

MIT Joint Program on the Science and Policy of Global Change



Ozone Effects on Net Primary Production and Carbon Sequestration in the Conterminous United States Using a Biogeochemistry Model

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This report is one of a series intended to communicate research results and improve public understanding of climate issues, thereby contributing to informed debate about the climate issue, the uncertainties, and the economic and social implications of policy alternatives. Titles in the Report Series to date are listed on the inside back cover.

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Abstract

The effects of air pollution on vegetation may provide an important control on the carbon cycle that has not yet been widely considered. Prolonged exposure to high levels of ozone, in particular, has been observed to inhibit photosynthesis by direct cellular damage within the leaves and through changes in stomatal conductance. We have incorporated empirical equations derived for trees (hardwoods and pines) and crops into the Terrestrial Ecosystem Model version 4.3 (TEM 4.3) to explore the effects of ozone on net primary production and carbon sequestration across the conterminous United States. Our results show up to a 5% reduction in Net Primary Production (NPP) in response to modeled historical ozone levels during the late 1980s to early 1990s. The largest decreases (over 20% in some locations) occur in the eastern U.S. and Midwest, during months with high ozone levels and high productivity. Carbon sequestration during the 1980s is reduced by 30 to 70 Tg C yr⁻¹ with the presence of ozone, or 5 to 23% of recent estimates of the total carbon sequestration for the U.S. Thus the effects of ozone on NPP and carbon sequestration should be factored into future calculations of the U.S. carbon budget.

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1. INTRODUCTION

Changes in atmospheric composition and land-use during the last century directly affected vegetation and soils and, therefore, the global carbon cycle. These changes have also indirectly affected the biota through influences on climate. While biogeochemical models have been used to study the effects of CO₂ fertilization, cropland establishment and abandonment, and climate variability as well as change on terrestrial ecosystems across the globe (*e.g.*, McGuire *et al.*, 2001), the damaging effects of air pollution on ecosystems have only been studied on a limited regional basis (Ollinger *et al.*, 1997, 2002). Over 90% of this damage may be the result of one air pollutant, tropospheric ozone (Adams *et al.*, 1986).

Tropospheric ozone is the product of photochemical reactions of carbon monoxide (CO), methane (CH₄), and other hydrocarbons in the presence of NO_x (NO + NO₂). Hydrocarbons are the product of fossil fuel emissions, solvent use, chemical manufacturing, and volatile organic carbon (VOC) emissions from natural vegetation. The primary sources of NO_x in the troposphere include fossil fuel combustion, as well as biomass burning, lightning, and microbial and geochemical processes in soils (Mauzerall and Wang, 2001). The production/destruction of ozone in the troposphere is determined by the concentrations of NO_x, CO, CH₄, and nonmethane hydrocarbons (NMHCs) (*e.g.*, Lui *et al.*, 1987; Lin *et al.*, 1988). Ozone can also be transported into a region by local winds and downward from the stratosphere (Oltmans and Levy II, 1994).

In the United States, ozone values reach their maximum in early spring (Singh *et al.*, 1978) to late summer, depending upon favorable meteorological or pollution conditions (Logan, 1989). Industrial continental regions tend to have maximum ozone values in the late afternoon and minimum in the early morning hours, whereas marine and high latitude sites have maximum ozone values before sunrise and lowest values in the afternoon (Oltmans and Levy II, 1994). Background ozone levels in unpolluted air can be anywhere from 20 to 60 ppb (Seinfeld, 1989; Lefohn *et al.*, 2001). Polluted regions contain ozone levels as high as 400 ppb (Seinfeld, 1989).

The effects of ozone on vegetation have been studied both within the laboratory and in field experiments (Heck *et al.*, 1984a,b; Pye, 1988; Pell *et al.*, 1990, 1993; Beyers *et al.*, 1992; McLaughlin and Downing, 1995; Tjoekler *et al.*, 1995; Fuhrer *et al.*, 1997; Lyons *et al.*, 1997; Zheng *et al.*, 1998; Lindroth *et al.*, 2001; Noormets *et al.*, 2001). Ozone affects vegetation by direct cellular damage once it enters the leaf through the stomates, so that ozone uptake is a function of both ambient ozone levels and stomatal conductance (Mauzerall and Wang, 2001). The cellular damage is probably the result of changes in membrane permeabilities and may or may not result in visible injury or reduced growth or yield (Krupa and Manning, 1988). A secondary response to ozone is a reduction in stomatal conductance, as the stomates close in response to increased internal CO₂ (Reich, 1987). Stomates generally open in response to light and warmth and close in response to aridity, water stress, and high CO₂ (Mauzerall and Wang, 2001). It has been suggested that the decrease in stomatal conductance caused by ozone is similar in magnitude to that caused by CO₂ increases since preindustrial conditions (Taylor and Johnson, 1994). Tjoekler *et al.* (1995) found a decoupling of photosynthesis from stomatal conductance as a result of long-term ozone exposure. Such a decoupling implies that ozone-induced reductions in photosynthesis would also be accompanied by decreased water use efficiency, resulting in even larger productivity reductions, particularly at arid sites (Ollinger *et al.*, 1997).

There have been few process-based modeling studies on the effects of ozone on vegetation. Reich (1987) developed a linear model using the experimental results of earlier studies to determine how pines, hardwoods, and crops respond to ozone. His results show that crops are the most sensitive to ozone and pines the least sensitive. Ollinger *et al.* (1997) used this model in the PnET-II forest ecosystem model to study the effects of ozone on hardwoods in the northeastern U.S. for the late 1980s to early 1990s. They found a reduction in net primary production (NPP) of between 3 to 16%, with less of a reduction on drier sites due to the lower stomatal conductance that generally occur at these sites. Ollinger *et al.* (2002) later applied their ozone algorithms to a version of PnET (PnET-CN) that includes nitrogen (N) cycling to evaluate the interactive effects of CO₂, O₃, and N within a context of historic land-use changes for the hardwoods in the northeastern U.S. They found that ozone counteracted the effects of increased CO₂ and N deposition on forest growth and carbon uptake in this region.

The current study expands the work of Ollinger *et al.* (1997, 2002). We incorporate the Reich (1987) and Ollinger *et al.* (1997) algorithms into an extant biogeochemical model, the Terrestrial Ecosystem Model (TEM 4.2) to explore the effect of ozone on net primary production and carbon sequestration across the conterminous U.S. during the 20th century, in the context of changing atmospheric CO₂ concentrations, climate, land cover, and agricultural management.

2. METHODS

To conduct this study, we first modified TEM 4.2 to include the effects of ozone on vegetation and developed a spatially-explicit historical ozone data set for the conterminous United States. We then conducted a series of simulations to partition the relative effects of ozone and other environmental factors. Finally we estimated the uncertainty in our results associated with the errors in the ozone parameters. Below we describe these procedures in detail.

2.1 Model Description

The Terrestrial Ecosystem Model is a process-based biogeochemistry model that simulates the cycling of carbon, nitrogen, and water among vegetation, soils, and the atmosphere. Vegetation incorporates carbon by the uptake of atmospheric CO₂ during photosynthesis (*i.e.* gross primary productivity, GPP). Soils obtain both organic carbon and nitrogen from litterfall that results when plant tissue dies. Carbon returns to the atmosphere through autotrophic respiration (R_A) from vegetation and heterotrophic respiration (R_H) associated with the decomposition of soil organic matter. A pool of available soil inorganic nitrogen provides the source of nitrogen to the vegetation and is replenished by nitrogen mineralization of soil organic nitrogen that results from decomposition (Raich *et al.*, 1991). Thus, nitrogen is recycled within the ecosystem. Vegetation nitrogen is divided into labile and structural components, which are the result of nitrogen resorption from dying tissues and nitrogen mobilization to create new tissues (Tian *et al.*, 1999). Further details of the model are described in Raich *et al.* (1991) and Tian *et al.* (1999, 2002).

In this study a new version of the Terrestrial Ecosystem Model (TEM 4.3) has been developed by modifying TEM 4.2 (Tian *et al.*, 2002) to include the effects of ozone on plant growth and to incorporate a new agriculture scheme. Specifically, the calculation of gross primary production (Raich *et al.*, 1991; Tian *et al.*, 1999) has been modified to include both direct and indirect effects of ozone on photosynthesis as follows:

$$GPP = Cmax f(PAR) f(LEAF) f(T) f(Ca, Gv, O_3) f(NA, O_3) f(O_3) \quad (1)$$

where $Cmax$ is the maximum rate of C assimilation, PAR is photosynthetically-active radiation, $LEAF$ is the leaf area relative to the maximum annual leaf area, T is the monthly air temperature, Ca is the atmospheric CO_2 concentration, Gv is the relative canopy conductance, O_3 is ozone, and NA is the feedback of nitrogen availability on carbon assimilation. The multiplier $f(O_3)$ incorporates both the direct immediate and lagged effects of ozone on GPP, whereas the multipliers $f(Ca, Gv, O_3)$ and $f(NA, O_3)$ include the indirect effects of ozone on GPP.

