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Impacts of climatic and atmospheric changes on carbon dynamics in the Great Smoky Mountains National Park

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Model simulations suggest that rising atmospheric CO₂ compensates for the adverse effects of ozone stress on ecosystem carbon dynamics in Great Smoky Mountain National Park.

Abstract

We used the Dynamic Land Ecosystem Model (DLEM) to estimate carbon (C) storage and to analyze the impacts of environmental changes on C dynamics from 1971 to 2001 in Great Smoky Mountain National Park (GRSM). Our simulation results indicate that forests in GRSM have a C density as high as 15.9 kg m⁻², about twice the regional average. Total carbon storage in GRSM in 2001 was 62.2 Tg (T = 10^{12}), 54% of which was in vegetation, the rest in the soil detritus pool. Higher precipitation and lower temperatures in the higher elevation forests result in larger total C pool sizes than in forests at lower elevations. During the study period, the CO₂ fertilization effect dominated ozone and climatic stresses (temperature and precipitation), and the combination of these multiple factors resulted in net accumulation of 0.9 Tg C in this ecosystem.

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1. Introduction

Forests have been major carbon (C) sinks in the United States (US) during the 20th century (Turner et al., 1995). The balance of this C sink can be affected by global climatic and atmospheric changes, and global forest NPP has increased in the last 20 years due to changes in these factors (Boisvenue and Running, 2006). Many natural forests in the US are in Class I Wilderness areas. These areas are generally located in more remote regions and are protected by Federal regulations (Department of the Interior (DOI), 1982), and include 16 national parks and other protected, "near-natural" environments. These forests can store large amounts of C, and play an

important role in the regional and global C balance. Global change effects that are primarily transmitted via the atmosphere are likely to be detectable in these protected mountainous-forested ecosystems, especially at high altitudes where the ecosystems are generally considered to be sensitive to climate change. These forested ecosystems, therefore, may serve as locations where the environmental impacts of climatic and atmospheric change can be studied directly. Furthermore, meteorological, hydrological, and forest types change strongly over relatively short distances in mountain regions. As a result, the ecosystem C storage and its responses to global change also differ dramatically along the altitudinal gradients. Therefore, the strong altitudinal gradients in mountainous environments provide unique and sometimes the best opportunities to analyze global change processes and their impacts on C dynamics of natural forests (Becker and Bugmann, 2001).

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The most significant atmospheric change during the last two centuries is the rapid rise of atmospheric CO₂ concentration which has been suggested to result in global climate change. Studies showed that the increased atmospheric CO₂ concentration can enhance forest growth and C sequestration capacity (Tian et al., 2000), thus providing a negative feedback at the atmospheric level. The beneficial effect of CO₂ fertilization, however, could be offset by the damaging effects of other air pollutants such as tropospheric ozone (Adams et al., 1986; Chappelka and Samuelson, 1998; Felzer et al., 2004). To understand the effects of global change on C dynamics of forests in national parks, the effects of CO₂ (Ellsworth, 1999; Loya et al., 2003), climate (Tian et al., 1998), ozone (Chappelka et al., 1988; Pye, 1988; Chappelka and Chevone, 1992), and their interactions (Ollinger et al., 1997; Tian et al., 1999, 2000; Boisvenue and Running, 2006) should be investigated. Furthermore, the various responses of different plant functional types to these stressors are also important (Reich, 1987; Chappelka and Samuelson, 1998; Weinstein et al., 2001). The large number of possible combinations and longterm periods over which they operate, however, make it nearly impossible to investigate the effects of multiple stresses on ecosystem C storage through controlled experiments (Ollinger et al., 2002). Integrated process models, which include the physiological responses of ecosystems to atmospheric and climatic changes can be quite useful in such multiple stressor studies (Ollinger et al., 1997, 2002; Martin et al., 2001; Felzer et al., 2004; Hanson et al., 2005; Karnosky et al., 2005).

In this study, we use the Dynamic Land Ecosystem Model (DLEM), an integrated ecosystem process model (Tian et al., 2005) that couples major biogeochemical and hydrological cycles to make daily and spatially-explicit estimates of carbon fluxes and pool sizes in Great Smoky Mountains National Park (GRSM) from 1971 to 2001. DLEM is able to address responses of terrestrial ecosystems to multiple stresses including changes in climate, atmospheric composition (CO₂ and ozone), land use, and natural disturbances. The GRSM represents forested ecosystems typical of the eastern mixed pine hardwood regions in the US (Whittaker, 1966), a region that has long been recognized as being strongly affected by elevated ozone concentrations (Neufeld et al., 1992; Mueller, 1994; Chappelka and Samuelson, 1998; Weinstein et al., 2001). GRSM is located downwind of large urban and industrial areas that generate large amounts of air pollutants or their precursors (Christine et al., 1994). Many field studies have revealed that GRSM forest growth has been inhibited by ozone pollution (Neufeld et al., 1992; Somers et al., 1998). Simulations have been conducted by Weinstein et al. (2001) to investigate the effect of ozone stress on photosynthesis and succession of a forest community in the Twin Creeks area of GRSM. Comprehensive evaluation of the impacts of multiple climate and atmospheric stresses on ecosystem productivity and C storage of the whole GRSM region has not yet been attempted. The purpose of this study was to use a model simulating approach to estimate the changes in GRSM C storage from 1971 to 2001 and to analyze forest responses to climate change, CO₂ fertilization, tropospheric ozone stress, and the interactions of these multiple stresses.

