Recent patterns of terrestrial net primary production in Africa influenced by multiple environmental changes

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Abstract. Terrestrial net primary production (NPP) is of fundamental importance to food security and ecosystem sustainability. However, little is known about how terrestrial NPP in African ecosystems has responded to recent changes in climate and other environmental factors. Here, we used an integrated ecosystem model (the dynamic land ecosystem model; DLEM) to simulate the dynamic variations in terrestrial NPP of African ecosystems driven by climate and other environmental factors during 1980–2009. We estimate a terrestrial NPP of 10.22 (minimum–maximum range of 8.9–11.3) Pg C/yr during the study period. Our results show that precipitation variability had a significant effect on terrestrial NPP, explaining 74% of interannual variations in NPP. Over the 30-yr period, African ecosystems experienced an increase in NPP of 0.03 Pg C/yr, resulting from the combined effects of climate variability, elevated atmospheric CO2 concentration, and nitrogen deposition. Our further analyses show that there is a difference in NPP of 1.6 Pg C/yr between wet and dry years, indicating that interannual climatic variations play an important role in determining the magnitude of terrestrial NPP. Central Africa, dominated by tropical forests, was the most productive region and accounted for 50% of the carbon sequestered as NPP in Africa. Our results indicate that warmer and wetter climatic conditions, together with elevated atmospheric CO2 concentration and nitrogen deposition, have resulted in a significant increase in African terrestrial NPP during 1980–2009, with the largest contribution from tropical forests.

Key words: Africa; climate change; dynamic land ecosystem model; elevated CO2 concentration; net primary production; terrestrial ecosystems.

Introduction

Net primary production (NPP) represents the amount of atmospheric carbon gained by vegetation during photosynthesis after losses through plant respiration (Mellilo et al. 1993). It represents the net carbon that is partly available for consumption as food, fuel, and feed. Terrestrial NPP is also an important component of the global carbon cycle and a driver of the most essential ecosystem services for mankind (Vitousek et al. 1986, Costanza et al. 1998). Research into terrestrial NPP has attracted much attention among the scientific community because it is an indicator of incoming energy to the biosphere and a measure of net carbon dioxide (CO2) assimilation, providing a basis to assess the status of a wide range of ecological processes (Pan et al. 2014a).

Africa is a continent increasingly recognized for its role in the global carbon cycle and has been identified as one of the regions most vulnerable to climate change and climate variability (Ciais et al. 2009, Müller et al. 2011, IPCC 2014). Understanding the response of NPP to environmental changes in African ecosystems is particularly important because Africa is well known for its widespread poverty, slow economic growth, and agricultural systems, which are particularly sensitive to frequent and persistent droughts (United Nations 2002, Cilliers 2009). Over the past decades, Africa has experienced a remarkable increase in population, with the current population five times its size in 1950 (UNICEF 2014). More than 40% of the population lives in arid and semiarid regions (Ciais et al. 2011), where insufficient rainfall limits agricultural and plant productions, resulting in an increased pressure on ecosystem...
services. Although Africa represents 20% of the global land mass, with substantial contribution to the global carbon cycle (Williams et al. 2007), our knowledge about the response of NPP to multiple environmental factors in Africa remains remarkably limited. In addition, tropical land clearing from deforestation (DeFries et al. 2002, Houghton 2003) and conversion of natural ecosystems to agriculture and cultivation practices (McGuire et al. 2001) have been increasingly recognized as important factors driving terrestrial primary production in previous studies; however, there is still limited understanding of how these factors, combined with changes in other environmental factors, have affected terrestrial NPP in Africa.