The direct ozone effect on photosynthesis is based upon Ollinger's Equation 1 for hardwoods and the dose response curves in figures 2 through 4 in Reich (1987), as follows:

$$rO_3 = 1 - (a \times g \times AOT40) \quad (2)$$

where rO_3 is the ratio of photosynthesis with and without ozone and is a value between 0 and 1, a is an empirically-derived ozone response coefficient, g is the mean stomatal conductance, and $AOT40$ is an ozone index based on accumulated hourly ozone values above a threshold of 40 ppb. The value of a is $2.6 \times 10^{-6} \pm 2.8 \times 10^{-7}$ for hardwoods (based on the value used by Ollinger *et al.*, 1997) $0.8 \times 10^{-6} \pm 3.6 \times 10^{-7}$ for conifers (based on pines), and $4.9 \times 10^{-6} \pm 1.6 \times 10^{-7}$ for crops which have been calculated from the empirical model of Reich (1987). The errors are based on the standard deviation of the slope from the dose response curves and the standard error of the mean of the stomatal conductances. As in Ollinger *et al.* (1997), stomatal conductance is calculated as follows:

$$g = -0.3133 + 0.8126 \times GPP. \quad (3)$$

The amount of O_3 entering the vegetation is itself limited by the previous month's ozone exposure due to reduced stomatal conductance. This reduction is accomplished using the following function:

$$rO_{3l} = (1 - 1/rO_{3c}) \times rO_{3p} + 1/rO_{3c} \quad (4)$$

where rO_{3c} is the current month's rO_3 value, rO_{3l} is a value between 1 and $1/rO_{3c}$ that counteracts the current month's rO_3 effect, and rO_{3p} is the previous month's ozone value. Overall, the direct immediate and lagged effects of ozone on GPP are described as follows:

$$f(O_3) = rO_3 \times rO_{3l}. \quad (5)$$

The change in stomatal conductance resulting from ozone exposure will also influence the uptake of atmospheric carbon dioxide and inorganic nitrogen by vegetation. This effect is applied using the previous month's ozone value (rO_{3p}) to incorporate the lag following initial ozone exposure, consistent with the approach taken by Ollinger *et al.* (1997). To reduce the amount of CO_2 entering the vegetation, Gv (Tian *et al.*, 1999) is reduced by multiplying evapotranspiration (EET) by rO_{3p} . To reduce the amount of N entering the vegetation, $NUPTAKE$ (McGuire *et al.*, 1992; Pan *et al.*, 1998) is reduced by multiplying it by rO_{3p} ; $NUPTAKE$ influences $f(NA)$ to affect GPP .

To estimate the net assimilation of CO_2 into plant tissues (*i.e.* plant growth), we calculate net primary production (NPP) as follows:

$$NPP = GPP - R_A. \quad (6)$$

To estimate carbon sequestration by the ecosystem, we calculate net carbon exchange as follows:

$$NCE = NPP - R_H - Ec - Ep \quad (7)$$

where Ec is the carbon emission during the conversion of natural ecosystems to agriculture, and Ep is the sum of carbon emission from the decomposition of products (McGuire *et al.*, 2001). For natural vegetation, Ec and Ep are equal to 0, so NCE is equal to net ecosystem production (NEP).

In addition to these revisions needed to incorporate ozone effects, TEM 4.3 also includes a new scheme to estimate NPP in agricultural ecosystems. In TEM 4.2, a spatially-explicit, empirically-derived relative agricultural productivity (RAP) database has been used to infer the effects of agricultural practices on crop productivity (McGuire *et al.*, 2001). Agricultural production was determined by simply multiplying the NPP of the original natural vegetation by a RAP value for the appropriate grid cell. In TEM 4.3, agricultural productivity is now no longer dependent upon the productivity rates of the original natural vegetation. Instead, the model uses the grassland parameterizations to describe carbon and nitrogen dynamics of crop plants. Soil organic matter dynamics of croplands, however, are still based on the parameterizations of the original natural vegetation. As in McGuire *et al.* (2001), forty percent of vegetation carbon in crops is assumed to be removed during harvest, and the remaining vegetation carbon is transferred to the soil organic carbon pool. Although the effects of different agricultural practices on crop productivity are not explicitly considered in TEM 4.3, two switches have been added that allow the model to estimate crop productivity if nitrogen is not limiting (*i.e.* optimum fertilization) and to estimate crop productivity if water is not limiting (*i.e.* optimum irrigation). Thus, the model can discern a range of crop productivities based on optimum agricultural management versus no management in the context of changing environmental conditions. The revisions are described in more detail in the Appendix. As with previous versions, TEM 4.3 is calibrated to each ecosystem using carbon and nitrogen pools obtained from the literature and previous studies (Raich *et al.*, 1991; McGuire *et al.*, 1992).

2.2 Dataset Development

Climatological data sets used by TEM in this study include the cloudiness, historical air temperature and historical precipitation data sets used by McGuire *et al.* (2001). The model also uses spatially-explicit data sets of soil texture, elevation, and potential vegetation (McGuire *et al.*, 2001), which is used to represent original natural vegetation. Historical changes in cropland distribution are prescribed using the data set developed for the McGuire *et al.* (2001) study.

To account for the effects of ozone on terrestrial carbon dynamics, we developed a spatially explicit data set of historical changes in the AOT40 index. First, hourly ozone data for the conterminous United States have been obtained from 71 stations of the Environmental Protection Agency's (EPA) Clean Air Status and Trends Network (CASTNET) (**Figure 1**). The CASTNET sites are located in rural regions away from urban emissions and are managed by both EPA and the National Park Service (NPS). The hourly ozone data are averaged for the three-year period of 1998–2000. The AOT40 index is calculated directly from the averaged hourly data for each site on a monthly basis. This index is the sum of the amounts by which ozone mole fractions exceed 40 ppb during daylight hours (07:00–19:00 GMT). The site data for each month is then interpolated to a $0.5^\circ \times 0.5^\circ$ grid using a thin plate spline interpolation (D. Nychka, personal

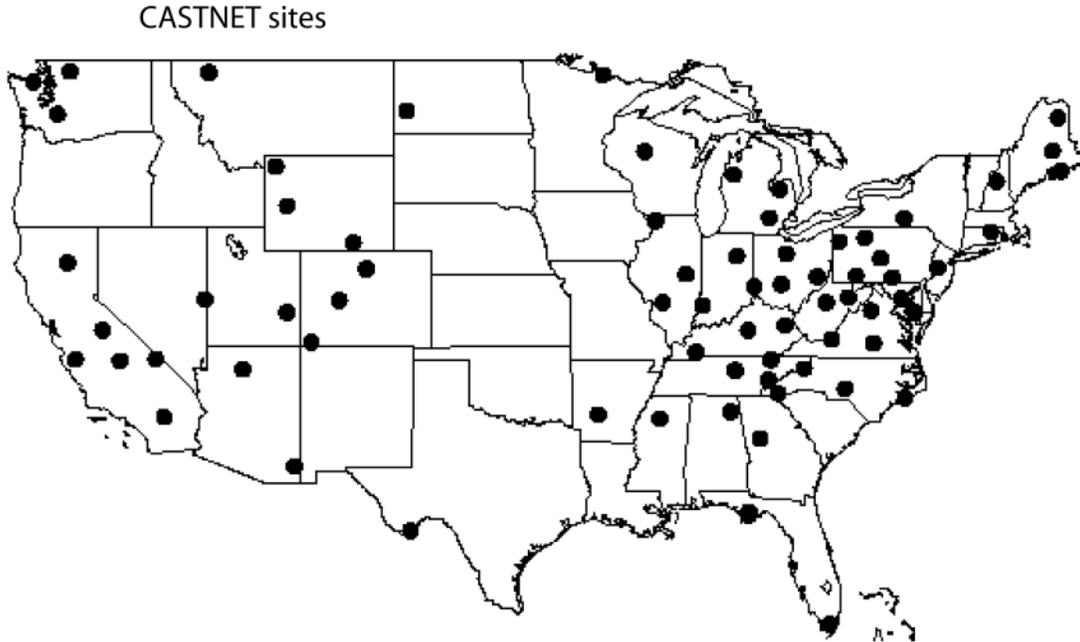


Figure 1. Location of CASTNET sites containing hourly ozone data for the U.S.