2. Methods

2.1. Study region

Great Smoky Mountains National Park, the largest Class I Wilderness area in the eastern US, was established along the border of western North Carolina and eastern Tennessee in 1934 to protect the 2079 km² continuous eastern mixed pine hardwood forests that consist of approximately 85% deciduous forest, 13% coniferous forest, and <2% in heath bald (MacKenzie, 1993; Figs. 1 and 2). Elevations in GRSM range from approximately 250 m along the outside boundary of the Park up to more than 2000 m in the center of the park (Fig. 1). The broad ranges of elevations in GRSM contribute to a wide variety of climates (Shanks, 1954; Busing et al., 2005). The climate is humid and warm at lower elevations, cool and wet at higher elevations (Thornthwaite, 1948). Annual precipitation at lower elevations is around 1200 mm while can be as high as 2000 mm at higher altitudes, similar to some of the wettest regions in the US (Busing et al., 2005). Overall annual average temperatures range from 10 to 12 °C.

The boreal or alpine coniferous forests [spruce-fir (*Picea abies*)] are located above 1400 m (Figs. 1 and 2). Northern Hardwood Forests dominate middle to upper elevations from 1000 to 1500 m in the park. Oak (*Quercus* spp.) is the major component in this region. Pine (*Pinus* spp.) forests grow within low-elevation regions, especially in the northwestern portion of the Park (Fig. 2).

Ozone exposures in the park are among the highest in the eastern US (Mueller, 1994; US EPA, 2001; DOI, 2002). The mean summer hourly ozone concentration was about 51 ppb (Look Rock ozone monitor site) to 55 ppb (Cove Mountain ozone monitor site) during the 1980s and early 1990s (Mueller, 1994), while damage to vegetation was found to occur at levels as low as 50 ppb. On average, ozone concentrations over the ridgetops of the park can be as high as or higher than in nearby cities, including Knoxville and Atlanta (DOI, 2002). The average ozone concentration measured in the summer of 1989-1991 at the Hendersonville station in metropolitan Nashville, for example, was 6-12 ppb lower than the value measured at Great Smoky Mountain stations (Mueller, 1994). Data from the Clean Air Status and Trends Network (CASTNET) (http://www.epa.gov/castnet/) shows that the SUM06 index [calculated as the sum of hourly O₃ concentrations above 60 ppb summed over 12 h (08:00 to 20:00) during a 3-month period] at the GRSM Look Rock ozone monitoring station in the summer of 2001 was about 27 (ppb-h). This value is higher than the 25 ppb-h that the US Environmental Protection Agency (US EPA) proposed as an alternative secondary standard (http://www.epa.gov/ castnet/). Ozone pollution results in visible injury in GRSM vegetation (Neufeld et al., 1992). In a survey conducted in GRSM, Chappelka et al. (1997) reported 47% of the over 1600 black cherry (Prunus serotina) examined showed visible foliar symptoms of ozone injury.

2.2. The Dynamic Land Ecosystem Model (DLEM)

The DLEM (Tian et al., 2005; Chen et al., 2006) is a process-based model which couples biophysical processes (energy balance), biogeochemical processes [water cycles, carbon cycles, nitrogen cycles, and trace gas (NO_x , CH₄)-related processes], community dynamics (plant distribution and succession), and disturbances (land conversion, agriculture management, forest management, and other disturbances such as fire, pests, etc.) into one integral model system (Fig. 3). DLEM can simulate the complex interactions of multiple stresses such as climate change, elevated CO_2 , tropospheric O_3 , N deposition, human disturbance, and natural disturbances.

In DLEM, the carbon balance of vegetation is determined by photosynthetic rate, autotrophic respiration, litterfall (related to tissue turnover rate and leaf phenology), and plant mortality rate. Plants assimilate carbon by photosynthesis, and then use this carbon to compensate for the loss through maintenance respiration, tissue turnover, and reproduction. The photosynthesis submodel of DLEM estimates net C assimilation rate, leaf daytime maintenance respiration rate, and gross primary productivity (GPP, unit: g C m⁻² day⁻¹). The photosynthetic rate is first calculated at the leaf level. The results are then multiplied by the leaf area index to scale up to the canopy level (Tian et al., 2005). To simulate the detrimental effect of air pollution on

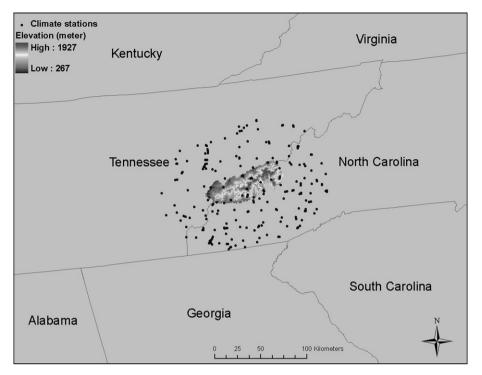


Fig. 1. Location of study region (Welch et al., 2002). Great Smoky Mountains National Park (GRSM) is located along the North Carolina-Tennessee border in the southeastern United States in the southern part of the Appalachian Mountains. Elevation ranges from approximately 250 m along the outside boundary of the Park up to more than 2000 m in the center of the park. Climate records from more than two hundred climate stations (black dots) were used to generate the climate datasets for the simulation.

ecosystem productivity, we developed the ozone submodel based on the work of other researchers (Ollinger et al., 1997; Martin et al., 2001; Felzer et al., 2004), in which we simulate the direct effect of ozone on photosynthesis.

