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Dynamic responses of African ecosystem carbon cycling to climate change

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ABSTRACT: Global climate change has been modifying ecosystem carbon cycling, which has produced feedbacks on climate by affecting the concentration of atmospheric CO_2. The importance of biospheric CO_2 uptake or release to climate change has generated great interest in quantifying the dynamic responses of terrestrial ecosystem carbon cycling to climate change. However, less attention has been given to Africa, although it accounts for about one-fifth of the global net primary production and is one of the regions that have the greatest climate change. Here we use a biogeochemical model to simulate the dynamic variations in the carbon fluxes and stocks of African ecosystems caused by changes in climate and atmospheric CO_2 from 1901 and 1995. We estimate that climate change reduces plant production and soil carbon stocks and causes net CO_2 release, but the fertilization effect of increasing atmospheric CO_2 on photosynthesis reverses the reduction and leads to carbon accumulation in vegetation. Therefore, the combined effect of climate change and increasing atmospheric CO_2 causes net CO_2 uptake, particularly in central Africa. The mean rate of the carbon sequestration in the period 1981–1995 is calculated to be 0.34 Gt C yr^{-1}. Nevertheless, Africa is not necessarily a significant carbon sink, because a large part of the carbon sequestration is offset by the carbon release arising from land use changes.

KEY WORDS: Carbon cycle · Climate change · Africa Ecosystem modeling

1. INTRODUCTION

Terrestrial ecosystems and climatic systems are closely coupled, particularly by carbon cycling between vegetation, soils, and the atmosphere. The exchanges of CO_2 between ecosystems and the atmosphere are responsible for a large fraction of both seasonal and interannual variations in atmospheric CO_2 (Conway et al., 1988, Keeling et al. 1993). Global environmental changes (such as global warming, atmospheric CO_2 increases, land transformation and anthropogenic N_2 fixation) affect plant photosynthesis, respiration, and decomposition, thus leading to changes in plant CO_2 fixation and the carbon stocks in vegetation and soils (Melillo et al. 1993, Schimel et al. 1995, Vitousek et al. 1997). It has been suggested that global environmental changes may have enhanced plant growth so as to render terrestrial ecosystems a substantial CO_2 sink (Tans et al. 1990, Dai & Fung 1993, Keeling et al. 1996), but some studies indicate that the changes may cause more CO_2 release (Oechel et al. 1993, Townsend et al. 1992). Quantification of terrestrial CO_2 uptake or release has become one of the most important areas in global change science in the last decade, and the studies will play a more and more important role in making environmental policy, because the Kyoto Protocol has included biological carbon sinks and sources in a legally binding framework for mitigating the anthropogenic greenhouse effect.

Although intensive studies on terrestrial ecosystem carbon cycling have been conducted, high uncertainties still exist in determining the magnitude and spatial distribution of the carbon sinks and sources. Most of the studies have concentrated on the ecosystems in northern high and middle latitudes and South America, but less attention has been given to Africa. Africa

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is one of the regions that have the greatest climate change, but the impacts on ecosystem carbon cycling have not been quantitatively estimated. In the African Sahel, the great drought that began in the late 1960s continued well into the 1980s, annual rainfall during 1961–1990 was from 20 to 40% less than that during 1931–1960 (Hulme 1992, Middleton & Thomas 1997). There has been an overall warming trend in Africa with global climate change, and the warmer years in Africa have been associated with drier condition (Hulme 1996a,b). The drought and warming may have resulted in land degradation or desertification (Schlesinger et al. 1990, Glantz 1994). About 60% of the continent has experienced increases in aridity, and about 7% of the lands has been classified as a drier aridity zone (Hulme 1992). The climate change and the consequent land degradation must affect the carbon fluxes and stocks of ecosystems. Because water availability limits plant growth in most parts of Africa, drying has reduced plant productivity (Schlesinger et al. 1990, Glantz 1994). Warming enhances microbial activity and thus can cause declines in the carbon stocks in soils (Oechel et al. 1993, Schimel et al. 1994). In subtropical and tropical Africa, where temperatures are often higher than the optimum for plant growth, warming may cause declines in plant net primary production. However, increasing atmospheric CO_2 may enhance plant productivity because it stimulates photosynthesis and increases water-use efficiency (Amthor 1995). Quantification of the responses of ecosystem carbon cycling to climate change requires understanding of the combined effects of changes in various climatic factors (e.g. precipitation, temperature, air humidity, and atmospheric CO_2) on all the ecosystem processes involved (e.g. evapotranspiration, photosyntheisis, respiration, and decomposition.