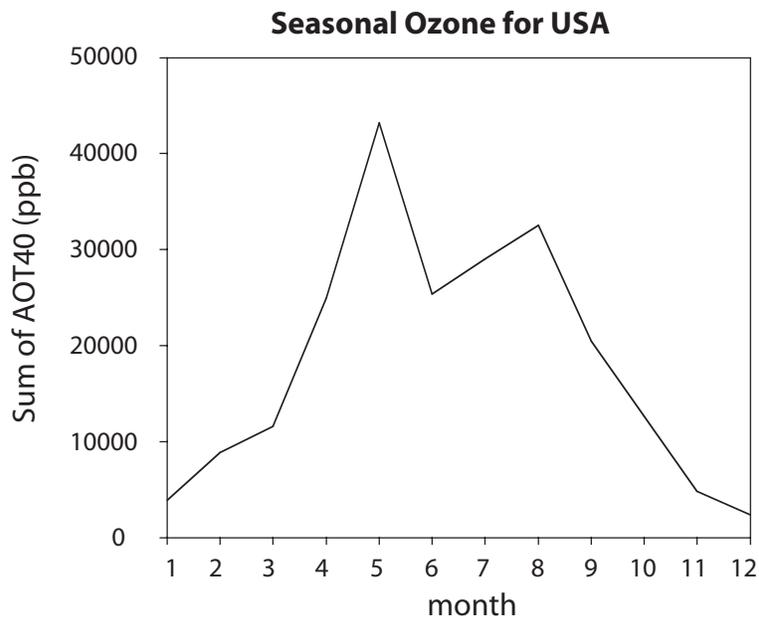


Figure 2. Monthly mean of AOT40 (ppb) calculated from CASTNET data averaged over the U.S. for 1998–2000.

communication). The resulting seasonal AOT40 signal (**Figure 2**) shows that during these three years, ozone levels are highest during May with a secondary peak in August and a minimum during the winter months. The map for May (**Figure 3**) shows highest AOT40 levels spreading eastward from the Los Angeles basin in the Southwest and in the region of the Southern Appalachians in the Southeast. The maximum in the Southwest is in part the result of transport from the Los Angeles urban center and natural VOC emission from chapparal, whereas the

May AOT40 (climatological ozone)

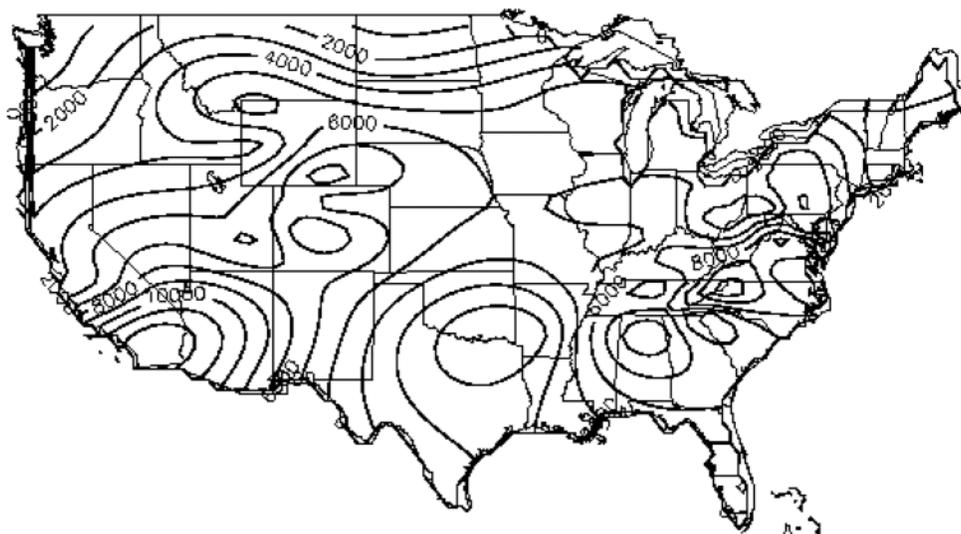


Figure 3. Mean of AOT40 (ppb) calculated from CASTNET data for 1998–2000 during May.

maximum in the Southeast is a factor of both transport from the Midwest and high natural VOC levels from local forests. The minimum in Texas is probably a result of the paucity of data in that region (Figure 1) and the fact that the two nearest sites have low ozone levels.

There are several ways of scaling ozone values to develop a historical ozone database. Since ozone is largely the product of gases produced by fossil fuel emissions, historical CO_2 concentrations may be used as a proxy for fossil fuel emissions, and therefore, ozone levels. This method would result in a 0.3% per year increase since 1950 and a 0.09% per year increase prior to the 1950s. Studies of ozone, however, have shown a much larger increase of 2.4% per year after the 1960s and a 1.6% per year increase earlier (Marenco *et al.*, 1994). A value of 1.1% per year after the 1960s is probably more representative for surface ozone at lower elevations in the mid-latitudes (Bojkov, 1988). To incorporate this information in our simulations, we have chosen to use a proportionate increase based on CO_2 concentrations as follows:

$$O_3(y)n = O_{395} \times (CO_2(y) - A)/(B - A) \quad (8)$$

where $O_3(y)n$ is the new ozone concentration in year y , O_{395} is the climatological ozone concentration used to represent the ozone value for 1995, $CO_2(y)$ is the CO_2 concentration in year y , $A = 286.596$ ppm, the CO_2 concentration in 1860 and $B = 359.62$ ppm, the CO_2 concentration in 1995. The resulting historical O_3 estimates increase by approximately 2.4%/year from the 1860s, though the changes tend to match the shape of the CO_2 curve. As the assumed 2.4%/year rate of ozone accumulation is on the high end of the measured rates, the ozone estimates in this study are conservative (*i.e.* a larger decrease from 1995 means there is less ozone in years prior to 1995 than there would be with a smaller assumed rate).

To develop a historical ozone data set to 1860, the climatological ozone data set (year 1995) must be scaled by the method described above. However, since AOT40 is a threshold index, it is necessary to scale the hourly ozone data and then calculate the AOT40 index from the newly scaled hourly data. In order to scale the hourly data, we chose to scale the hourly ozone values

from the sites with the maximum AOT40 value for each month, and then recalculate the AOT40 values based on the scaled hourly values to create representative historical AOT40 curves for each month. The AOT40 values at each grid point from the 1995 dataset are then scaled for each month based on these representative AOT40 curves. The result is that during the winter and early spring, AOT40 does not get greater than zero until the 1970s, whereas during the summer and autumn, it occurs in the 1950s. Prior to 1950, therefore, there is no ozone effect on vegetation.

2.3 Experimental Design

To examine the relative effect of ozone on net primary production and carbon sequestration by terrestrial ecosystems in comparison to other environmental factors, we have devised six model simulations. The first simulation examines the effect of CO₂ fertilization using historical atmospheric CO₂ concentrations (Keeling *et al.*, 1995; Etheridge *et al.*, 1996, updated) (denoted CARBON). We then examine the influence of CO₂ fertilization and climate variability (Jones, 1994; Hulme, 1995, updated) on terrestrial carbon dynamics in the second simulation (denoted CLIMATE). In the next two simulations, we examine the influence of CO₂ fertilization, climate variability, and land-use change (until 1993, then constant at 1993 values) with and without optimal irrigation (I) and fertilization (F) on crop productivity, (denoted LAND, LANDIF). The final simulations include the influence of CO₂ fertilization, climate variability, land-use change with and without irrigation and fertilization, and ozone (denoted OZONE, OZONEIF) (**Table 1**). There is also a reference experiment containing the pre-industrial value of CO₂ for each year, climatological temperatures and precipitation, and natural vegetation (denoted REF).

In this experimental scheme, the ozone effects are determined with and without agricultural management. Although optimal irrigation and fertilization may be the best assumption for the present, that is not necessarily true historically, so these two scenarios can be considered two end member cases. As ozone will not affect terrestrial carbon dynamics until the 1950s, we focus our analysis on the time period 1950 to 1995. The experiments without ozone are done to determine how the effects of CO₂, climate, and land-use change compare to the ozone effect.

For each simulation, carbon and nitrogen dynamics of terrestrial ecosystems are initialized to equilibrium conditions assuming the land is covered with the original natural vegetation. The model is then run in transient mode for 120 years using the historical climate data during the initial 40 years. If a grid cell was cultivated in 1860, the grid cell is converted during the first year of this spinup period, and terrestrial carbon and nitrogen dynamics are allowed to come back into a dynamic equilibrium state before starting our historical analysis from 1860 to 1995.

Table 1. Experimental setup, showing application of CO₂, climate (temperature and precipitation), land-use (agriculture), IF (irrigation and fertilization), and O₃.