The following equations and parameters are used in the model:

$$A = \min(w_i, w_c, w_e) \tag{1}$$

$$A' = A \times O_{3\text{eff}} \tag{2}$$

$$\mathbf{O}_{3\mathrm{eff}} = F(g_s, \mathbf{O}_3, a) = 1 - a \times g_s \times \mathbf{O}_3 \tag{3}$$

$$g_s = G(A') \tag{4}$$

$$g_c = g_s f(\text{LAI}, T_{\min}, W, \text{CO}_2) \tag{5}$$

where w_j, w_c, w_e are the electron transport (or light)-limited, carboxylationlimited and export-limited rates respectively; *A* is the rate of photosynthesis; g_s is stomatal conductance and g_c is canopy conductance; LAI denotes leaf area index; T_{\min} is the minimum temperature; and *W* is wind speed. O_{3eff} denotes the effects of ozone on photosynthesis; *a* is the ozone plant functional type-specific sensitivity coefficient (deciduous trees and heath bald: 2.6×10^{-6} ; coniferous trees: 0.7×10^{-6} ; Felzer et al., 2004). GPP is used to estimate net primary productivity (NPP) by subtracting the autotrophic respiration (*R*_A):

$$NPP = GPP - R_A \tag{6}$$

DLEM estimates the annual net carbon exchange (NCE) of the terrestrial ecosystem with the atmosphere using the following equation:

$$NCE = NPP - R_{\rm H} - E_{\rm NAD} - E_{\rm AD} - E_{\rm P} \tag{7}$$

where E_{NAD} is the magnitude of the carbon loss from a natural disturbance, E_{AD} is carbon loss during the conversion of natural ecosystems to agriculture, and E_P is the sum of carbon emission from the decomposition of products (Tian et al., 2003). Since GRSM is relatively undisturbed, E_{NAD} , E_P and E_{AD} are equal to 0. Therefore, NCE in GRSM is equal to net ecosystem production (NEP).

2.3. Input data

2.3.1. Base maps

Input base maps include: (1) elevation, slope, and aspect maps which are derived from the 7.5 min USGS National Elevation Dataset (http://edcnts12.cr. usgs.gov/ned/ned.html); (2) soil datasets (pH, bulk density, depth to bedrock, soil texture represented as the percentage content of loam, sand, and silt) derived from the 1 km resolution digital general soil association map (STATSGO map) developed by the United States Department of Agriculture (USDA) Natural Resources Conservation, while the texture information of each map unit was estimated using the USDA soil texture triangle (Miller and White, 1998); and (3) a vegetation map (Fig. 2b) for the late 1980s which was developed by MacKenzie. MacKenzie (1993) developed this 100 m resolution and 14 category vegetation type map of the GRSM based on satellite imageries. We aggregated these vegetation types into the deciduous, pine, spruce-fir, and heath types that were used as our model input (Fig. 2b). All of these input maps were aggregated into a 1×1 km resolution.

2.3.2. Generating daily climate dataset

The model simulation requires 1 km resolution daily climate information (precipitation, maximum and minimum temperatures) in the study region. We generated the climate dataset from 1949 to 2001 based on climate data (Cooperative Summary of the Day, TD-3200 dataset, compiled by the National Climatic Data Center, http://www.ncdc.noaa.gov/oa/ncdc.html) from 216 stations that were located <50 km from GRSM (Fig. 1). We adopted the interpolation method developed by Thornton et al. (1997), with the following modifications:

 Unlike the original approach that assesses the daily temperature lapse rate using least-squares regression technique, we used a fixed monthly lapse rate for minimum and maximum air temperatures, based on the study results of Busing et al. (2005) who used historical climate records of five GRSM stations of different elevations to analyze the elevation-climate pattern of GRSM.

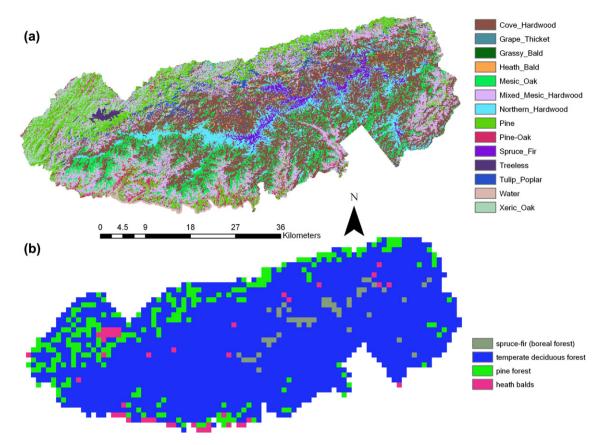


Fig. 2. The distribution of major vegetation types in GRSM (late 1980s) (a) Original 100 meter resolution vegetation map developed by MacKenzie (1993) and (b) the $1 \times 1 \text{ km}^2$ resolution 4-category vegetation map aggregated from map (a) by us to drive the model.

Unlike the original approach that assesses the daily precipitation-elevation relationship using a least-squares regression technique, we used the following empirical model to estimate the elevation-precipitation relationship of GRSM:

$$\begin{split} \text{PPT} &= -0.0002 \times \left(\text{ELEV}^2 - \text{ELEV}_{\text{ref}}^2\right) + 0.9612 \times \left(\text{ELEV} - \text{ELEV}_{\text{ref}}\right) \\ &\quad + \text{PPT}_{\text{ref}} \end{split} \tag{8}$$

where PPT and PPT_{ref} are the predicted precipitation in the target grid and the precipitation of the climate station, respectively. ELEV and ELEV_{ref} are elevation of the grid and the climate station, respectively. The coefficients are derived based on the monthly precipitation and elevation relationship of GRSM reported by Busing et al. (2005). The R^2 for the regression fit was 0.98.