Ecosystem modeling is perhaps the only feasible way to investigate the impacts of climate change on the spatial-temporal dynamics of ecosystem carbon cycling at the continental and long-term scale. Ecosystem biogeochemical models have been developed to simulate the biological and physiological processes involved in ecosystem carbon and nutrient cycling and have been used to estimate the changes in carbon fluxes and stocks arising from the shifts of equilibrium ecosystem states (Raich et al. 1991, Running & Gower 1991, Parton et al. 1993, Smith & Shugart 1993). However, most ecosystems rarely reach and maintain the equilibrium state, because they are always disturbed by environmental variations; and it is the information on seasonal and interannual variations in ecosystem carbon fluxes that is most important for predicting the real time changes in atmospheric CO_2. In recent years, the development of dynamic ecosystem models (Cao & Woodward 1998a, Tian et al. 1998, Woodward et al. 1998) has made possible quantification of the dynamic changes in ecosystem carbon exchanges. In this study we report our estimates for the dynamic responses of African ecosystem carbon fluxes and stocks to climate change from 1901 to 1995. The estimates are made based on the simulations of plant photosynthesis, respiration, litter production, and soil decomposition with the CEVSA (carbon exchange between vegetation, soil, and the atmosphere) model (Cao & Woodward 1998a,b).

2. MODELING APPROACHES

Biological carbon cycling occurs via the processes of photosynthesis, respiration, litter production and decomposition, which are controlled by plant ecophysiological characteristics (e.g. photosynthetic pathway, leaf form, and phenology) and by environmental conditions (e.g. radiation, temperature, and water and nutrient availability). To couple the biological and environmental controls over carbon cycling, the CEVSA model (Cao & Woodward 1998a,b) includes 4 modules: a biophysical module calculating canopy conductance, evapotranspiration and soil moisture; a plant growth module describing photosynthesis, respiration, carbon allocation among plant organs, and litter production; a biogeochemical module simulating the transformation and decomposition of organic materials and nitrogen inputs and outputs in soils; and a vegetation module determining vegetation distribution and composition. The model is run with a time-step of 1 mo, except that the environmental influences on carbon and nitrogen allocation among plant organs and on litter quality are estimated on an annual basis. The modeling strategies and key processes of the CEVSC model are described in the following sections.

2.1. Plant photosynthesis and net primary production (NPP)

Rates of plant CO_2 assimilation depend on the balance between the CO_2 demand by photosynthetic biochemical processes, which is controlled by the efficiency of photosynthetic enzyme systems (Farquhar et al. 1980), and CO_2 supply by diffusion from the atmosphere into leaf intercellular air spaces, which is the function of stomatal conductance (Jones 1992, Harley et al. 1992). Plant photosynthetic processes and stomatal conductance interact with each other and both are affected by environmental factors, such as radiation, temperature, air humidity, soil moisture, and atmospheric CO_2 concentration (Collatz et al. 1992, Harley et al. 1992). A part of the carbon assimilated in photosynthesis is consumed in autotrophic respiration for maintaining living tissue and synthesizing new tissue. The difference between gross photosynthesis and autotrophic respiration is defined as NPP, which represents the net carbon flux from the atmosphere to the vegetation. The CEVSA model (Cao & Woodward 1998b) uses the methods described by Woodward et al. (1995) to calculate rates of plant photosynthesis, stomatal conductance, and autotrophic respiration and to determine the leaf area index (LAI). In the calculations, the plant canopy is divided into layers, each having unity LAI and the rates of CO_2 assimilation, respiration, and stomatal conductance of each layers are calculated separately. The LAI is determined based on the carbon balance between photosynthesis and respiration and the water balance between precipitation and water losses through evapotranspiration and runoff. The CEVSA model determines vegetation distribution based on the temperatures of the coldest and warmest month, growing degree days, and water availability (Prentice et al. 1992).

Plants allocate fixed carbon proportionally among leaves, stems and roots for balancing carbon assimilation and the uptake of nutrients and water. The CEVSA model calculates the carbon allocation based on the leaf mesophyll resistance to CO_2 assimilation and the stomatal resistance to water loss for forests and on fractional parameters for grasses (Cao & Woodward 1998b). The allocated carbon in various plant organs is given a mean residence time with a statistical distribution upon which the carbon pool of plant organs and rates of litter production are calculated. The seasonality of litter production is determined according to the phenological characteristics of vegetation types (Cao & Woodward 1998b). Litter entering soils is transformed into soil organic matter and is decomposed into CO_2 through heterotrophic respiration. The CEVSA model divides soil organic matter into pools of surface litter, root litter, microbes, and slow and passive carbon materials. Microbial decomposition and the carbon transformations between those pools are considered to be first-order rate reactions, and each of the reactions has a specific decay rate that is adjusted according to litter quality, temperature, soil moisture, nitrogen availability, and soil texture (Cao & Woodward 1998b). The difference between plant NPP and soil heterotrophic respiration, defined as net ecosystem production (NEP), represents the net carbon fluxes between ecosystems and the atmosphere. When NEP is positive, ecosystems are taking up CO_2 from the atmosphere; otherwise they are releasing CO_2 into the atmosphere.