The impact of climate change in Africa is likely to be severe compared to other continents due to high rain-fed agricultural dependence and limited ability to mitigate and adapt to climate change (Müller et al. 2011). In recent decades, warming in Africa has been more pronounced and faster than the global average, and this trend is likely to continue in the future (Collier et al. 2008). Air temperatures have increased by more than 0.5°C during the previous 100 years over most of Africa (Funk et al. 2011, Nicholson et al. 2013, IPCC 2014). In particular, Anyah and Qiu (2012), analyzing climate data from the 11 Coupled Model Intercomparison Project version 3 (CMIP3), found a significant increase in temperature since the early 1980s in the equatorial and southern regions of eastern Africa, indicating that there has been dramatic climate change in some parts of Africa during recent decades. On the other hand, precipitation shows large spatial variations, with increases in eastern Africa, as well as parts of central Africa (Collier et al. 2008), and decreases in others, such as the northern region of North Africa and the Sahel (Barkhordarian et al. 2013, Biasutti 2013). Also, many of the semiarid regions in Africa are vulnerable to periodic droughts, resulting in strong biophysical feedback to the climate systems (Bonan 2008) and subsequent declines in terrestrial NPP (Zhao and Running 2010). In addition to climate change and variability, atmospheric CO₂ concentration has increased substantially from the preindustrial level of 280 ppm to 380 ppm by 2005 (IPCC 2007). Such changes in climate and rising atmospheric CO₂ have profound influences on the magnitude and spatiotemporal patterns of terrestrial NPP in Africa.

Land-use changes, such as cropland expansion and deforestation, also play a profound role in determining the variabilty of terrestrial NPP in the African continent. For example, land-use change contributed to 25–35% of the total tropical land clearing caused by deforestation in the last decades (DeFries et al. 2002, Houghton 2003). It has been suggested that conversion of natural ecosystems to agricultural land and cultivation practices, combined with changes in surface air temperatures, may alter natural sources of ozone gases, resulting in higher tropospheric ozone levels (Zeng et al. 2008), which could subsequently affect vegetation dynamics and terrestrial NPP in Africa. In addition, nitrogen deposition has also been widely recognized as a major factor contributing to plant diversity (Bobbink et al. 2010), which could ultimately lead to changes in NPP. Although land-use practices, such as pastoralism, agriculture, and domestic wood harvest (Houghton 2003), and changes in environmental factors, such as nitrogen deposition (Bobbink et al. 2010) and tropospheric ozone (Zeng et al. 2008), are widely recognized as factors driving changes in African NPP, they are rarely considered in the regional carbon balance assessment. Therefore, quantifying the response of terrestrial NPP to multiple environmental factors in Africa is imperative and could provide a deeper insight into the processes and underlying mechanisms that regulate ecosystem services critical for human well-being (Melillo 2015).

Ground-based monitoring and measurements of terrestrial NPP in Africa are scarce and incomplete. Some in situ measurements, such as biomass inventories in a few countries (FAO 2007), ecosystem-scale measurements for savannas and forests (Abbadie et al. 2006, Liu et al. 2014), and biomass measurements based on the international geosphere biosphere program (IGBP; Koch et al. 1995), are available in Africa. In addition, in situ measurements of carbon fluxes through the use of eddy covariance techniques are becoming available across a few sites in Africa. Although these measurements provide relatively precise and accurate estimates at the plot, stand, or biome level, they are incomplete over broader temporal and spatial scales, due to complexity of upscaling plot-, stand-, and biome-level measurements to regional scales. Therefore, satellite observation and ecosystem modeling form an important basis for understanding and quantifying NPP and its response to environmental changes in continental Africa.

In this study, we use a process-based ecosystem model, the dynamic land ecosystem model (DLEM; Tian et al. 2010a) to simulate changes in the magnitude and spatiotemporal patterns of terrestrial NPP as well as their response to multiple environmental factors in the African continent during 1980–2009. The multiple environmental factors we considered include climate change, increasing atmospheric CO₂ concentration, nitrogen deposition, tropospheric ozone, land-cover and land-use change (LCLUC), and land management practices (e.g., nitrogen fertilizer use and irrigation). The major objectives of this study are (1) to estimate the magnitude and temporal and spatial patterns of terrestrial NPP in Africa, (2) to better understand mechanisms controlling spatial and temporal patterns of terrestrial NPP, (3) to assess the biome NPP response to changes in multiple environmental factors, and (4) to identify uncertainties and knowledge gaps associated with NPP estimation in Africa.
Model and Data