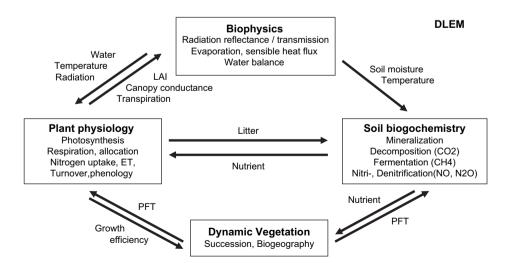


Fig. 3. Dynamic Land Ecosystem Model (DLEM). The DLEM (Tian et al., 2005) is a process-based model which couples biophysical processes (energy balance), biogeochemical processes (water cycles, carbon cycles, nitrogen cycles, and trace gases (NO_x , CH_4)-related processes), community dynamics (plant distribution and succession), and disturbances (land conversion, agriculture management, forest management, and other disturbances such as fire, pest etc.) into one integral system. DLEM can simulate the complex interactions of multiple stresses such as climate change, elevated CO_2 , tropospheric O_3 , N deposition, human disturbance, and natural disturbances.

2.3.3. Atmospheric composition datasets

Standard IPCC CO_2 concentration history data set (Enting et al., 1994) was used in this simulation. We did not consider the intra-annual CO_2 concentration change. The spatial pattern of atmospheric CO_2 concentration was assumed to be homogeneous.

DLEM required a daily AOT40 input as the index of tropospheric ozone stress. AOT₄₀ is the accumulated dose over a threshold of 40 ppb during daylight hours (Felzer et al., 2004). In DLEM, we used an accumulation period of 30 days back-trajectory. 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 in GRSM. First, hourly ozone data for five stations over 1988 to 2004 in the park were obtained from the National Park Service Air Resources Division (NPS, AQD, Lakewood, CO). These 5 stations are located across the park at various elevations including Cades Cove (564 m), Look Rock (793 m), Cove Mountain (1242 m), Purchase Knob (1500 m), and Clingmans Dome (2021 m). Due to limited hourly ozone data for the Purchase Knob site, this location was excluded from the development of the ozone spatially explicit data set. The AOT40 index was calculated directly from the averaged hourly data for each site on a monthly basis. Second, we developed an AOT_{40} index regression model for each month using the calculated AOT₄₀ index data. In these models, the AOT 40 index was the response variable while elevation was the only explanatory variable because ozone concentration is correlated with elevation, i.e., higher concentrations at higher elevations and greater exposure of forested ecosystems (Gilliam et al., 1989; Gilliam and Turrill, 1995; Mueller, 1994; Chappelka et al., 1999). The regression model for each month was then interpolated to a $1 \times 1 \text{ km}^2$ grid based on the elevation map. A linear interpolation method is used to interpolate the monthly AOT40 into a daily data set which is required by DLEM. Using this method, we developed the AOT_{40} index transient data over the entire park for the period of 1988 to 2004. Prior to 1988, we used the AOT₄₀ dataset developed by Felzer et al. (2004) which was modified by us so that the 1998 AOT_{40} matched our interpolated result.

2.4. Simulation design

To address the objectives of the study we designed the following seven simulation scenarios for this study as described in Table 1. The last scenario (i.e., CLMCO2O3) simulates the environmental change and carbon dynamics of GRSM ecosystems. We used it to assess the change of C storage of the system. We estimated the effects of climate, ozone, CO_2 factors, and their interactions respectively by analyzing the differences between CLMCO2O3 and CO2O3, between CLMCO2O3 and CLMO3, between CLMCO2O3 and CLMCO2, and between CLMCO2O3 and the sum of CLM, CO2, and O3. The CLM, CO2, and O3 scenarios estimate the general impacts of these single factors on the C dynamics of GRSM ecosystems. Besides identifying the impacts and interactions of different environmental factors, we also analyzed the responses of different vegetation types (pine forest, spruce-fir forest, deciduous forest, and heath bald) in GRSM to these environmental stresses.

In this simulation, we first used the long-term climate normal data and preindustrial CO_2 concentration data (288 ppmv) as model inputs and ran the model to the equilibrium state to build the simulation baseline for soil C pools and soil water pools. Then, for those scenarios involving transient climate we set up a spin-up run of 88 (22×4) years to prevent any abnormal fluctuation due to the sudden switch from the equilibration state to the transient state. Only the climate data were allowed to vary in the spin run. Finally, we set up the simulation of each scenarios described above. The 21-years simulation from 1949 to 1970 developed the historical background. Our analysis of simulation output focused on the period from 1971 to 2001.

3. Results and discussion

3.1. Climatic change and the atmospheric change

Our climate data shows no obvious trend of climate change in the GRSM occurred from 1971 to 2001, although an interannual fluctuation of temperature and precipitation was observed (Fig. 4a). The average temperature was 11 °C. The most rapid interannual temperature rise (by 1.59 °C) took place during the years 1997-1998 when a strong El Niño happened. The average precipitation was 1640 mm (Fig. 4b). The largest increase in precipitation was observed during the years 1988–1989, a period when the strongest La Niña in the last two decades of the 20th century took place. According to our data set, the study region experienced a long-term drought from 1985 to 1988 when annual precipitation fell to 1277 mm in 1988, the driest year. We also found that spatial patterns of climate factors were closely related to elevation (Fig. 4c,d). Precipitation in GRSM tended to increase with elevation (Fig. 4d), while temperature declined with elevation with a lapse rate of about 2.9 to 5.6 °C km⁻¹ (Busing et al., 2005).

Our ozone data set shows that the annual average AOT_{40} increased from 1418 ppb-h in 1971 to 3194 ppb-h per 30 days in 2001. Ozone concentrations in GRSM fluctuated from season to season and from year to year. Fig. 5a shows the interannual pattern of the AOT_{40} index from 1971 to 2001. Ozone concentrations increased linearly from 1418 ppb-h in 1971 to 2216 ppb-h in 1977. From 1977 to 1994, the AOT_{40} fluctuated around 2200 ppb-h, and only increased slightly (8.7%) during the 18 years. In the late 1990s, ozone stress in GRSM increased dramatically. The annual average AOT_{40} nearly doubled in the four years from 1994 to 1998. After that, it dropped back quickly to 3194 ppb-h in 2001.