	CO ₂	climate	land-use	IF	O ₃
CARBON	historical	constant	constant	no	0
CLIMATE	historical	historical	constant	no	0
LAND	historical	historical	historical	no	0
LANDIF	historical	historical	historical	yes	0
OZONE	historical	historical	historical	no	historical
OZONEIF	historical	historical	historical	yes	historical

2.4 Uncertainty Analysis

We have conducted an uncertainty analysis to ascertain the error in NPP and NCE due to the empirically-derived ozone response coefficient (a) in Equation 2. The variable rO_3 determines the ozone effect in TEM4.3, and the magnitude of this effect depends upon a . There is also uncertainty in $AOT40$, but the idea behind this analysis is to calculate the uncertainty for the given set of ozone data. We have used the means and standard deviations of a for hardwoods, conifers, and crops (see Section 2.1) to develop three Gaussian distributions, which are the probability distribution functions (PDFs) that describe the uncertainty of each of the coefficients. From these PDFs, we have applied a Latin Hypercube (Morgan and Henrion, 1992) to generate ten random combinations from ten equally distributed probability bins to develop a random Monte Carlo scheme (Clark, 1961). These ten combinations then constituted ten individual simulations that were used as the basis for uncertainty statistics. A second set of ten samples was also run to ensure consistency of the first set. This analysis was performed on the ozone experiment using optimal agricultural management (OZONEIF).

3. RESULTS

3.1 Ozone Effects on Net Primary Production

Ozone effects on NPP in the conterminous United States result in a 3.0% decrease in annual NPP (without agricultural management) to a 5.0% decrease (with agricultural management) (**Table 2**). Although the absolute NPP values are higher with agricultural management both with and without ozone, the percentage decrease is larger in the case with agricultural management. The seasonal decrease (**Figure 4a,b**) is largest during the summer months, with the largest monthly decrease of 5.2 to 7.9% in August (**Table 2**). During the winter months, when productivity and ozone levels are low in many parts of the U.S., there is very little ozone effect on NPP (**Figure 4a,b**).

These simulations show that agricultural management increases the magnitude of the ozone effect. With optimal irrigation and fertilization, crop plants do not experience the water and nitrogen limitations imposed on natural vegetation during the summer and are therefore

Table 2. Comparison of mean annual net primary productivity (NPP) and mean monthly NPP during August for the period 1989 to 1993 among different scenarios.

Scenario	Annual NPP (Tg C yr ⁻¹)	August NPP (Tg C mo ⁻¹)
CO₂		
without ozone (CARBON)	3517	469
CO₂ + climate		
without ozone (CLIMATE)	3462	443
CO₂ + climate + land-use		
with ozone (OZONE)	2451	311
without ozone (LAND)	2526	328
CO₂ + climate + land-use + IF		
with ozone (OZONEIF)	3811	604
without ozone (LANDIF)	4012	656
Reference (no changes)		
without ozone (REF)	3315	422

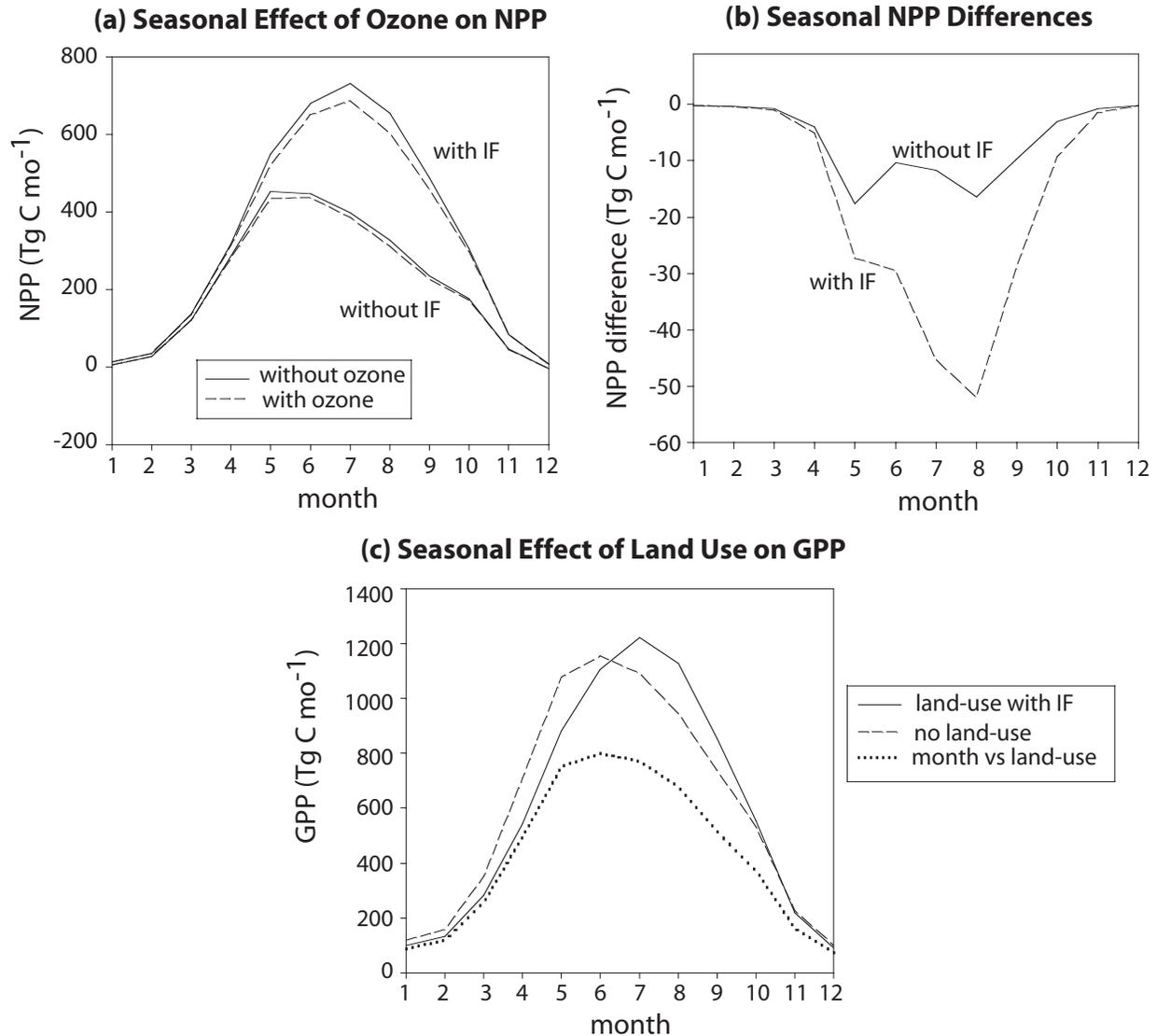


Figure 4. (a) Mean monthly NPP from 1989–1993 over the U.S. for CO₂+climate+land-use with irrigation and fertilization with ozone (OZONEIF) (dashed, complete), and without ozone (LANDIF) (solid, complete), CO₂+climate+land-use with ozone (OZONE) (dashed, no IF), and without ozone (LAND) (solid, no IF) in Tg C mo⁻¹, showing the decrease of NPP due to ozone exposure. (b) NPP differences in Tg C mo⁻¹ between the experiments with and without ozone in panel (a). (c) Mean monthly GPP from 1989–1993 over the U.S. for CO₂+climate+land-use with irrigation and fertilization (LANDIF) (solid), CO₂+climate+land-use (LAND) (dotted), and CO₂+climate (CLIMATE) (dashed) in Tg C mo⁻¹, showing the shift in peak photosynthesis due to irrigation and fertilization.

responsible for a large proportion of the carbon uptake (*i.e.* GPP) during this time. Since the reduction in NPP is primarily the result of the imposed linear reduction on GPP (Equations 1–5), when irrigation and fertilization are applied, the larger GPP contributes to the larger ozone effect (Figure 4c). Agricultural management also shifts the largest response from late spring to mid summer (Figure 4a,b). While ozone levels are largest during May with a secondary peak in August (Figure 2), the GPP reaches its peak in July with irrigation and fertilization and during June without irrigation and fertilization (Figure 4c). Therefore, with irrigation and fertilization,

the relatively high ozone during August combines with the relatively high GPP during August to produce the maximum reduction during that month. Without irrigation and fertilization, the highest ozone levels during May combine with the relatively high GPP during May to produce the maximum reduction during that month (Figure 4a,b).