Model description

The DLEM 2.0 model is a highly integrated, process-based terrestrial ecosystem model that couples biophysical characteristics, plant physiological processes, and biogeochemical cycles to make daily, spatially explicit estimates of carbon, nitrogen, and water fluxes and pool sizes in terrestrial ecosystems from site to regional and global scales. The DLEM model has been widely applied in many regions worldwide, such as North America, the United States, tropical Asia, China, and India. A detailed model description can be found in our previous publications (Tian et al. 2010a, b, 2011, 2015, Pan et al. 2015a, b). It is capable of simulating the structural and functional dynamics of land ecosystems as influenced by multiple environmental factors, such as climate, atmospheric compositions (CO₂, nitrogen deposition, and tropospheric ozone), LCULC, and land management practices (harvest, rotation, fertilization, etc.). The NPP is calculated as the difference between gross primary productivity (GPP) and autotrophic respiration. The DLEM 2.0 is an updated version of the DLEM model and is characterized by the improved representation of ecosystem structure and processes, such as cohort structure, multiple soil layer processes, coupled carbon, water, and nitrogen cycles, multiple greenhouse (GHG) emissions, and dynamic linkages between terrestrial and riverine ecosystems. This model has been extensively evaluated against various field data covering forest, grassland, and cropland from the Chinese Ecological Research Network, the U.S. Long Term Ecological Research (LTER) sites, the AmeriFlux network, and other field sites (Tian et al. 2010a, Pan et al. 2014c).

Before model simulation, we calibrated the DLEM to get fitting parameter values for each plant functional type by minimizing the differences between the simulated and observed carbon, nitrogen, and water fluxes. In this study, model calibration is particularly done with reference to observed data from various biomes across the globe. After model calibration, we evaluated model performance by comparing the simulated carbon stocks and fluxes with observations across a range of biomes. In general, DLEM-simulated GPP is closer to eddy covariance observations for hardwood forests, coniferous forests, and grasslands. Detailed information on how the DLEM simulates these processes is available in our published papers (Lu et al. 2012, Ren et al. 2012, Tian et al. 2012, Tao et al. 2013, Pan et al. 2014b, Yang et al. 2015).

Input data sets

During model simulation, the DLEM is driven by both transient (climate, atmospheric CO₂ concentration, nitrogen deposition, tropospheric ozone, LCULC, and land management practices) and static (elevation, slope, aspect, and soil properties, such as soil texture, bulk density, soil pH, etc.) data sets to simulate the response of NPP to climate and other environmental factors. All data were compiled at a spatial resolution of 0.5° × 0.5°. The contemporary vegetation map was derived from an integration of multiple land-cover and land-use maps, with 12 plant functional types in Africa (Fig. 1). To generate a contemporary vegetation map, we first identified constant fractional cover of land and water within each grid based on a global water mask derived from remote sensing (data from the Global Land Cover Facility, University of Maryland, Greenbelt, Maryland, USA). We assume that surface areas of rivers, lakes, streams, oceans, glaciers, and bare ground in each grid do not change over time. The lake and stream surface areas were estimated from the Shuttle Radar Topography Mission (SRTM) Water Body Data (SWBD) products (data from the NASA Jet Propulsion Laboratory, La Cañada Flintridge, California, USA). The fractional distributions of the glacier and bare ground were quantified with the GLC2000 (Global Land Cover 2000; data from the European Commission Joint Research Centre, Brussels, Belgium). Second, percentages of each natural plant functional type within each grid were calculated through merging a static satellite-based land-cover product (SYNMAP; Jung et al. 2006) with the time-varying land use harmonization (LUH) data from the fifth assessment report (AR5) of the Intergovernmental Panel on Climate Change (IPCC; Hurrт et al. 2011). We converted SYNMAP-LUH to DLEM land-cover classification (Liu and Tian 2010, Tian et al. 2011) through integrating with multiple data sources, such as a global potential vegetation map (Ramankutty and Foley 1999), a global C₄ percentage map (Still et al. 2003), and the Global Lakes and Wetlands Database (GLWD; Lehner and Döll 2004). The daily climate data (including average, maximum, minimum air temperature, precipitation, relative humidity, and shortwave radiation) were from the CRU-NCEP data set that combines the Climatic Research Unit (CRU) and National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalysis products and provides global gridded six-hour time-varying climatology products for the period of 1901–2009 (Figs. 2 and 3; CRU-NCEP data set available online).¹ When a land conversion occurs, such as crop and forest conversions, a new cohort is formed and disturbed land area within the grid cell is then proportionally subtracted from the undisturbed potential vegetation. Monthly CO₂ concentrations during 1901–2009 were derived from the Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MSTIMP; Wei et al. 2014). Nitrogen deposition data in Africa was obtained from global data sets as developed by Dentener et al. (2006). Three time-period data sets