We conducted dynamic simulations of carbon cycling in Africa with the CEVSA model using the climate data from 1901 to 1995 supplied by the Climatic Research Unit, University of Norwich, UK. The climate data sets included monthly-mean values of the variables of temperature, precipitation, water vapor pressure, wet day frequency, diurnal temperature range, and sunshine duration with a spatial resolution of 0.5° latitude × 0.5° longitude. The data on soil texture and unit needed by the model were derived from the digitized FAO map of the world soils (Zobler 1989). We first ran the model with the average climate from 1901 to 1920 until an ecological equilibrium was reached, that is when the differences between annual NPP, litter production, and decomposition and the interannual variations in soil moisture, carbon stocks in vegetation and soils were less than 0.1%. After reaching equilibrium, we conducted dynamic simulations with the transient changes in climate and atmospheric CO_2 from 1901 to 1995. Because the CEVSA model cannot simulate the dynamic changes in vegetation distribution and composition, we used a fixed potential vegetation pattern that was determined with the average climate from 1901 to 1920. Therefore, this study does not take into account the effects of the changes in vegetation composition and distribution caused by either natural or anthropogenic disturbances. For separating the influences of climate change and CO_2 increase, we make simulations with 2 scenarios: climate change with and without CO_2 increase. In addition to analyses for the whole of Africa, the results were also integrated into 3 latitudinal regions, northern (>10° N), central (10° N to 10° S) and southern Africa (>10° S), to investigate the differential responses of different climate-vegetation zones.

3. RESULTS

3.1. Vegetation distribution and the carbon stocks with the equilibrium status

Fig. 1 shows the vegetation distribution, NPP, and carbon stocks in vegetation and soils as the ecosystems reach equilibrium under the average climate between 1901 and 1920. The equilibrium status represents the baseline of our dynamic simulations of the responses of ecosystem carbon cycling to transient changes in climate change and atmospheric CO_2. The potential distribution of forests and woodlands we estimate from climatic conditions is similar to that based on the vegetation classification scheme (Lanly 1982, Matthew 1983), but our estimated area of forests and woodlands—about 8.6×10^6 km^2—is 22% higher than the current one calculated from land-use grouping (FAO 1993) and remote sensing data (DeFries & Townshend 1994). Annual NPP ranges from about 10 g C m^{-2} for deserts to 400 g C m^{-2} for savanna and to 1000 g C m^{-2} for evergreen forests. In most regions of the continent,