Ozone concentrations varied significantly from season to season (Fig. 5b–d). The AOT_{40} increased quickly in the spring, reached a first peak in May, and then dropped slightly

Table 1						
Description	of the	seven	scenarios	in	this	study

Scenario	Description	Environmental factors					
		Climate change	CO ₂ fertilization	Ozone stress			
CLIMATE	Climate only	+	_	-			
CO2	CO ₂ fertilization only	_	+	-			
O3	Ozone stress only	_	_	+			
CLMCO2	Climate and CO ₂ combination	+	+	-			
CLMO3	Climate and ozone combination	+	_	+			
CO2O3	CO_2 and ozone combination	_	+	+			
CLMCO2O3	All environmental factors	+	+	+			

+ indicates that transient effect of the environment factor is considered; - indicates that value of the environment factor is keep constant and its transient effect is not included in the simulation.

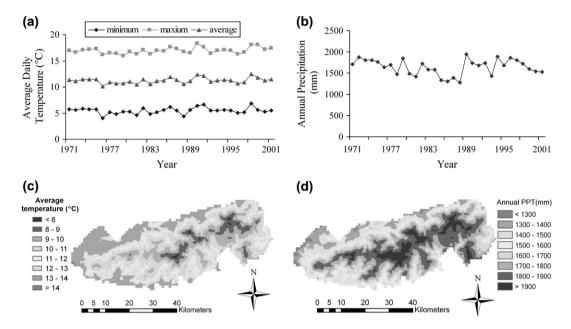


Fig. 4. The temporal and average spatial pattern of temperature and precipitation in GRSM: (a) Temporal variation of yearly average temperature from 1971 to 2001, (b) Temporal variation of annual total precipitation from 1971 to 2001, (c) Spatial pattern of average daily temperature during study period, (d) Spatial pattern of average annual precipitation during study period.

in summer. In late summer, the AOT_{40} rose to a second peak, and then decreased linearly to September.

Fig. 5c and d show the spatial pattern of ozone within the GRSM. Ozone concentrations are higher at the high

elevation regions of GRSM (Mueller, 1994; Chappelka et al., 1999; DOI, 2002). CO_2 concentrations increased from 326.3 ppmv in 1971 to 371.0 ppmv in 2001 (Enting et al., 1994).

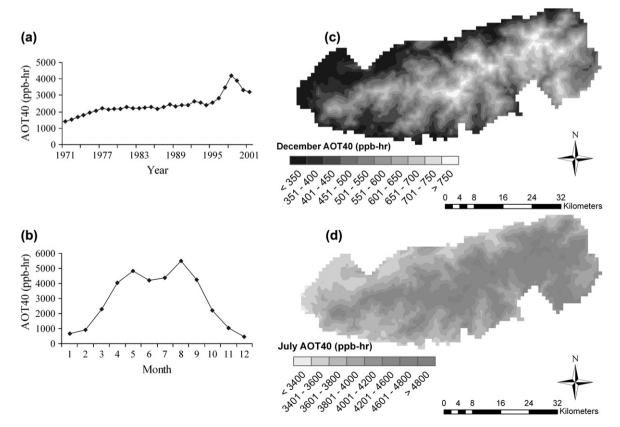


Fig. 5. The interannual, intra-annual, and seasonal pattern of tropospheric ozone (AOT₄₀, ppb-h) in GRSM: (a) Interannual variation of average AOT₄₀ from 1971 to 2001, (b) Intra-annual variation of AOT₄₀, (c) Spatial pattern of AOT₄₀ in December, (d) Spatial pattern of AOT₄₀ in July. The AOT₄₀ increases with altitude.

3.2. Changes in carbon storage from 1971 to 2001

Our simulation result shows that from 1971 to 2001 the total C storage of GRSM increased slightly from 61.3 Tg $(1 \text{ Tg} = 10^{12} \text{ g})$ to 62.2 Tg [calculated by multiplying the average total C (TOTC) density in Table 2 with area of GRSM]. In 2001, about 54% of the C was stored in the living vegetation C pool (VEGC); about 44% was stored in the soil organic C pool (SOC). The rest of the C was stored in the litter C pool (LTRC). If the ozone stress is not considered (CLMCO2 scenario), however, the combined effects of climate and CO₂ fertilization together could have resulted in a 3% (or 1.8 Tg) increase of total C storage during these 30 years. This suggests that ozone stress could have reduced the C sequestration rate by 50% (about 0.9 Tg) in GRSM. If the CO₂ fertilization effect is not considered (CLMO3), the combination effects of climate and ozone result in a 1.4 Tg loss of C from 1971 to 2001. This means that the CO₂ fertilization effects may have contributed to about 2.3 Tg C of sequestration in GRSM from 1971 to 2001.

Different vegetation types responded differently to ozone in our model results. The TOTC of deciduous forests decreased by 2.5% from 1971 to 2001, while the TOTC of pine forests decreased by only 1.4% for the same period. In another study on a lower slope forest of the GRSM, current ambient levels of ozone were predicted to accelerate forest succession by suppressing the growth of ozone sensitive species (Weinstein et al., 2001).

