPP and NCE, which averaged 1192 g m⁻² year⁻¹ and 186 gC m⁻² year⁻¹, respectively, increases of 28 and 76% over preindustrial conditions. Simulating increases in all factors simultaneously, which represents the most complete of all scenarios, produced NPP estimates ranging from 1030 to 1220 g m⁻² year⁻¹ (mean = 1116 g m⁻² year⁻¹) and NCE values of 139–188 gC m⁻² year⁻¹ (mean = 161 gC m⁻² year⁻¹), increases of 19 and 53% with respect to the control runs (Fig. 4a,b). These values are similar to those observed under rising CO₂ alone, indicating that the regional effect of N deposition on carbon sequestration was largely offset by ozone-induced declines in photosynthesis. Ozone effects on photosynthesis were slightly greater in the presence of elevated N deposition

because the added N inputs caused increased foliar N concentrations, which caused higher leaf gas exchange and ozone uptake. When compared to the scenario of elevated CO₂ and N deposition, the combined scenario indicated an ozone effect on NCE of from -10 to -45 gC m⁻² year⁻¹ with a mean of -25.0 gC m⁻² year⁻¹ or -13% (Fig. 4b).

Effects of CO₂, O₃ and N deposition under timber harvest site history

When all sites were simulated with a history of timber harvesting, overall predictions of NPP were higher, while overall predictions of NCE were lower than those following agriculture (Fig. 4). Under background atmospheric conditions, NPP averaged 1096 g m⁻² year⁻¹ and NCE averaged 42 gC m⁻² year⁻¹ (Fig. 4c,d). Differences between predictions under the agriculture vs. timber harvesting reflect the lower intensity of disturbance to soil C and N pools imposed by the timber harvest scenario than by the agriculture scenario. The simulated agricultural disturbance included continuous biomass removals for the 100-year period from 1750 to 1850. This caused depletion of soil nitrogen which had not recovered after 150 years of regrowth, even when the last half of that period experienced rising N deposition. Following the less severe effects of the timber harvest scenario, faster recovery of N cycling and higher foliar N concentrations led to higher rates of productivity. Because soil pools were disturbed to a lesser degree, soil respiration remained higher, keeping total carbon fluxes more tightly balanced than were observed following agriculture.

Interactions among CO₂, O₃ and N deposition were qualitatively similar following timber harvesting to those observed following agriculture (Fig 4c,d). However, because N limitations were weaker in the timber harvest simulations, plant C:N ratios were lower, causing plant growth to become more responsive to CO₂ relative to N deposition. The historical rise in CO₂ produced increases in NPP and NCE of 14 and 232% (reaching values of 1246 g m⁻² year⁻¹ and 134 gC m⁻² year⁻¹, respectively) while N deposition had a relatively small effect. Declines in growth due to ozone were greater than those observed following agriculture because of higher foliar N concentrations which led to greater ozone uptake by foliage. Compared to the scenario of increased CO₂ and N deposition, the combined scenario produced a mean ozone effect on NCE of -33.6 gC m⁻² year⁻¹ or -23% (Fig. 4c,d).

Relative influence of land use history and atmospheric chemistry

Model simulations conducted with no land use allow us to evaluate the extent to which carbon flux estimates