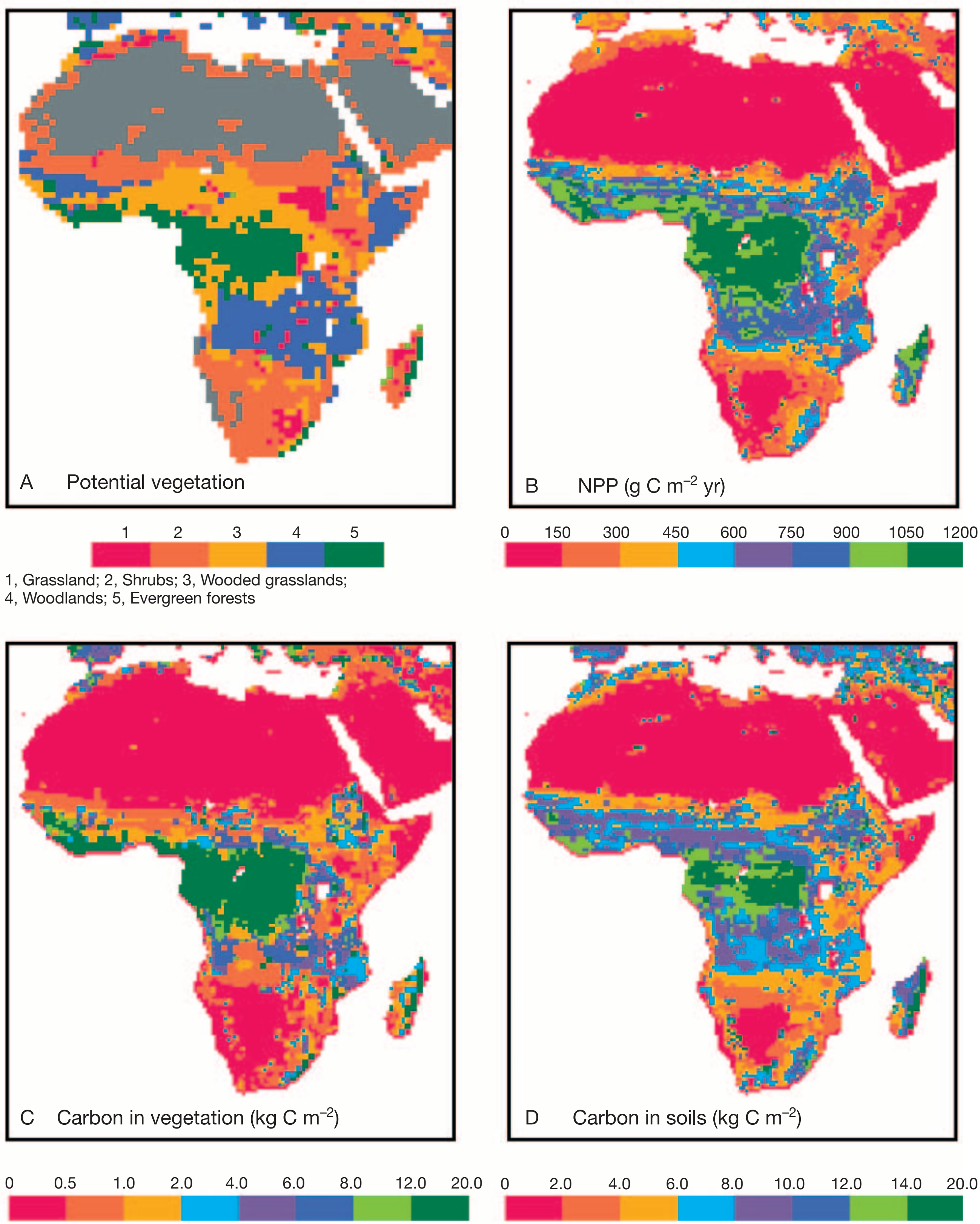

Fig. 1. Vegetation distribution (A), net primary productivity (NPP) (B), and carbon storage in vegetation (C) and soils (D) as the ecosystems reaches the equilibrium with the mean climatic conditions from 1901 to 1920

annual NPP is below 400 g C m^{-2}, but central Africa is one of the most highly productive regions in the world. The total NPP of Africa is about 11 Gt C yr^{-1}, and total carbon stocks are 275 Gt C, of which 170 Gt is in soils and 105 Gt is in vegetation. Our estimated carbon stocks in soils are close to that calculated from measured soil organic carbon content and world life zone distribution (Post et al. 1982), but the estimated carbon stocks in vegetation biomass are higher than other estimates using current vegetation distribution (FAO 1993, Millington et al. 1994, Gaston et al. 1998). Gaston et al. (1998) calculated that the current carbon stocks in vegetation are about 50 Gt, which is only a half of our result. The difference between the potential vegetation distribution and carbon stocks as we estimate and the current actual ones may reflect the effect of human activities. In Africa, deforestation has reduced the area of original forests by half, and other human activities such as logging, fuel-wood gathering, grazing, and anthropogenic burning cause forest degradation and reductions in the carbon density in both vegetation and soils (FAO 1993, Millington et al. 1994, Gaston et al. 1998). By comparing the difference between the potential and current existing vegetation distribution, Defries et al. (1999) estimated land use change may have caused a total loss of 30 to 40 Gt organic C from Africa.

3.2. Climate change and the effect on soil moisture

The changes in climate and atmospheric CO_2 from 1901 to 1995 are shown in Fig. 2A. During this period, atmospheric CO_2 concentration increased from 296 to 365 ppmv. The mean temperature for the whole of Africa increased by 0.5°C, and the greatest warming occured in southern Africa, with an increase of 0.8°C. Precipitation reached its maximum in the 1950s and then declined until late 1980s. In northern and central Africa, precipitation declined after the 1960s but started to recover in the 1990s; in southern Africa, precipitation reached its maximum in the 1970s and decreased in the 1980s and 1990s. Although the stomatal conductance per unit leaf area reduced by 4% as atmospheric CO_2 increased from 296 ppmv in the 1900s to 365 ppmv in the 1990s, the evapotranspiration demand still increased because of warming and drought; therefore, we predict a decreasing trend in soil moisture (Fig. 2A). The mean soil moisture (relative to soil water holding capacity) of the continent in the 1980s was 0.37, 9% lower than the average at the beginning of the century. Soil moisture in northern and southern Africa has decreased by about 12% since the 1960s. Therefore, climate change has reduced the availability of soil moisture in Africa.