The C density of GRSM forest ecosystems was high (Whittaker et al., 1974). Based on our results, in 2001, the spruce-fir boreal forests at higher elevations had an average VEGC density of 16 992 g C m⁻² (Table 2). This value agrees with

Whittaker's (1966) estimate of 13 000–22 100 g VEGC m^{-2} in GRSM spruce-fir forest biomass (by assuming a ratio of root to woody shoot dry biomass of 0.3, and a C to dry biomass ratio of 0.5). Our result shows that deciduous forests had an average C density of about 16.7 kg VEGC m^{-2} in 2001. This value falls in the range of $8.4-39 \text{ kg VEGC m}^{-2}$ estimated by Whittaker (1966). Whittaker (1966) reported the pine-heath forest biomass to have 3.4-5.5 kg VEGC m⁻², and our estimation is about 4.9 kg VEGC m⁻². Our estimation of pine forest biomass is 11.8 kg VEGC m⁻², which also falls within the range of 8.4–12 kg VEGC m⁻² for pine forest biomass as estimated by Whittaker (1966). Our estimation of soil organic carbon (SOC) in GRSM was about 13 kg SOC m⁻² (Table 2), higher than the 11.2 kg C m^{-2} reported by Miller et al. (2004), but close to the Post et al. (1982) estimation of 12.1 kg SOC m^{-2} for overall cool, moist temperate forests. Daniels et al. (1987), however, found the SOC of a protected mesic southern Appalachian forest in North Carolina could be as high as 28 kg SOC m^{-2} .

Fig. 6 shows the temporal pattern of C storage from 1971 to 2001. Since the SOC was relatively stable, the temporal pattern on total C dynamics was decided primarily by the change in the VEGC pool, which followed the general pattern of climate change, especially the interannual change in precipitation. The late 1980s drought (Fig. 4b), for example, may have resulted in a loss of C storage in GRSM. The negative effect of ozone stress and positive effect of CO_2 fertilization on ecosystem C sequestration become more and more evident through time and their combined effects resulted in a slight increase of C storage according to our analysis.

Fig. 7 shows the spatial pattern of the GRSM C storage, and its net change from 1971 to 2001. Except for the scattered

Table 2 Overall change in GRSM forest carbon density (g C m^{-2}) from 1971 to 2001

		CLMCO2O3				CLMCO2				CLMO3			
		1971	2001	Change	Change (%)	1971	2001	Change	Change (%)	1971	2001	Change	Change (%)
VEGC	Pine	11782	11789	7	0.06	11786	11787	0	0.00	11649	11459	-190	-1.63
	Spruce-fir	16266	16992	726	4.46	16352	17304	952	5.82	16031	15909	-121	-0.76
	Deciduous	16475	16661	186	1.13	16596	17115	518	3.12	16235	15634	-601	-3.70
	Heath bald	4734	4903	169	3.57	4750	4911	162	3.40	4761	4756	-6	-0.12
	Average	15706	15884	179	1.14	15811	16276	464	2.94	15483	14951	-532	-3.44
SOC	Pine	8981	9418	437	4.87	8989	9470	481	5.35	8845	8901	56	0.63
	Spruce-fir	14413	14463	50	0.35	14417	14502	86	0.59	14574	14504	-70	-0.48
	Deciduous	13420	13642	221	1.65	13440	13773	332	2.47	13564	13446	-118	-0.87
	Heath bald	10681	10971	290	2.71	10694	11083	389	3.64	10423	10295	-128	-1.23
	Average	12902	13144	242	1.88	12920	13264	344	2.66	13007	12908	-98	-0.76
LTRC	Pine	958	983	25	2.58	964	1005	41	4.25	917	748	-169	-18.46
	Spruce-fir	1396	1412	16	1.16	1382	1416	35	2.51	1443	1406	-37	-2.55
	Deciduous	878	890	13	1.43	875	913	38	4.34	878	843	-34	-3.93
	Heath bald	626	676	49	7.84	631	698	67	10.62	602	577	-25	-4.22
	Average	893	908	15	1.65	891	930	39	4.36	889	840	-49	-5.51
TOTC	Pine	21722	22190	468	2.16	21739	22261	522	2.40	21411	21108	-303	-1.41
	Spruce-fir	32075	32867	792	2.47	32151	33223	1072	3.33	32048	31820	-228	-0.71
	Deciduous	30773	31193	420	1.36	30912	31801	889	2.87	30677	29924	-753	-2.46
	Heath bald	16041	16549	508	3.17	16074	16692	618	3.84	15787	15627	-160	-1.01
	Average	29500	29936	435	1.48	29622	30469	847	2.86	29379	28700	-679	-2.31

Area of pine forest is 226 km²; area of deciduous forest is 1760 km²; area of spruce-fir alpine/boreal forest is 48 km²; area of heath bald is 45 km²; total area of GRSM is 2079 km².

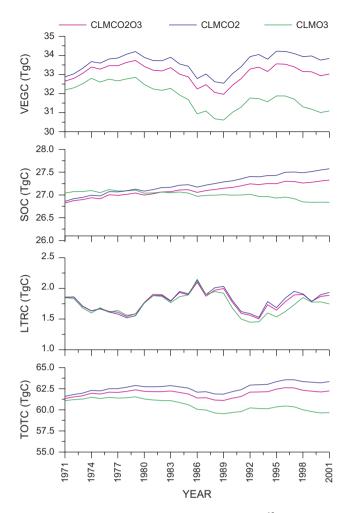


Fig. 6. Changes in GRSM carbon pools (unit: Tg; $1 \text{ Tg} = 10^{12} \text{ g}$) from 1971 to 2001. VEGC denotes vegetation carbon pool; SOC denotes soil carbon pool; LTRC denotes litter C pool; TOTC denotes total carbon storage. Scenarios: CLMCO2, climate + CO₂ effect; CLMO3, climate + ozone effect; CLMCO2O3, combination of climate + CO₂ + ozone effect.