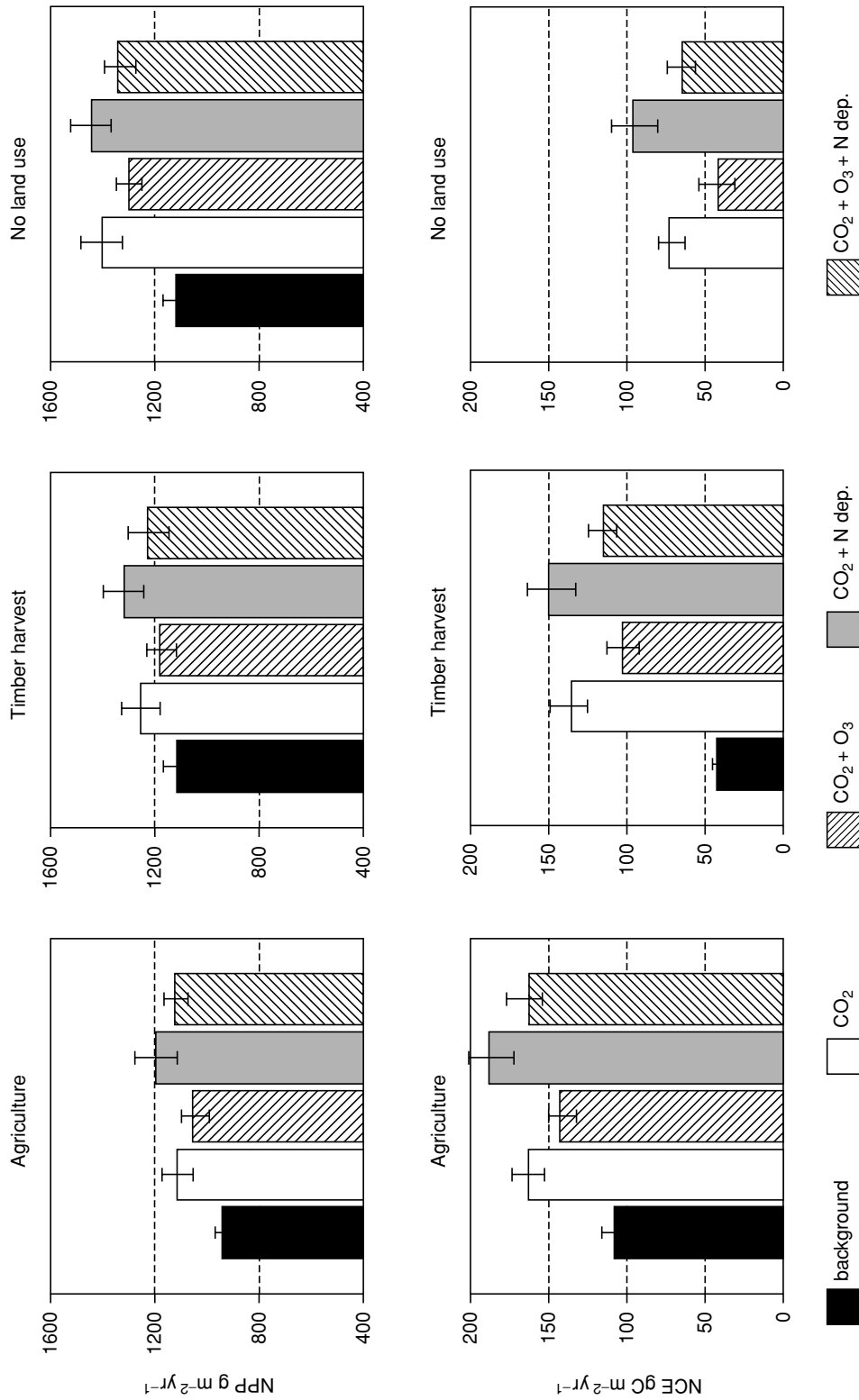


Fig. 4 Predicted mean net primary production (NPP, $g\ m^{-2}\ yr^{-1}$) and net carbon exchange (NCE, $gC\ m^{-2}\ yr^{-1}$) under different combinations of CO_2 , O_3 and N deposition and three land use history scenarios. Positive values for NCE indicate net uptake by the ecosystem. Values shown are means ($n = 64$) of predictions for the year 2000, at the end of 300-year simulations (1700–2000). Bars indicate standard deviations.

were affected by physical disturbances vs. changes in atmospheric chemistry. With no land use and background atmospheric conditions, predicted NPP averaged $1109 \text{ g m}^{-2} \text{ year}^{-1}$, which is slightly higher than that obtained under background atmospheric conditions in the timber harvest scenario, and considerably higher than under background conditions in the agricultural scenario. Interactions among pollution stressors were qualitatively similar to those seen under the previous two scenarios (Fig. 4e,f). Adding all three pollutants together resulted in a regional mean NPP of 1325, a 20% increase over that under background conditions.