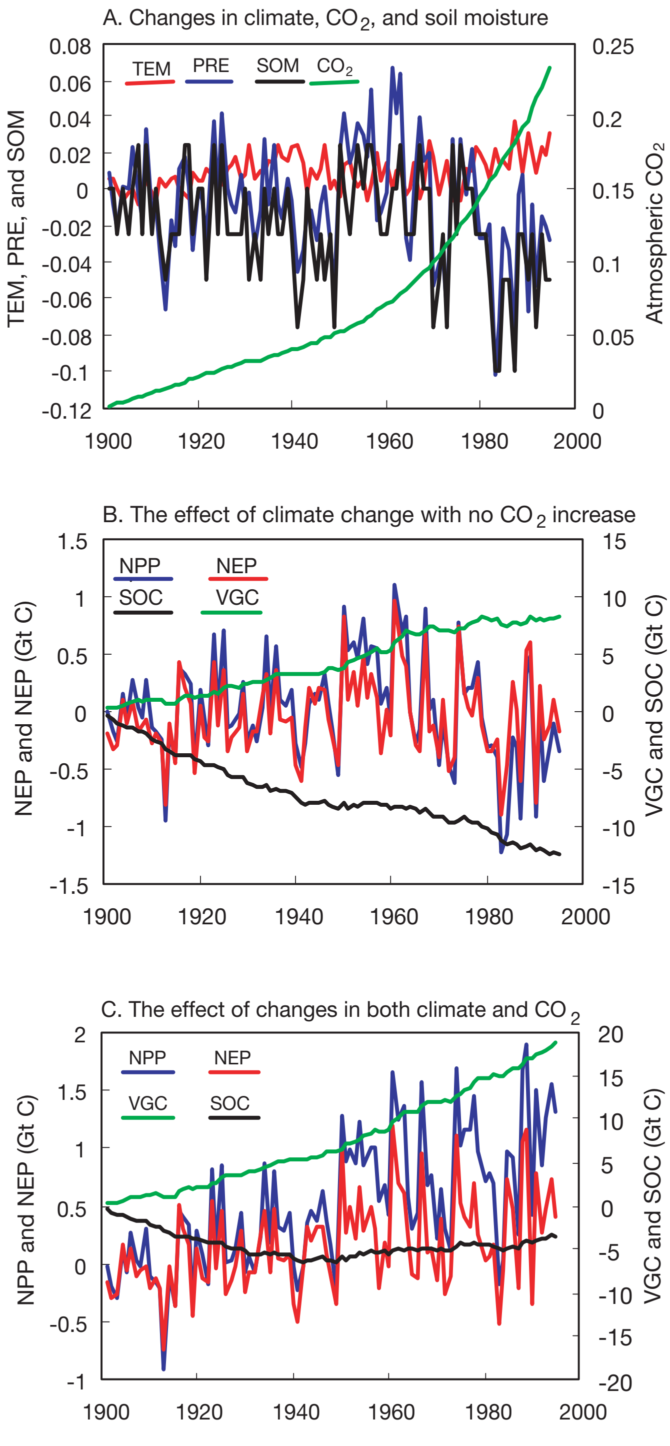

Fig. 2. Climate change and the effects on soil moisture and carbon exchange. (A) Variations in atmospheric CO_2, air temperature (TEM), precipitation (PRE), and soil moisture (SOM). All values represent the proportional changes of the variables relative to the averages from 1901 to 1920. (B) Variations in net primary production (NPP), net ecosystem production (NEP), and carbon stocks in vegetation (VGC) and soils (SOC) resulting from climate change with no atmospheric CO_2 increase. (C) Variations in NPP, NEP, VGC and SOC caused by the changes in both climate and atmospheric CO_2

3.3. Responses of carbon cycling to climate change with no CO_2 increase

Interannual climatic variations affects NPP and NEP strongly and lead to changes in the carbon stocks in soils and vegetation (Fig. 2B). Precipitation plays a dominant role in the changes in NPP. Annual NPP responds positively to the variations in precipitation (R = 0.92) but negatively to temperature (R = –0.38). From the beginning of this century, NPP had an increasing trend until the 1960s, then it decreased in response to the decreases in soil moisture caused by warming and drought. The decadal-mean NEP for the whole of Africa is positive only in the 1950s and 1960s, when there was high precipitation. The mean NEP from 1981 to 1995 was –0.15 Gt C yr^{-1}, so climate change and the resultant decreases in soil moisture caused a net CO_2 release from Africa. Although the carbon in vegetation has slightly increased, soil carbon stocks have been greatly reduced by warming, which enhances soil organic carbon decomposition (Fig. 2B).

In most regions of Africa, climate change caused reductions in NPP and NEP (Fig. 3A). The highest reduction in NPP and NEP occurred in northern Africa due to the drought in the 1970s and 1980s, causing substantial decreases in soil organic carbon (Table 1). In the period 1981–1990, NPP was only 82% of that in the 1950s, and the mean NEP was –0.13 Gt C yr^{-1} (Table 1); however, both NPP and NEP started to increase in the 1990s due to the recovery of precipitation. In central Africa, NPP had no clear changing trend, soil carbon losses were offset by the carbon gains in vegetation, the total organic carbon stocks increased slightly. In southern Africa, NPP was high in the period 1961–1970, but has decreased since the 1980s because of decreasing precipitation. The decreases in NPP and the warming-induced increases in soil decomposition caused carbon losses in southern Africa (Fig. 3A, Table 1).

3.4. Responses of carbon cycling to changes in both climate and atmospheric CO_2

For the changes in both climate and atmospheric CO_2, we predict that both NPP and NEP are increasing (Fig. 2C). Because of the CO_2 fertilization effect on photosynthesis, annual total NPP in Africa increased from 11.4 Gt C in the 1900s to 12.7 Gt C in the 1990s. The CO_2 fertilisation factor β, a logarithmic response in NPP to an atmospheric CO_2 increase, is estimated to be 0.52, which is consistent with experimental data (Amthor 1995). According to the biochemical kinetics of photosynthetic processes, a relatively large stimulation of photosynthesis by CO_2 enrichment occurred in high-temperature regions (Kirschbaum 1994). Increases in water-use efficiency by elevated atmospheric CO_2 (Eamus 1991, Kirschbaum 1994) also contributed to the strong NPP increases. We calculated that the plant water-use efficiency (the carbon fixed per millimeter of actual evapotranspiration) increased by 14%. The CO_2-induced increases in NPP led to carbon accumulation in vegetation, and the consequent increases in litter production reversed the decreasing trend of soil organic carbon caused by warming (Fig. 2C). NEP has been enhanced, and the carbon stocks in vegetation and soil increase by 15.5 Gt from 1901 to 1995. African ecosystems took up CO_2 at a mean rate of 0.34 Gt C yr^{-1} in the period 1981–1995.