With irrigation and fertilization, the NPP in large portions of the Midwest and Great Plains appears to be the most affected by ozone with reductions between 5 to 10% (Figure 5a). This pattern represents a combination of regions with high ozone exposure (*i.e.* large AOT40), high productivity (*i.e.* large GPP), and a large proportion of the area in cropland or abandoned cropland, which occur primarily in the eastern two thirds of the U.S. Without irrigation and fertilization, the pattern changes where NPP in the Midwest and Great Plains are not as influenced by ozone as in the optimal agricultural management case (Figure 5b). The regional and seasonal pattern of NPP reduction (Figure 6a,b) shows significant percentage decreases in NPP over most regions of the country, with the largest decreases during mid-summer. When irrigation and fertilization are not used, there are smaller decreases in the mid-summer in some of the regions, because NPP is limited by other environmental factors such as water or nitrogen availability. The large percentage changes in the West (especially with irrigation and fertilization) are insignificant because the absolute differences are so small due to low productivity in these areas.

3.2 Ozone Effects on Carbon Sequestration

From 1950 to 1995, ozone exposure decreased carbon sequestration by 1572 Tg C (34.2 Tg C yr⁻¹) over the U.S. with agricultural management. Because of the reduced productivity without agricultural management, the decrease in carbon sequestration, represented by NCE, is only 694 Tg C (15.1 Tg C yr⁻¹) (Table 3) over the same time period for the U.S. This reduction is due primarily to a reduction in vegetation carbon. The increase in soil carbon is the result of reduced nitrogen uptake (see Section 4). At the grid-cell scale, significant reductions in carbon sequestration (10 to 25 g C m⁻² yr⁻¹) (Figure 7a,b) occur throughout most of the region where NPP has also been reduced.

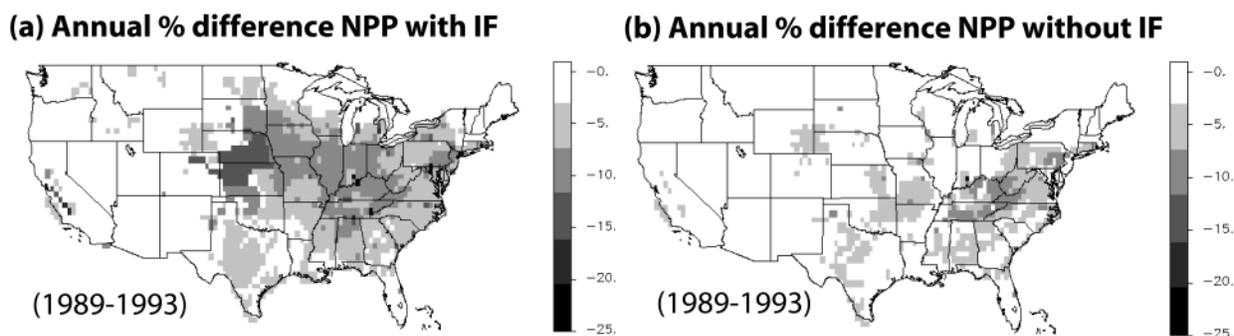


Figure 5. (a) Map of mean annual NPP percent difference between CO₂+climate+land-use with irrigation and fertilization with ozone (OZONEIF) and without ozone (LANDIF) for the years 1989–1993. Largest decrease is –23.82% (corresponding to 224.7 Tg C yr⁻¹) and largest increase is 0.81%, which occurs for only 15 grids. (b) Map of mean annual NPP percent difference between CO₂+climate+land-use with ozone (OZONE) and without ozone (LAND) for the years 1989–1993. Most significant decreases in NPP occur in the eastern half of the U.S., where productivity is the highest.

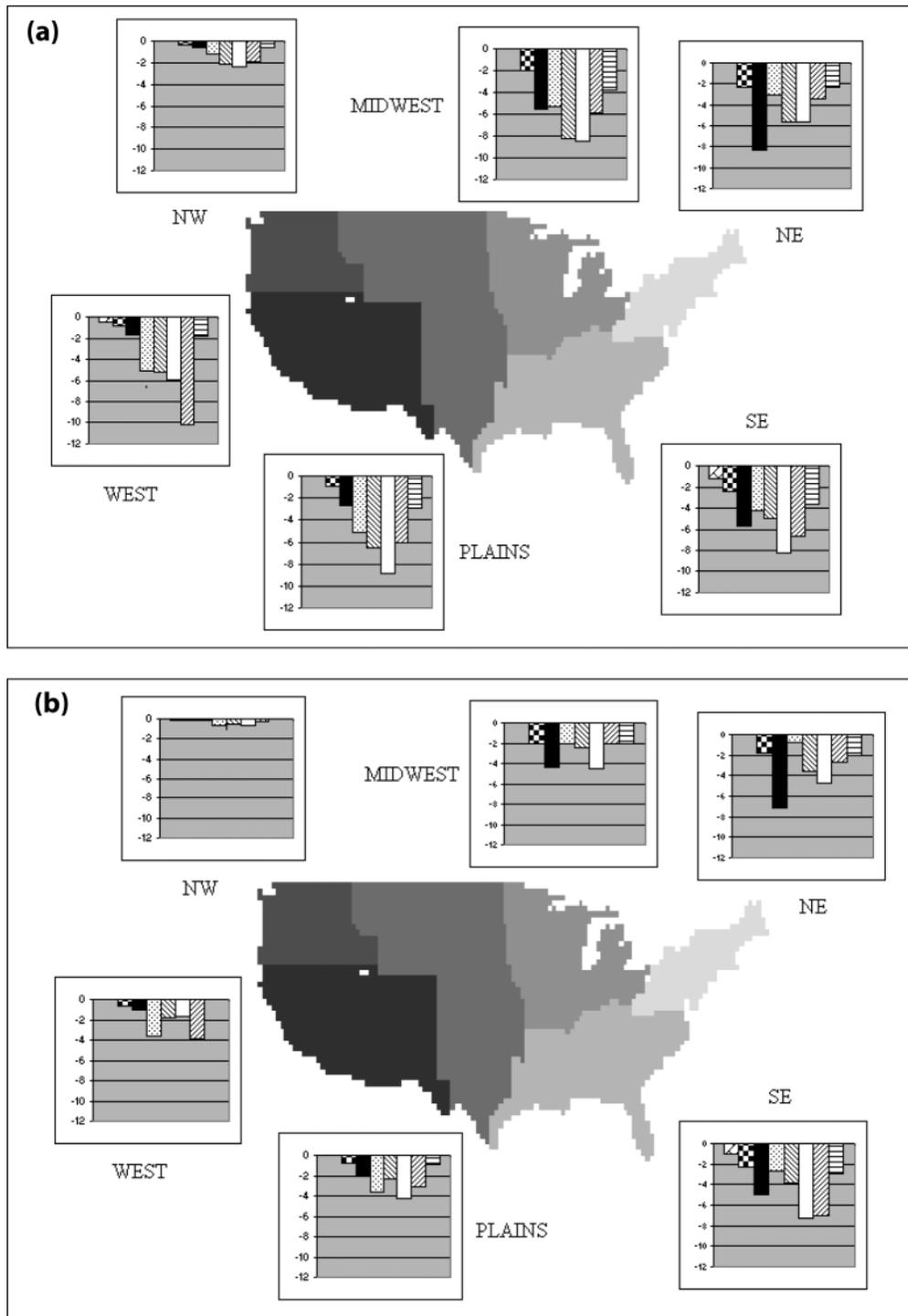


Figure 6. (a) Regional and seasonal decreases in percent NPP between CO_2 +climate+land-use with irrigation and fertilization with ozone (OZONEIF) and without ozone (LANDIF) for 1989–1993. Largest decreases occur during mid-summer and are in the range of 5 to 10%. **(b)** Regional and seasonal decreases in percent NPP between CO_2 +climate+land-use with ozone (OZONE) and without ozone (LAND) for 1989–1993. Largest decreases are in the range of 4 to 8%. March = diagonal brick, April = checkerboard, May = solid black, June = dots, July = back diagonals, August = white, September = forward diagonals, October = horizontal lines.

Table 3. Partitioning of cumulative changes in carbon storage between 1950 and 1995 among effects attributable to CO₂ fertilization, climate variability, cropland establishment and abandonment, agricultural management, and ozone exposure (units = Tg C).