Comparison of changes in predicted growth across pollution scenarios with changes across land use scenarios suggests that their effects can be relatively similar in magnitude, albeit with considerable variation resulting from differences in the intensity and timing of disturbance (Fig. 4). Note, for example, that predicted NPP in the absence of any disturbance (no land use and preindustrial atmospheric conditions, $1109 \text{ m}^{-2} \text{ year}^{-1}$) was very similar to that obtained under the most disturbance-intensive scenario of agricultural land use with all pollutant stressors ($1116 \text{ m}^{-2} \text{ year}^{-1}$). This indicates that, on average, the enhancement effects of CO_2 and N deposition were almost entirely offset by the negative effects of disturbance and ozone stress on site quality and photosynthetic capacity.

In the absence of any disturbance, predicted NCE was zero, illustrating a state of equilibrium between carbon fixation and ecosystem respiration. Adding all three pollutant stressors increased regional mean NCE to $64 \text{ gC m}^{-2} \text{ year}^{-1}$. Although this shows a substantial enhancement effect, NCE estimates resulting from pollution stressors along with agricultural and timber harvest disturbance scenarios were greater still (115 and $161 \text{ gC m}^{-2} \text{ year}^{-1}$, respectively). This suggests an important influence of each mechanism, but indicates a decline in their relative importance in the order of: agricultural scenario > atmospheric effects > timber harvest scenario.

Transient effects at Hubbard Brook and Harvard Forest

Results in Fig. 4 represent the endpoints of 300 years-long model simulations, but we were also interested in examining transient dynamics leading up to those values. Additional model runs for the Harvard Forest and Hubbard Brook research sites are shown in Figs 5 and 6 and demonstrate the transient effects of each land use and pollution scenario over the period of 1880–2000. In Fig. 5(a), which shows predictions for Hubbard Brook, NCE under each pollution scenario was at or near zero coming into the 20th century. This stems from the absence of disturbances throughout the 18th and 19th centuries,

with the exception of a weak CO_2 effect through the 1800s. In the baseline scenario (no disturbance of any kind), NCE remained at zero over the entire period. In the land use scenarios, the effects of each disturbance event are clearly visible and their combined influence persisted to the end of the simulations. The combined effects of atmospheric perturbations are more continuous and had a slightly greater influence on present-day NCE than did land use. The highest NCE predictions occurred when all atmospheric and physical disturbance factors were included together.

In the Harvard Forest simulations (Fig. 5b), NCE in the early 20th century was at or near zero in the absence of land use, but scenarios that included land use began the period with positive carbon balances. This was caused by continued long-term recovery following the 18th century agricultural treatments (not shown so that 20th century trends be more easily identified). Physical disturbances in Fig. 5 (b) represent the salvage harvest following the 1938 hurricane and the 1950 ground fire which occurred during recovery from the salvage harvest. The combined effects of all physical disturbances produced greater NCE than the combined effects of atmospheric disturbances, which is consistent with results in Fig. 4.

Figure 6 shows the result of adding climate variability over the period of 1895–2000 to simulations that included all land use and pollution effects. In both 6a and 6b, the baseline and combined (land use + atmospheric effects) simulations are the same as those in Fig. 5 and are included to provide a reference for climate variation effects. Although climate variation did not substantially alter mean levels of NCE, the degree of temporal variation in predicted values increased considerably. This was particularly true for Harvard Forest, where lower rainfall and higher temperatures, relative to Hubbard Brook, resulted in greater prediction of mid-summer water limitations. This is important because it suggests that short-term climatic effects can be similar in magnitude to the long-term effects of pollution (CO_2 + ozone + N deposition) and nearly as great as that of physical disturbance. We should note, however, that a previous application of PnET suggested that the model overestimates the importance of drought at Harvard Forest. Mid-summer drought was predicted by the model, but was less evident in the tower CO_2 flux data (Aber *et al.*, 1995). It was suggested that this discrepancy stemmed either from an underestimation of water holding capacity or from lateral flow of soil moisture at the HF site, a process that is not accounted for in the model.