NPP and NEP increased mainly in central Africa (Fig. 3B), particularly since the 1950s as atmospheric CO_2 rose rapidly. The current NPP is 17% higher than in the 1900s. The NEPs in the 1980s and 1990s were

Table 1. Net primary production (NPP), net ecosystem production (NEP), and changes in vegetation carbon (VGC) and soil organic carbon (SOC), in response to climate change with no atmospheric CO_2 increase

	Northern Africa (>10° N)				Central Africa (10° N–10° S)				Southern Africa (>10° S)			
	NPP	NEP	VGC	SOC	NPP	NEP	VGC	SOC	NPP	NEP	VGC	SOC
	(Gt C yr^{-1})				(Gt C yr^{-1})				(Gt C yr^{-1})			
1900s	2.25	–0.12	0.00	–0.12	6.34	0.03	0.04	–0.01	2.78	0.03	0.05	–0.02
1910s	2.22	–0.11	0.01	–0.10	6.23	–0.05	–0.02	–0.03	2.79	0.03	0.05	–0.02
1920s	2.37	–0.07	0.01	–0.08	6.32	0.02	0.05	–0.03	2.76	–0.03	0.04	–0.07
1930s	2.38	–0.10	0.00	–0.10	6.30	0.02	0.03	–0.01	2.78	0.04	0.06	–0.02
1940s	2.36	–0.02	0.01	–0.03	6.28	0.01	0.03	–0.02	2.74	0.01	0.01	0.00
1950s	2.58	–0.01	0.02	–0.03	6.32	0.03	0.05	–0.02	2.88	0.07	0.07	0.00
1960s	2.36	–0.11	0.00	–0.11	6.48	0.17	0.12	0.05	2.79	0.05	0.06	–0.01
1970s	2.15	–0.12	0.00	–0.12	6.29	0.00	0.00	0.00	2.95	0.10	0.09	0.01
1980s	1.96	–0.14	–0.01	–0.13	6.27	–0.03	–0.01	–0.02	2.68	–0.03	0.02	–0.05
1990s	2.19	0.00	0.04	–0.04	6.30	0.01	0.03	–0.02	2.61	–0.06	–0.01	–0.05