Effect	Vegetation Carbon	Soil Organic Carbon	Products	Total Carbon Storage
CO ₂	1604	1048	0	2652
climate	1262	-458	0	804
land-use change	40	-1259	-455	-1674
ozone	-724	34.8	-4.8	-694
total (no IF)	2182	-642	-452	1088
Irrigation, Fertilizer	1602	1721	57	3380
total with IF	3784	1079	-395	4468

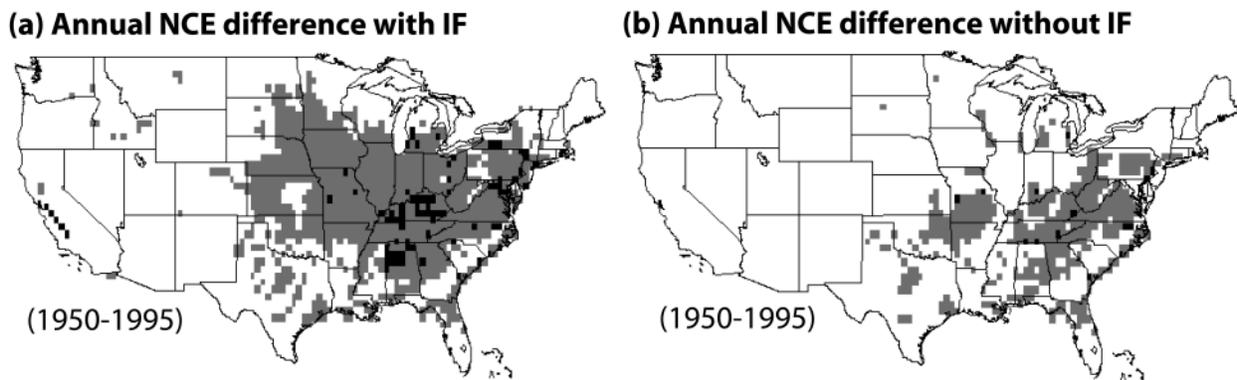


Figure 7. (a) Map of annual NCE difference between CO₂+climate+land-use with irrigation and fertilization with ozone (OZONEIF) and without ozone (LANDIF) for 1950–1995 in g C m⁻² yr⁻¹. The largest decrease is -72 g C m⁻², and there are a few grids (12) with an increase in NCE no larger than 0.4 g C m⁻². (b) Map of annual NCE difference between CO₂+climate+land-use with ozone (OZONE) and without ozone (LAND) for 1950–1995 in g C m⁻² yr⁻¹. White are values greater than -5 g C m⁻² yr⁻¹, gray are values between -5 and -20 g C m⁻² yr⁻¹, and black are values less than -20 g C m⁻² yr⁻¹. The largest total C sequestration during this time period is decreased significantly in the eastern U.S. as a result of ozone exposure.

3.3 Relative Importance of Ozone Effects on NPP and Carbon Sequestration

A comparison of the annual NPP for the different simulations shows that the ozone reduction in NPP (-3.0% from 1989–1993) compensates the effects of CO₂ fertilization on NPP (+6.1%, CARBON-REF) (Figure 8a). The reduction is also significantly larger when irrigation and fertilization are applied (-5.0%). The climate effect on NPP is dominated by year-to-year variability. This variability also influences the effects of land-use change and agricultural management. The magnitude of the ozone effect (-3.0 to -5.0%) is greater than the influence of climate variability (-1.6%, CLIMATE-CARBON), but less than the influence of agricultural management (+58.8%, OZONEIF-LAND) and land-use change (-27.0%, LAND-CLIMATE) (Table 2, Figure 8a).

Likewise, over the period 1950–1995, carbon sequestration has increased as a result of irrigation and nitrogen fertilization, climate, and CO₂ fertilization, but decreased as a result of land-use change and ozone exposure (Table 3). However, the relative importance of these factors are changing over this period (Figure 8b). The effect of the interaction between agricultural

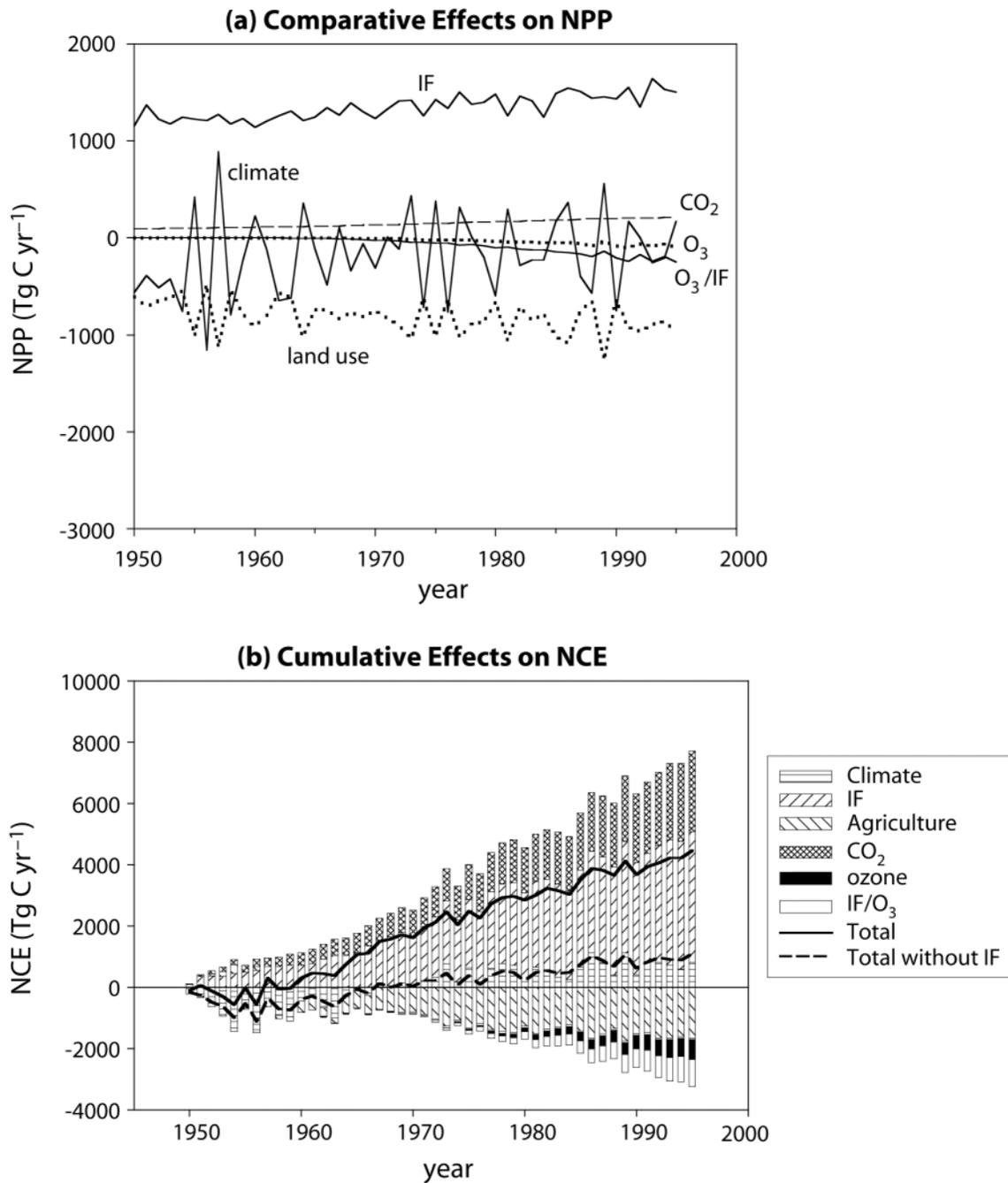


Figure 8. Transient NPP and NCE responses from 1950–1995, showing how ozone effect compares to other disturbances. **(a)** Effect of CO₂ fertilization (CARBON-REF), climate variability (CLIMATE-CARBON), land-use (LAND-CLIMATE), agricultural management (LANDIF-LAND), and ozone (OZONEIF-LANDIF) on NPP. **(b)** Cumulative carbon sequestration from each of the factors in (a). All units in (Tg C yr^{-1}) .

management and ozone has grown over this period such that by 1995 the interaction is larger than the ozone effect itself without irrigation and fertilization. In general, the reduction of NPP and NCE by ozone is larger when the vegetation is most productive, as occurs when croplands are irrigated and fertilized. Both the ozone effect (with or without the added effect from

agricultural management) and the CO₂ effect are increasing with time, though in opposite directions. As long as ozone levels continue to rise, the reduction in carbon sequestration caused by ozone will continue to counterbalance the future benefits of CO₂ fertilization.

3.4 Uncertainty Analysis

We ran two sets of 10 random Monte Carlo simulations based on the Latin Hypercube. From the first set of 10 random Monte Carlo simulations, we estimate NPP of the conterminous United States to be $3811 \pm 16.8 \text{ Tg C yr}^{-1}$ from 1989–1993 and NCE to be $97.1 \pm 3.1 \text{ Tg C yr}^{-1}$ from 1950–1995 when optimal agricultural management is applied. Therefore ozone causes NPP to decrease by $5\% \pm 0.42\%$ and carbon sequestration to decrease by $34.2 \text{ Tg C yr}^{-1} \pm 3.1 \text{ Tg C yr}^{-1}$. Because the mean NPP and NCE values are less when agricultural management is not used, we can expect even smaller errors in that case. The second random set of ten yields slightly lower errors (NPP uncertainty of $14.7 \text{ Tg C yr}^{-1}$ and NCE uncertainty of 2.7 Tg C yr^{-1}), yet are still consistent with the first set. These uncertainties associated with the ozone coefficient are clearly much less than the uncertainties due to agricultural management.