At Hubbard Brook, predicted drought stress was generally less important than at Harvard Forest, which explains the lower amplitude of variation in predicted NCE. One noteworthy exception occurred in the mid 1960s when a prolonged period of drought caused

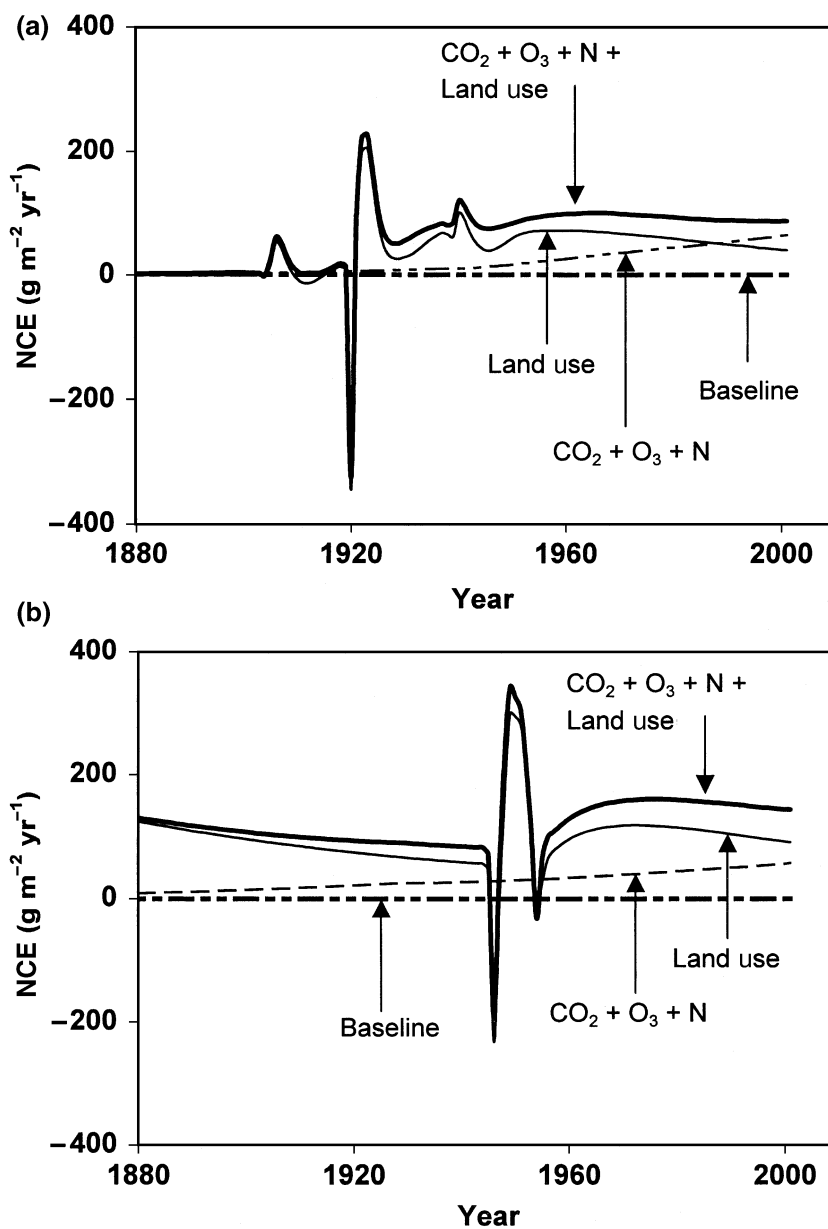


Fig. 5 Transient effects of various land use and atmospheric chemistry scenarios on net carbon exchange (NCE, $\text{g m}^{-2} \text{ year}^{-1}$) at (a) Hubbard Brook and (b) Harvard Forest. The baseline scenario included no disturbance of any kind. The land use scenario includes physical disturbances only (Table 3), the $\text{CO}_2 + \text{O}_3 + \text{N}$ scenario includes atmospheric effects only and the combined scenario (upper line) includes all factors together.

large reductions in predicted NCE. This effect is evident in Fig. 6(a), and was due to increased water limitations on carbon assimilation. This was followed by a period of higher-than-normal NCE immediately after the drought subsided. This response was driven by elevated rates of soil respiration and indicates that the drought caused greater reductions in decomposition than in litter production and carbon addition to soils.