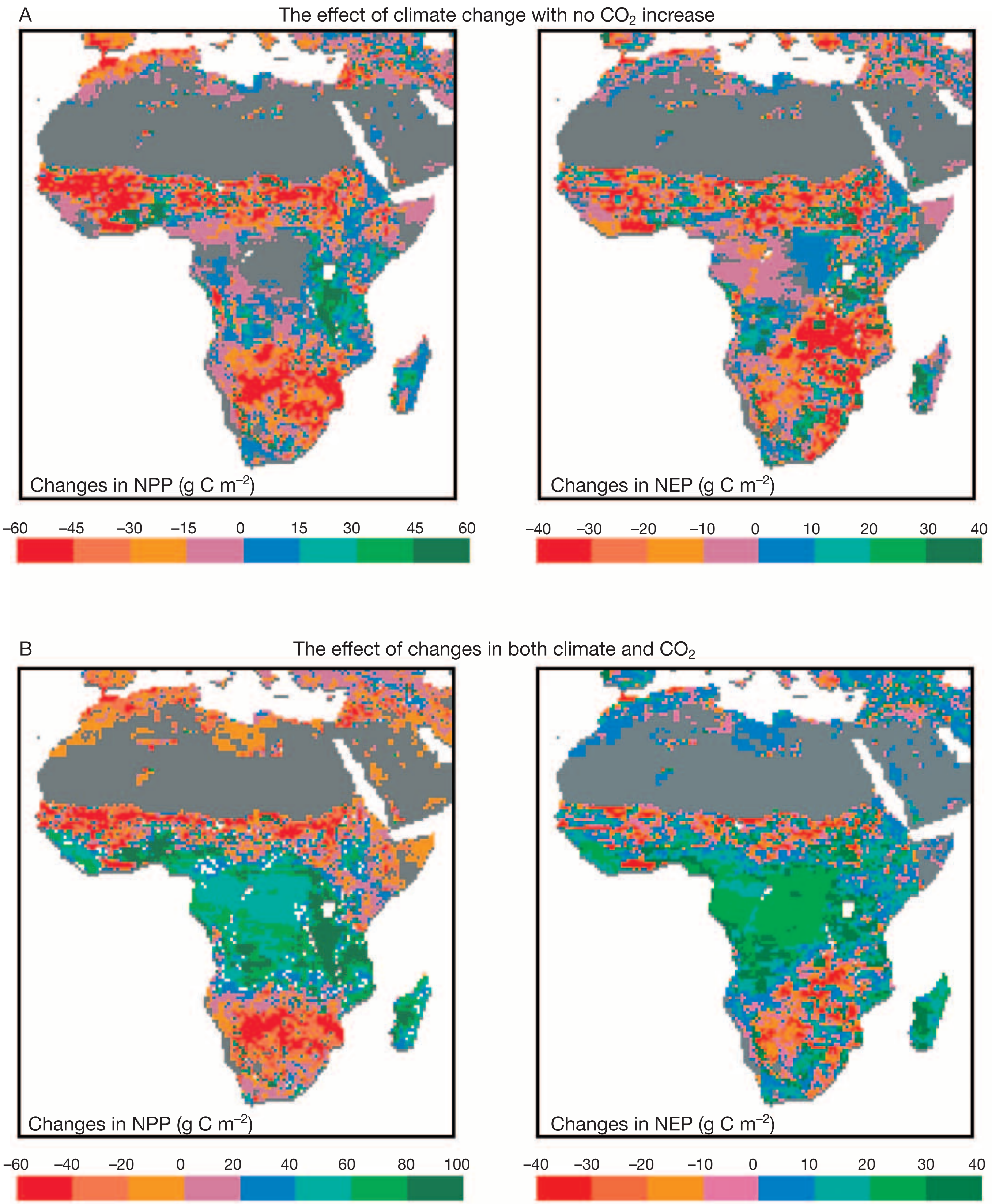

Fig. 3. Changes in NPP (difference between the mean in the period 1981–1995 and that in 1901–1920) and the mean NEP from 1981–1995, in response to (A) climate change alone and (B) changes in both climate and atmospheric CO_2

mostly positive, and the mean rate of carbon sequestration in this period was 0.29 Gt C yr^{-1}. The total carbon stocks increasd by 14.3 Gt C from 1901 to 1995, of which 76% was in vegetation and 24% was in soils. The strong increases in NPP and vegetation carbon stocks in central Africa were related to the high vegetation density that took full advantage of the CO_2 fertilization effect and the large area of forests that have high carbon-holding capacity. Although warming enhances soil organic carbon decomposition, the increases in litter production resulting from the carbon accumulation in vegetation leads to increases in soil carbon stocks. In northern Africa, the carbon stock in vegetation is barely changing, but soil organic carbon is still decreasing because of the enhanced decomposition by warming (Table 2). Therefore, northern Africa released 6.4 Gt C in the period from 1901 to 1995. In southern Africa, NPP reached its maximum in the 1970s and then decreased with declining precipitation, but the NPP in the 1990s was still higher than early in the century (Table 2). From 1981 to 1995, the mean NEP in southern Africa was 0.08 Gt C yr^{-1}, and the carbon stocks increasd by 6.7 Gt C in vegetation and 0.7 Gt C in soil in the period 1901–1995.

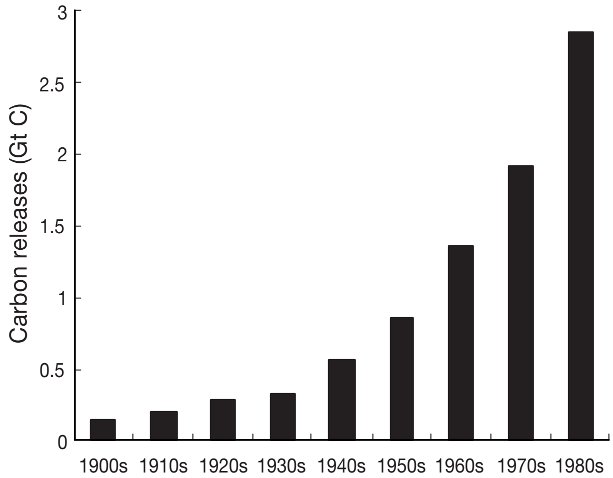

Fig. 4. Carbon releases in Africa arising from land-use changes. The estimate is based on the studies of FAO/UNEP (1981), FAO (1993), Houghton (1993), and Mayaux et al. (1998)

4. CONCLUSION AND DISCUSSION

African ecosystems play an important role in the global carbon cycle by accounting for about one fifth of the global NPP and vegetation carbon stocks. Changes in climatic factors reduce NPP and soil carbon stocks, but atmospheric CO_2 increases enhance NPP and cause carbon accumulation in vegetation. The combined effect of the changes in climate and atmospheric CO_2 caused a total carbon sequestration of 15.5 Gt C from 1901 to 1995, and the sequestration occurs mainly in central Africa. However, atmospheric measurements have not shown substantial terrestrial carbon sinks in the tropics (Ciais et al. 1995, Keeling et al. 1996). This inconsistency may arise from the carbon release caused by human activities, which may conceal the carbon uptake caused by the changes in climate and atmospheric CO_2. According to the data from FAO/UNEP (1981), FAO (1993) and Houghton (1993), carbon release from Africa due to land-use changes was 8.5 Gt C from 1901 to 1990 (Fig. 4). A recent study even suggested that land-use changes in Africa caused a carbon release of 6.6 Gt in the 1980s alone (Gaston et al. 1998). If the effects of land-use changes are taken into account, African ecosystems may have not taken up much carbon and are probably a net carbon source in the last decade because of the high rate of deforestation.