heath balds, the ecosystem total C storage generally increased with altitude. This pattern could be explained by the unique climate patterns of the GRSM. While the lower temperatures at the higher altitudes limited ecosystem C loss through respiration, the high precipitation enhanced plant C sequestration capacity (Fig. 4c,d). It seems that this climate effect dominated over the negative effect (on C sequestration) of high ozone concentrations in high elevations (Fig. 5c,d). Our simulation results also indicate that the northern region of GRSM sequestrated more C than the southern part of GRSM (Fig. 7c). The low altitude and the mountain-top forests may store C, while some of the mid-altitude forests, especially those in the southwestern and southeastern regions, may lose small amounts of C in comparison with the magnitude of C sequestration during the simulation period. Our analysis shows that from 1971 to 2001, the average annual precipitation increase rate in the southeastern and northeastern GRSM could be about 20% lower than the rate of increase for precipitation of the whole park. As the result, in these regions, C sequestration due to CO₂ fertilization and climate change could not compensate

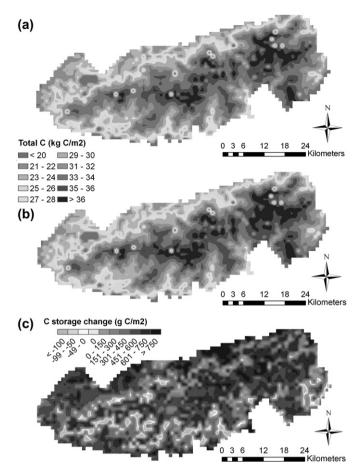


Fig. 7. The spatial pattern of the GRSM C pool. (a) C storage in 1971; (b) C storage in 2001; (c) C storage changes from 1971 to 2001.

for the C loss due to increased ozone exposures in the mid-latitudes (Fig. 5).

According to our estimation, the average TOTC of GRSM could be as high as 30 kg C m⁻² in 2001, much higher than the regional average C density (McNulty et al., 1994). The average VEGC density was approximately 15.9 kg C m⁻². Whittaker (1966) reported that in GRSM "Cove forest biomasses are larger than any reported for either temperate or tropical forests". The VEGC stored in undisturbed cove forests growing in GRSM valleys ranges from 25 to 30 kg C m^{-2} . The average VEGC and TOTC of North Carolina and Tennessee forests in 1997, as reported by Birdsey and Lewis (2003), were 7.3 kg C m⁻² and 15.8 kg C m⁻², respectively, only half of the C density in GRSM. The total C pool size of the US is 37,210 Tg, whereas the Southeastern US stores 5280 Tg, about 5269 g C m $^{-2}$, including both forested and non-forested land (Potter et al., 2006). Therefore, the C density of GRSM could be about 6 times that of the regional average value (McNulty et al., 1994; Potter et al., 2006). With such high C density, any climate change or atmospheric change could lead to significant amounts of C flux from GRSM. The analyses of impacts of climate change, CO₂ fertilization, and ozone stress on C fluxes are, therefore, important for evaluating GRSM C dynamics in the past, its current C pool size, and its C sequestration capacity in the future.

3.3. Carbon fluxes

According to our simulation, the average annual net primary productivity (NPP) of GRSM was about 738 g C m⁻². close to the average of 700-840 g C m⁻², by assuming that the belowground NPP to aboveground NPP ratio equals to 0.4 (Nadelhoffer et al., 1985); and C:dry biomass ratio equals 0.5 for well-stocked, mesic southern Appalachian forests reported by Whittaker (1966). The average annual NPP of spruce-fir and pine forests were about 642 g C m^{-2} and 715 g C m⁻², respectively. These estimations fall in the range of 514-980 g C m⁻² NPP for coniferous forests reported by Whittaker (1966). The average annual NPP of deciduous forests was about 748 g C m⁻², close to the average NPP (714 g $C m^{-2}$) of nine eastern deciduous forests reported by Whittaker (1974), and was within the range of GRSM deciduous forest NPP (581-854 g $C m^{-2}$) reported by Busing et al. (1993).

Our simulation results indicate that the pattern of interannual variation of NPP in the CLMCO2O3 scenario was probably driven by climate variation (Fig. 8a). The average annual NPP of the CLM, CO2, and O3 scenarios (Table 1; see Section 2.4) are 699 g C m⁻², 756 g C m⁻², and 675 g C m⁻²,

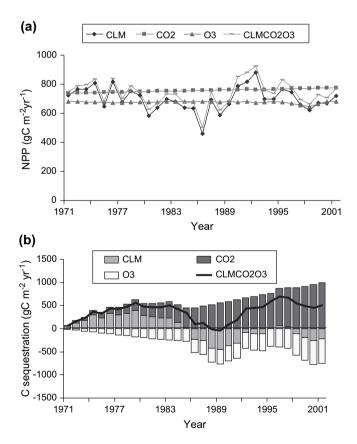


Fig. 8. Transient responses of net primary productivity (NPP) and carbon storage to multiple environmental stresses. Scenarios under comparison: CLM, climate only; O3, ozone only; CO2, CO₂ only, CLMCO2O3, combination effects of climate, ozone, and CO₂. (a) Effect of climate, CO₂-fertilization, and O₃ damage on NPP; (b) Cumulative carbon storage from each of the factors in (a).

respectively. Their combined effect was 4% higher than their average value. There is evidence that elevated CO_2 concentrations cause partial stomatal closure, especially in C3 plants, that survive solely on C3 carbon fixation (Mott, 1988; Allen, 1990) and thus possibly reduce the stomatal uptake of O_3 (Paoletti and Grulke, 2005), although this mechanism may not work for all GRSM plant species, especially if injured by ozone (Grulke et al., 2007).