The implication of these results is that changes in NCE driven by anthropogenic factors may be difficult to identify without long-term measurements and, even then, will likely require that considerable effort be put towards

separating anthropogenic effects from natural responses to climate variability.

Comparison with existing carbon balance estimates

The predicted rate of present-day carbon accumulation under the combined scenario following agriculture (regional mean = $161 \text{ gC m}^{-2} \text{ year}^{-1}$) is within, but on the low end of, the measured range of $140\text{--}280 \text{ gC m}^{-2} \text{ year}^{-1}$ from eddy flux tower measurements at the Harvard Forest (Wofsy *et al.*, 1993; Goulden *et al.*, 1996), and is in close agreement with an estimate for the north-east

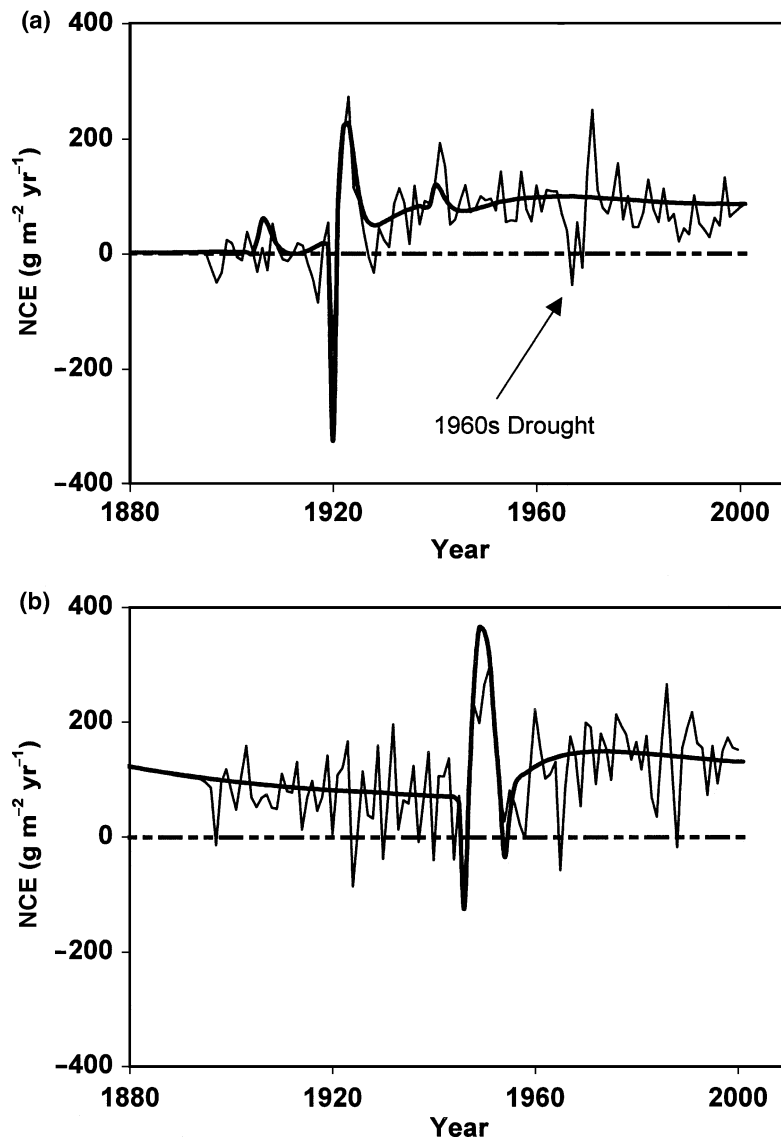


Fig. 6 Transient predictions of net carbon exchange (NCE, $\text{g m}^{-2} \text{ year}^{-1}$) at (a) Hubbard Brook and (b) Harvard Forest with the inclusion of interannual climatic variation as an additional treatment (along with all land use and pollution effects). Also shown for reference are results from the baseline and combined scenarios in Fig. 5. The predicted decline in NCE at Hubbard Brook during the 1960s results from a prolonged period of drought.