4. DISCUSSION

These results expand upon the site-specific modeling of Ollinger *et al.* (1997, 2002) to provide estimates of the effects of ozone on net primary production and carbon sequestration at the continental scale. The magnitude and even timing of the ozone reduction of NPP and NCE are highly dependent upon whether or not irrigation and fertilization are applied to croplands. The ozone effect compensates for the effects of increased CO₂ fertilization and, similar to the CO₂ effect, is increasing with time. Below, we examine how our simulated ozone effects for different vegetation types compare to observational estimates. We then compare the results of this study to those of Ollinger *et al.* (1997, 2002) and other modeling studies and provide further insights into important mechanisms affecting carbon sequestration in the conterminous United States. Finally, we suggest what kinds of measurements are needed in the future to effectively evaluate the effects of ozone on vegetation using biogeochemical models.

4.1 Comparison of Simulated Ozone Effects with Observational Studies

Overall, the values from our modeling study are in the same range as the experimental values (**Figure 9**; Pye, 1988; Heck *et al.*, 1984b). Deciduous trees are more sensitive to ozone than coniferous in both simulations (growing season) and experiments, though TEM 4.3 shows a larger range of values for deciduous trees than the experimental results. Median crop yield is also more sensitive to ozone in our simulations than deciduous trees, but is less sensitive in the observations. The higher sensitivity of crop yield is entirely consistent with the Reich (1987) model that serves as the basis for TEM 4.3. For trees, the TEM 4.3 results contain a small number of grid cells with increases in biomass, which skews the maximum end of the range from the experimental values, though as evident in the median, most grid cells experience a decrease in biomass as a result of ozone exposure.

Perhaps the largest source of uncertainty in this comparison is due to the differences between controlled experiments and model output. The observational data are mostly the result of

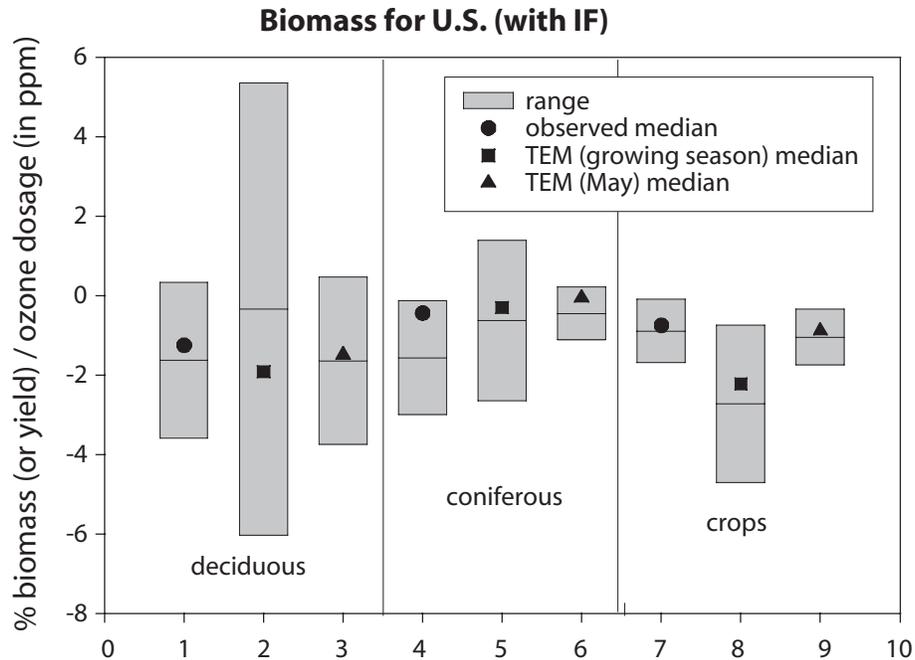


Figure 9. Ratio of percent change in biomass for trees or yield for crops to the increase in ozone dosage in ppm. Observational data for trees are from Pye (1988) and include only the statistically significant data. Observational data for crops are from Heck *et al.* (1984b); 7 hour/day mean ozone concentrations are multiplied by the number of hours over the season to derive dosages. The TEM 4.3 results are based on NPP as a measure for biomass of trees and C flux coming into agricultural products as a measure for crop yield.

seedlings grown under controlled, experimental conditions, rather than mature trees in a natural setting. Therefore, a comparison of model data to the observational data can be done using any month during the growing season for the model data, all of which yield different values (the mean from May–September was used here). For example, if we use May values from TEM 4.3 as representative of the start of the growing season (Figure 9), the deciduous and crop values are improved, but the coniferous values are too low.

There are other sources of uncertainty in the comparison as well. The TEM results contain values from all grid cells within the range of a vegetation type, whereas the observed range is based on a very limited number of site-specific data. The ozone index is also a source of error, since TEM correlations are based upon the AOT40 index, while the Pye (1988) data are based on actual dosages and the Heck *et al.* (1984b) data are based upon mean concentrations. Also, there is considerable uncertainty in the historical AOT40 estimates developed for this modeling study. As discussed in the methods, this error is probably on the conservative side, which would increase the model sensitivity to ozone.

4.2 Comparison to Estimates of Ozone Damage from Other Modeling Studies

The only other regional model simulation of the effects of ozone on vegetation is the PnET model used by Ollinger *et al.* (1997, 2002). They ran the model for 64 specific sites in the northeastern U.S. In the original version Ollinger *et al.* (1997), only the effects of climate and ozone were considered for the period 1987–1992. They found an annual NPP reduction of

3–16%, with a mean reduction of 11%. For the Northeast region, we found a reduction of 4.1% in annual NPP for the same time period, which is on the lower end of their range.

In their more recent study, Ollinger *et al.* (2002) incorporated the effects of N deposition and land-use history (both agriculture and timber harvest) into the PnET model for the same sites in the northeast U.S. TEM 4.3, while including croplands and abandonment, does not include timber harvest or N deposition. They found that including ozone offset some of the increase in NPP (from 17.4% to 12.0%) and NCE (12% lower) caused by CO₂ fertilization over the period 1860–1995 for the northeast region. Our simulations with all disturbances included (LANDIF) show a 16% increase in NPP without ozone and a 10.1% increase with ozone over this same period. NCE for the same period and region is 9.2% lower with ozone. Both of these results are comparable to the Ollinger *et al.* (2002) values. Ollinger *et al.* (2002) also found that for carbon sequestration, the effects of N deposition offset the effects of ozone exposure, and that for net primary production, the combined enhancement by CO₂ and N deposition were equally offset by the combined negative effects of ozone exposure and land-use disturbance.

Our study, however, has extended the analysis of ozone effects from the northeast U.S. to the entire conterminous U.S. Over the entire U.S. from 1860–1995 (with agricultural management), NPP increases 31% without ozone and only 24% with ozone, which is about twice the percentage increase over the northeast region alone. Although carbon sequestration has occurred over the period 1860–1995 in the northeast with or without ozone, carbon has generally been lost from terrestrial ecosystems over the conterminous U.S. during this same period because of conversion of natural vegetation to agricultural land. Ozone enhanced these losses during this same period by 49.5%. Because of cropland abandonment in the early 1800s, carbon has accumulated in the forests of the northeastern U.S. over the period 1860–1995. However, in more recent times (1950 to 1995), carbon has also been sequestered in the conterminous U.S., though less sequestration has occurred with exposure to ozone (by 26%). During the latter part of the century, cropland abandonment and CO₂ fertilization are contributing to carbon sequestration across the United States. Therefore, even the net exchange of carbon between terrestrial ecosystems and the atmosphere is highly dependent upon the particular time period and region because of the heterogeneous nature of land-use change and temporal nature of CO₂ fertilization.

4.3 Relative Role of Ozone on Carbon Sequestration in the Conterminous United States

Our estimates of carbon sequestration in the conterminous United States during the 1980s (24.1 Tg C yr⁻¹ without agricultural management to 68.4 Tg C yr⁻¹ with agricultural management) are an order of magnitude smaller than the 300 to 580 Tg C yr⁻¹ estimated by Pacala *et al.* (2001) for the same time period using a suite of inverse models. However, the inverse modeling studies inherently include the effects of processes not included in this study, such as cropland soils, wood products, and sediments, and our results are on the same order as some of these individual terms that are part of the total (Pacala *et al.*, 2001). Their results are also larger than estimates from previous studies because they include processes not included in other studies, such as accumulation of carbon in sediments of reservoirs or rivers. The Vegetation Ecosystem Modeling and Analysis Project (VEMAP) process-based modeling estimate for the U.S. carbon sequestration is 80 Tg C yr⁻¹ for 1980–1993 (Schimel *et al.*, 2000) but includes only the effects of CO₂ and climate on terrestrial carbon dynamics.