Cumulative carbon sequestration from climate change and atmospheric change is shown in Fig. 8b. Unlike NPP, the temporal pattern of net C sequestration from 1971 to 2001 not only followed the fluctuations of climate change, but was also controlled by the cumulative effect of CO_2 fertilization, which constantly increased during the study period. Since the mid 1980s, the positive CO_2 fertilization effect on C sequestration might have dominated the ozone stress and the negative effect of climate change, even though the C storage of the GRSM forest ecosystem decreased slightly in 1988 due to negative climate stress (Fig. 8b).

3.4. Comparisons of the simulation results with other studies

3.4.1. Ozone effects

Our results (Table 2) show that ambient ozone stress could reduce GRSM vegetation biomass by approximately 2.5% (CLMCO2CO3 - CLMCO2). In a long-term field study with loblolly pine (Pinus taeda) in North Carolina, Shafer and Heagle (1989) found that the near-ambient ozone concentrations $(0.05 \ \mu L^{-1})$, seasonal 12-h mean) reduced the forest biomass by about 2-19%. Our results show that from 1971 to 2001, ozone stress (CLMCO2O3 - CLMCO2) could reduce NPP by 3.1%. Based on a 6-year uncontrolled field study of mature loblolly pine growing in eastern Tennessee, McLaughlin and Downing (1995, 1996) reported that the forest productivity could be reduced by 0-15% (average 5%) due to the ambient ozone stress. Teskey (1995) reviewed the literature for southern coniferous forests, and concluded that the ambient ozone could reduce forest productivity by 2-5%. Chappelka and Samuelson (1998) reviewed the ambient ozone effects on forest trees of the eastern United States and suggested that the ozone may reduce the growth of mature trees by about 2-9%.

Most of the field studies conducted were only short-term in nature. The majority of these studies focused on vegetation growth, but did not include the measurement of the soil C pool which is important for the estimation of the ecosystem carbon sequestration rate (or net carbon exchange, NCE). To validate our simulation, we also compared our results to other large-scale, long-term regional simulation studies conducted in the US. Ollinger et al. (1997) simulated the effects of ozone using 64 ozone monitoring sites across the northeastern US for the period 1987–1992, and found an annual NPP reduction of 3-16%. The results of a 300-year (1700–2000) simulation study in the same region (Ollinger et al., 2002) further suggested that the ozone stress could have reduced NCE by about 46.7%. Felzer et al. (2004) used a monthly time-step terrestrial ecosystem model to estimate the effects of ozone on NPP and NCE across the conterminous US, and estimated a mean 2.6-6.8% reduction for the annual NPP in response to historical ozone levels during the late 1980s to early 1990s. Their results also suggested that ozone exposure could have decreased US carbon sequestration by 49.3% (but did not consider agricultural management). These results agree with our estimation of a 3.1% reduction of NPP and 50% decline of carbon sequestration (see Section 3.2) due to ozone stress in GRSM.

3.4.2. CO₂ fertilization effect

Our results suggest that during the 1971-2001 time period CO₂ fertilization (CLMCO2O3 - CLMO3) may have enhanced GRSM ecosystem productivity by about 8%. A comparison of the FREE Air Enrichment Sites (FACE site) from their inception (Norby et al., 2005) showed a median increase of 23% in NPP across sites exposed to elevated CO₂ (550 ppm) in comparison with control sites (370 ppm). By assuming a linear interpolation of these FACE site results, Boisvenue and Running (2006) estimated that the CO_2 fertilization effect since 1950s could have increased global forest productivity by about 4%. Considering the acclimation of plants to rising CO₂ (Moore et al., 1999; de Graaff et al., 2006; El Maayar et al., 2006), however, the CO₂ fertilization effect in a lower concentration (e.g. the ambient atmospheric CO₂ concentration during the past 50 years) could be stronger than the effect observed in enrichment experiments (550 ppm). Therefore, we expect the actual enhancement on NPP due to rising CO₂ concentrations since 1950s could be higher than 4%, and be close to our estimation. Similarly, in a modeling study across the conterminous US, Felzer et al. (2004) estimated that the CO₂ fertilization effect could have resulted in a 6% increase in NPP from 1989 to 1993.

4. Conclusions

The carbon density of GRSM could be as high as 15.9 kg m⁻² in 2001, twice the regional (NC and TN) average C density. Although these forests are protected from landconversion and catastrophic fire disturbances, the C storages in these forests are still affected by climatic and atmospheric changes such as CO₂ fertilization and tropospheric ozone pollution. The climatic and atmospheric environments of mountainous ecosystems also vary by elevation. The precipitation and ozone concentrations of GRSM, for example, increase with elevation. The total C density may increase with altitude as a result of climate control along the altitudinal gradient (i.e., high precipitation, which enhances forest growth and low temperatures, which inhibit respiration and decomposition). We estimated that ozone has reduced C sequestration by about 0.9 Tg C in GRSM, while the CO₂ fertilization effects contributed to a sequestration of about 2.3 Tg C in GRSM from 1971 to 2001. The combined effects of climatic and atmospheric change during this 30-year period could have resulted in about a 0.9 Tg C increase in the GRSM C pool. The average annual net primary productivity of GRSM was about 738 g C m⁻². The interactions among climatic and atmospheric factors enhanced the positive effects of CO₂ fertilization on GRSM C sequestration using modeled responses of stomatal conductance to elevated CO_2 . Our simulation shows that the temporal pattern of NPP was controlled by the climate factors (temperature and moisture), while the temporal pattern of net C sequestration not only followed the fluctuations of climate change, but also was controlled by the cumulative effect of CO_2 fertilization, which was constantly rising during the study period. In the long run, the positive CO_2 fertilization effect on C sequestration dominated the ozone stress and the negative effect of climate stresses.

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