region of approximately $175 \text{ gC m}^{-2} \text{ year}^{-1}$ from analysis of forest inventory data (Turner *et al.*, 1995). Predicted carbon accumulation following the timber harvesting scenario (regional mean = $115 \text{ gC m}^{-2} \text{ year}^{-1}$) fell below both of these estimates. This may stem from the predominance of agricultural site histories across the north-eastern US region, which should be reflected in forest inventory data, and the fact that the Wofsy *et al.* (1993) and Goulden *et al.* (1996) studies were conducted at Harvard Forest, a site known for its history of agricultural cultivation.

Predicted rates of NCE at Harvard Forest for individual years under the variable climate scenario (Fig. 6) fall from within to below the measured range and underestimate measured values for 4 of the 5 years where data were available (Table 4). The greatest discrepancy occurred in

1994, when the model predicted the lowest NCE of the 5-year period. This resulted from the effects of below-average precipitation in 1993, which carried forward in the model through reduced allocation to buds to cause reduced canopy production and reduced C uptake in 1994. The model agreed well with measured NCE for 1993, which had the lowest measured NCE of the period, but the recovery implied by the high measured NCE in 1994 does not support the lag effect predicted by the model.

We should also emphasize that the disturbance scenarios we simulated represent available information on major disturbances at two well-documented sites, but also include important assumptions for parameters where information was lacking (e.g. precise biomass removal rates). Although Harvard Forest and Hubbard Brook are believed to have fairly typical histories among

Table 4 Predicted and observed net carbon exchange (NCE) for the Harvard Forest for the period from 1991 to 1995 (observed values from Goulden *et al.*, 1996). Positive values indicate net uptake by the ecosystem

Year	Predicted NCE (gCm ⁻² year ⁻¹)	Observed NCE (gCm ⁻² year ⁻¹)
1991	217	280
1992	163	220
1993	155	140
1994	78	210
1995	160	270

north-eastern forests, we should not assume that our results reflect differences between agriculture and timber harvesting generally. Further, although major disturbances were included in our simulations, it is likely that measured rates of NCE are also influenced by a variety of minor disturbances. Physical disturbances such as small wind-throw events, insect defoliations, soil frost and winter ice storms are known to occur in these ecosystems, but specific records of such events are very limited and were not included in our analysis.

Conclusions and implications for other regions

Our analysis suggests that over the past several decades, elevated atmospheric CO₂ and N deposition have caused increases in present-day rates of growth and carbon accumulation across north-eastern forests, but that the magnitude of these gains has been considerably reduced by concurrent increases in ozone (Fig. 7). The larger

relative declines in NCE than NPP stems from the fact that ozone has a proportionately greater effect in the model on predicted wood growth than on leaf or root growth. Hence, relatively small reductions in biomass production can translate to greater reductions in present-day ecosystem carbon gain because of the decades to centuries required before reductions in wood growth translate to reduced soil respiration.