4.4 Partitioning of Carbon Sequestration between Vegetation and Soils

Agricultural management also has an important effect on the carbon partitioning between vegetation and soils. Carbon accumulation in vegetation occurs as a result of CO₂ fertilization, climate variability, cropland abandonment, and agricultural management, but decreases with ozone exposure (Table 3). Vegetation carbon in TEM 4.3 increases so much more with agricultural management than without it because the assumption of optimal irrigation and fertilization since 1860 has resulted in an accumulation of soil organic nitrogen in croplands that then decompose to enhance nitrogen availability for plant growth of the natural vegetation when croplands are abandoned. Land-use change itself involves harvesting of crops to remove litterfall from the system, and vegetation productivity is not compensated by the irrigation and fertilization.

Carbon accumulation in soils occurs as a result of CO₂ fertilization, agricultural management, and ozone exposure, while reductions occur as a result of climate variability and land-use change (Table 3). To understand why ozone exposure slightly increases carbon in soils, we ran some new simulations with TEM 4.3. These new sensitivity experiments were also developed to examine the role of the indirect ozone effects of reduced stomatal conductance, including reduced CO₂ and N uptake (which increase the ozone effect) and reduced O₃ uptake (which decreases the ozone effect). In particular, individual simulations were performed without the indirect effects of ozone on nitrogen and carbon uptake and the lagged effect on ozone uptake.

The results confirm that the primary effect of ozone on primary production in TEM 4.3 is still the direct reduction on GPP, while the other indirect and lagged effects slightly perturb this overall reduction. One consequence of the reduced N uptake in TEM 4.3 is to increase C/N of plant tissues and resulting detritus, which reduces R_H (*i.e.* less decomposition) and therefore increases carbon accumulated in soils, if nitrogen fertilization is not applied. Although there is some evidence of increased C/N with ozone exposure (Lindroth *et al.*, 2001), more observational studies are needed to further explore the effects of ozone on N uptake and C/N.

4.5 Future Requirements

This study has clearly identified several observational requirements for the future. The network of ozone monitoring stations in the U.S., even when accounting for stations other than CASTNET, is still underrepresented in the Great Plains. In order to compare models to observations, the experimental data should contain hourly indices such as AOT40 rather than simple concentration or dosage information. The most useful results are those that report some measure of biomass, rather than tree size, so it would be useful for authors to include allometric equations that can be used to compute biomass. Ultimately more open-top chamber (OTC) or even ambient air experiments on mature forests are required, rather than controlled-chamber experiments with seedlings. Experimental results should also include error estimates (for *e.g.*, pertaining to ozone dose response curves) to enable easier error analysis in future model simulations. This study also points to the need for a georeferenced time series of irrigation and fertilization in croplands throughout the U.S., since the ozone effect is so highly dependent upon agricultural management.

5. CONCLUSIONS

This research has explored the effects of tropospheric ozone on NPP and NCE over the U.S. during the latter half of the 20th century. Tropospheric ozone results in a 3 to 5% reduction in annual NPP over the U.S. during the late 1980s to early 1990s. With agricultural management, this reduction is largest during August, when the combination of ozone levels and GPP is high. Without agricultural management, the largest NPP reduction occurs during May, which is the month of peak ozone concentrations. The reduction in NPP is largest in the Southeast, Midwest, and Great Plains, corresponding to regions with both moderate to high ozone levels and the largest productivity.

Carbon sequestration in the conterminous United States during the 1980s has been reduced by 24.1 to 68.4 Tg C yr⁻¹ as a result of ozone exposure, which is 5 to 23% of the total modeled range for this period. The largest reductions in carbon sequestration coincide with regions of decreased NPP, with decreases in the range of 10 to 25 g C m⁻² yr⁻¹ common in some areas. The decrease in NCE is primarily due to the reduced carbon accumulation in vegetation.

The effects of ozone on net primary production and carbon sequestration within the conterminous U.S. are similar in magnitude to those of CO₂ fertilization and climate variability, though less than the effects of land-use change and agricultural management. Clearly these effects should be considered in future estimates of greening due to CO₂ fertilization and carbon sequestration, especially in ozone-rich regions such as Europe and China. The developing world, in particular, will have to consider the effects of ozone on carbon sequestration to accurately estimate their obligations under international agreements.

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APPENDIX

Improvements in the Simulation of Agricultural Carbon and Nitrogen Dynamics by the Terrestrial Ecosystem Model

In version 4.2 of the Terrestrial Ecosystem Model (TEM), initial attempts have been made to incorporate the effects of human activities, particularly row crop agriculture, on terrestrial carbon and nitrogen dynamics (McGuire *et al.*, 2001). These effects include: 1) the loss of carbon and nitrogen from ecosystems associated with conversion of forests to agricultural fields; 2) the changes in carbon and nitrogen stocks and fluxes associated with agricultural practices; 3) the loss of carbon as a result of the decomposition of agricultural products or wood products that were obtained during conversion; and 4) the sequestration of carbon associated with regrowth of natural vegetation when agricultural fields were abandoned. To simulate the changes in carbon stocks and fluxes associated with land-use change, we have used an approach similar to that described in the Terrestrial Carbon Model (Houghton *et al.*, 1983; Melillo *et al.*, 1988) except that initial biomass levels and the recovery of the biomass of natural vegetation after agricultural abandonment varied on a $0.5^\circ \times 0.5^\circ$ grid cell basis in response to spatial and temporal variations in environmental conditions. To simulate carbon dynamics in agricultural ecosystems, we have used the relative agricultural productivity (RAP) approach of Esser (1995) where simulated agricultural productivity was a multiplier of the original natural vegetation. The RAP multiplier varies spatially and attempted to incorporate the effects of agricultural practices and their variation across the surface of the earth. Thus, the RAP multiplier can be greater than 1.0 in areas where agricultural fields were irrigated and fertilized, but will be a fraction of the natural productivity in areas with less intense management. While the RAP approach has been useful in examining the relative effects of human activities on historical changes in terrestrial carbon dynamics, the approach is limited in examining potential future changes, especially if changes in albedo and greenhouse gases associated with land-use change had an influence on future climate.

To improve our ability to assess the effects of agricultural activities on future terrestrial carbon dynamics, we have replaced the RAP approach with a more process-based approach. First, we use the extant grassland parameterizations of TEM 4.2 to simulate vegetation dynamics (*e.g.*, gross primary production, respiration, nitrogen uptake, litterfall) of crop plants. As in TEM 4.2, soil organic matter dynamics in crop fields are parameterized based on the type of the original natural vegetation. Unlike TEM 4.2, we use growing-degree days above 5°C (GDD) to determine when crops are planted (GDD = 300) and harvested (GDD = 2000). The GDD approach allows us to simulate variations in the timing of planting and harvest of crops across a region. In addition, the simulation of multiple crops within a year is possible by resetting GDD to zero whenever a crop is harvested in areas with favorable climatic conditions. Similar to TEM 4.2, we assume that 40 percent of the vegetation biomass is removed from the fields during harvest and the remaining biomass enter the soil organic matter pools.

While our process-based approach allows us to consider the effects of changing atmospheric CO_2 concentrations and climatic conditions on crop metabolism and agricultural productivity, the evaluation of the effects of management (*e.g.*, irrigation, application of fertilizers and pesticides)

on agricultural productivity still requires the development of additional time-varying spatially explicit data sets that describe these activities. However, if we assume that the purpose of irrigation and fertilization is to alleviate water and nitrogen limitations of crop plants, respectively, we can estimate the optimum effects of various management strategies if we run TEM for croplands without water and/or nitrogen limitations. To maintain mass balance, we calculate how much water and nitrogen are required to alleviate these limitations and then add these amounts to the crop ecosystem as irrigation and fertilizer, respectively.

To determine the amount of irrigation required, we determine both potential evapotranspiration (PET) and estimated evapotranspiration (EET) for a grid cell as described in Pan *et al.* (1996) and examine the relationship between these two variables. If EET is less than PET, then water availability is limiting crop production. To overcome this limitation, we subtract EET from PET and add this amount as irrigation to supplement precipitation.

To determine the amount of nitrogen fertilizer required, we determine nitrogen uptake by crops as described by McGuire *et al.* (1992) for both of the situations where nitrogen availability is limiting productivity (NUPTAKE) and where nitrogen availability is not limiting productivity (NUPTAKE_p) during a particular month. If NUPTAKE is less than NUPTAKE_p, we then subtract NUPTAKE from NUPTAKE_p and add this amount to the ecosystem as N fertilizer.

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