Table 2. Net primary production (NPP), net ecosystem production (NEP), and changes in vegetation carbon (VGC) and soil organic carbon (SOC), in response to changes in both climate and atmospheric CO_2

	Northern Africa (>10° N) (Gt C yr^{-1})				Central Africa (10° N–10° S) (Gt C yr^{-1})				Southern Africa (>10° S) (Gt C yr^{-1})			
	NPP	NEP	VGC	SOC	NPP	NEP	VGC	SOC	NPP	NEP	VGC	SOC
1900s	2.26	−0.19	0.01	−0.20	6.37	0.06	0.06	0.00	2.87	0.05	0.06	−0.01
1910s	2.24	−0.13	0.01	−0.14	6.31	0.00	0.02	−0.02	2.89	0.05	0.06	−0.01
1920s	2.41	−0.06	0.02	−0.08	6.43	0.09	0.10	−0.01	2.86	0.00	0.05	−0.05
1930s	2.43	−0.09	0.01	−0.10	6.46	0.09	0.07	0.02	2.88	0.07	0.07	0.00
1940s	2.43	0.00	0.01	−0.01	6.48	0.08	0.08	0.00	2.86	0.04	0.03	0.01
1950s	2.68	0.02	0.02	0.00	6.58	0.13	0.11	0.02	3.03	0.11	0.09	0.02
1960s	2.50	−0.08	0.01	−0.09	6.85	0.32	0.21	0.11	2.98	0.10	0.09	0.02
1970s	2.33	−0.06	0.01	−0.07	6.79	0.21	0.13	0.08	3.24	0.19	0.13	0.06
1980s	2.19	−0.08	0.00	−0.08	6.96	0.25	0.17	0.08	3.04	0.08	0.07	0.01
1990s	2.51	0.10	0.06	0.04	7.17	0.37	0.26	0.11	3.06	0.07	0.04	0.03

Other modeling studies and field measurements also indicate that undisturbed tropical ecosystems take up CO_2 from the atmosphere. A micrometeorological study suggesed that mature Amazonian forests are substantial carbon sinks (Grace et al. 1995), and a long-term monitoring of tropical forests in Southern America revealed that the carbon stock in vegetation is increasing by 71 ± 34 g C m^{-2} yr^{-1} (Phillips et al. 1998). A model simulation of Amazonian ecosystem carbon cycling indicated that the ecosystems took up CO_2 in all but 4 years from 1980 to 1994 (Tian et al. 1998). Nevertheless, whether changes in climate and atmospheric CO_2 cause a substantial CO_2 uptake depends largely on the extent at which the estimated CO_2 fertilization effect on photosynthesis could be realized. Like other ecosystem models, the CEVSA model describes the effects of atmospheric CO_2 on photosynthesis and stomatal conductance based on the currently available results from controlled experiments in which annual plants or tree seedlings are normally used to test the plant responses to elevated atmospheric CO_2; however natural vegetation and big trees may respond differently (Korner 1995, Bazzaz 1996). The CO_2 fertilization at the ecosystem level may be smaller than that at the individual plant level (Norby et al. 1992, Jenkinson et al. 1994, Bazzaz 1996). Early increases in plant photosynthesis and growth due to elevated atmospheric CO_2 may disappear as plant growth becomes limited by other environmental factors, such as nutrient supply (McGuire et al. 1995, Bazzaz 1996). Increasing atmospheric CO_2 also affects the carbon/nitrogen ratio of plant tissues, rates of organic decomposition, and nitrogen mineralization in the longterm (Amthor 1995, McGuire et al. 1995). Currently, the long-term effects of elevated atmospheric CO_2 at the ecosystem level are still poorly understood; the influences on ecosystem cycling warrant further research.

The results of this study show the responses of ecosystem functions (e.g. photosynthesis, respiration, and decomposition) to changes in climate and atmospheric CO_2. We do not consider the possible changes in vegetation composition and distribution, which also affect ecosystem functions and hence carbon exchanges (Melillo et al. 1996). Changes in climate and atmospheric CO_2 can cause variations in vegetation composition and distribution because they determine which plant species survive and prevail in a given region (Woodward 1987). For example, variations in precipitation can lead to shifts of the boundaries between tropical evergreen and deciduous forests and the tree-grass balance in savannas (Lauenroth et al. 1993). Warming favors C_4 plants, but elevated atmospheric CO_2 favors C_3 plants (Jackson et al. 1994). Increasing atmospheric CO_2 may cause expansion of tropical forests but shrinkage of savannas because high CO_2 concentration favors C_3 trees more than C_4 grasses (Jackson et al. 1994, Prentice & Sykes 1995). The interest in the effects of the ecosystem structure on carbon cycling has lead to efforts to develop global dynamic vegetation models (GDVM) that can describe the transient changes in vegetation composition and distribution (Foley et al. 1996, Friend et al. 1997). In addition, human activities also have modified the ecosystem distribution and composition in Africa: over 40 % of original forests and woodlands have been transformed, and arable lands and permanent pasture occupy about 30 % of the continent (Houghton 1994). Degraded forests, pastures, and crops are quite different from natural vegetation in the exchanges of energy, water, and carbon with the atmosphere (Cole et al. 1996, Xue 1997, Bonan 1998). Therefore, more accurate quantification of African ecosystem carbon cycling requires that the effects of ecosystem structural changes arising from both natural and anthropogenic disturbance be taken into account.

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