These results have potentially important implications for areas beyond the north-eastern US because many regions experience higher-than-background ozone levels and because the spatial distributions of nitrogen deposition and tropospheric ozone are often related. Whereas cycles of carbon and nitrogen are coupled within the biosphere, patterns of N deposition and surface ozone concentrations are linked in the atmosphere through the dependence of ozone formation on nitrogen oxide emissions. Tropospheric ozone is formed by photochemical reactions involving volatile organic compounds (VOCs) and the nitrogen oxides NO and NO₂ (NO_x). In the eastern United States, where biogenic VOC emissions are high, ozone production is controlled to a greater extent by NO_x emissions (National Research Council 1992). This has been demonstrated at local scales by analysis ozone formation in power plant smoke plumes (Ryerson *et al.*, 2001) and is evident at broader scales across our study region by a strong correlation between N deposition and ozone exposure levels (Fig. 8). This relationship has also been predicted to occur globally, wherever N deposition comes principally from industrial NO_x emissions (Chameides *et al.*, 1994; Holland *et al.*, 1997) as opposed to agricultural ammonium emissions. Variation in this trend should also result from climatic factors that affect

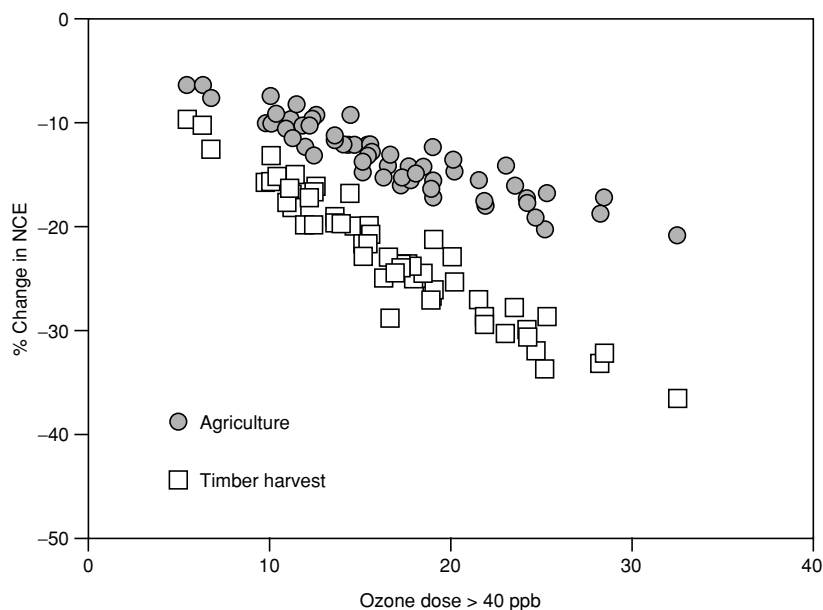


Fig. 7 Predicted change in current annual net carbon exchange (NCE) in response to ambient ozone concentrations across the north-eastern US under two land use history scenarios. Reductions in NCE represent the difference between predictions under rising CO₂ + N deposition + O₃ and those under rising CO₂ + N deposition only. Ozone Dose > 40 ppb is the sum of hourly daytime concentrations above a threshold concentration of 40 ppb, accumulated over one growing season.

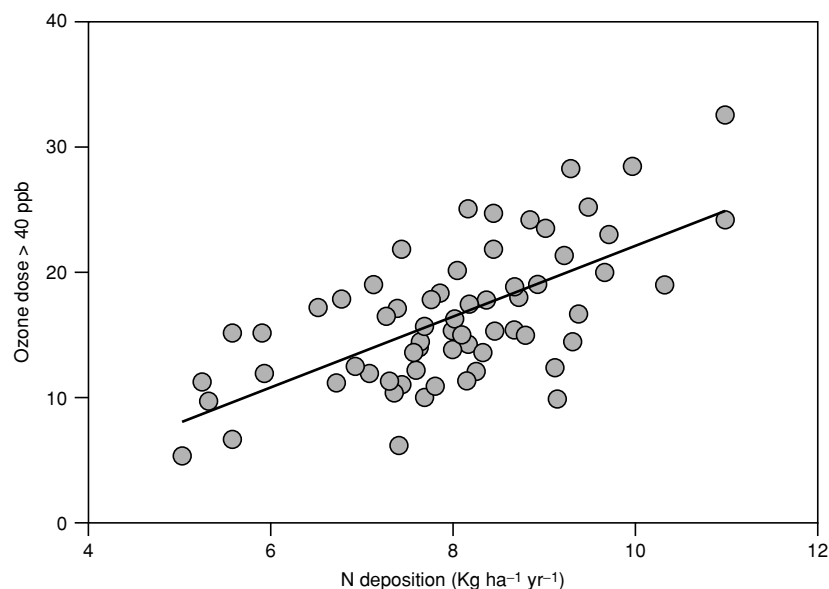


Fig. 8 Mean ozone Dose > 40 ppb in relation to annual wet + dry nitrogen deposition ($\text{kg ha}^{-1} \text{ year}^{-1}$) for the 64 study sites across the north-eastern US region. $R^2 = 0.42$, $P < 0.001$.

the kinetics of ozone formation independently of N emissions. Nevertheless, given the importance of industrial N emissions globally, these results raise the question of whether the reduction of N-induced carbon sinks by ozone may be a common phenomenon across other industrialized regions.

Comparison of model predictions across different disturbance history scenarios vs. predictions across pollution scenarios suggests that all factors have an important influence on present-day growth and carbon gain. In the case of NPP, factors that caused growth enhancements (CO_2 and N deposition) were similar in magnitude to factors that caused growth reductions (ozone and historical disturbance). Although substantial variation in their relative effects at any given site can result from differences in disturbance intensity and pollution exposure levels, the implication of these results is that intact forests may show relatively little evidence of altered growth since preindustrial times and that identifying the effect of any single factor may be a very challenging task. This may help to explain discrepancies that have emerged in the literature between experimental data and field observations of forest biomass production. Although CO_2 exposure studies and analysis of leaf $\delta^{13}\text{C}$ concentrations both indicate increased photosynthesis over the past several centuries (e.g. Polley *et al.*, 1992; Beerling, 1996), analysis of forest inventory data show little change in aboveground production at the stand level (Casperson *et al.*, 2000).

For net ecosystem carbon exchange (NCE), atmospheric effects and disturbance effects both contributed to the positive rates of present-day carbon gain, and by relatively similar magnitudes. Identifying the influence of individual mechanisms is important because each can

have very different consequences for future rates of carbon uptake and storage. The effects of physical disturbances typically involve transient changes in NCE that diminish as forests mature, whereas growth enhancements or reductions due to atmospheric effects are likely to persist for longer periods of time. Although positive carbon balances that stem from past land use activities represent a transfer of carbon from the atmosphere to the ecosystem over the short-term, they do not represent a net gain over the long-term because the acquired carbon may simply replace that which was present in the ecosystem prior to disturbance. Atmospheric effects, however, can represent novel changes with very different long-term implications.

Finally, although this analysis was intended to raise interesting questions about interactions between human activities and ecosystem processes, it is also important to recognize the uncertainties that are inherent in such a study. Our aim was to expand the range of environmental factors that are normally included in model analyses, but we should recognize that the number of mechanisms acting in real ecological systems is substantially greater. Although the processes we included in PnET-CN have all been identified as important responses, other processes that are either beyond the scope of the model or for which too little information is presently available may prove to be equally important. Nevertheless, the synthesis of existing information and advancement of new hypotheses can be an important contribution to scientific understanding and is one for which models are particularly well suited. Developing methods for testing these hypotheses poses a greater challenge and will likely require a variety of techniques such as eddy covariance, multifactorial field experiments and large-scale gradient analyses.

Acknowledgements

This research was supported by the USDA Forest Service Southern Global Change Program and the USDA Forest Service Northern Global Change Program. We received valuable input and helpful comments from a number of individuals including Glenn Bernston, Christy Goodale, Tom Lee, Gary Lovett, Alison Magill and Marie-Louise Smith. Access to the VEMAP historical climate dataset was provided by the Climate System Modelling Program, University Corporation for Atmospheric Research, and the Ecosystem Dynamics and the Atmosphere Section, Climate and Global Dynamics Division, National Center for Atmospheric Research. This project is a contribution to the Harvard Forest and Hubbard Brook Long-Term Ecological Research Programs.

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