¹ ftp://nacp.ornl.gov/synthesis/2009/frescati/model_driver/cru_ncep/analysis/readme.htm
(1860, 1993, 2050) from Dentener et al. (2006) were used to interpolate the annual nitrogen deposition data set during 1980–2009, assuming that the interannual variability of nitrogen deposition is consistent with that of NH₃ and NOₓ emission from 10 anthropogenic sources (Wei et al. 2014). Similarly, consumption of nitrogen fertilizers from 1961 to 2008 was derived from the country-level Food and Agriculture Organization of the United Nations (FAO) statistical database. For the African continent, Dentener et al. (2006) used nitrogen deposition rates from eight stations available through IDAF (International Global Atmospheric Chemistry [IGAC] Deposition of Biogeochemically Important Trace Species [DEBITS] AAFrica) to validate the atmospheric transport model. Since the simulated nitrogen deposition data were validated against a few observations, most of which came from west-central Africa, there are potential uncertainties associated with low station density and nitrogen exchange mechanisms at the land surface (Holland et al. 2005). Annual nitrogen fertilization rate was then calculated as the ratio of nitrogen fertilizer application amount to total cropland area in each country (Tian et al. 2011). The ozone data set from 1980 to 2009 was derived from a global historical AOT40

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**Fig. 1.** Contemporary distribution of dominant plant functional types in Africa used for driving the dynamic land ecosystem model (DLEM).
(ozone exposure index) data set based on Felzer et al. (2005). Other data sets, including river network, soil bulk density, soil texture, soil pH, and topographic layer, are consistent with our previous work (Tian et al. 2011, Pan et al. 2014b). Although there are limitations of using Dentener et al. (2006) and Felzer et al. (2005) data sets for carbon balance assessment in Africa, they are still the best data sets widely used at regional and global scales. The purpose of this study is not to evaluate data uncertainty but to investigate how terrestrial NPP has responded to changes in climate and other environmental factors.

Fig. 2. Anomalies in temperature and precipitation during 1980–2009 relative to the 30-yr mean (1980–2009). The mean is presented as a horizontal dashed line, with the magnitude of temperature and precipitation anomalies shown by distance from the mean.

Fig. 3. Spatial pattern of average annual precipitation and average annual temperature in Africa for the period 1980–2009.
Experimental design and implementation

To investigate NPP changes in Africa as influenced by multiple environmental factors, we performed an all-combined experiment driven by changes in climate, land-cover/land-use change (LCLUC; including land management practices), and atmospheric chemical components (including CO2, ozone, and nitrogen deposition) during 1980–2009. The model simulation follows three important stages: an equilibrium simulation stage, a 100-yr spin-up stage, and a transient simulation stage. The model simulation begins with an equilibrium run with long-term average climate data for the period 1901–1930. The initial point for sensitivity analysis is achieved when the net carbon exchange between the atmosphere and terrestrial ecosystem is less than 0.1 g C/m², the change in the soil water pool is less than 0.1 mm, and the difference in the soil mineral nitrogen content and nitrogen uptake is less than 0.1 g N/m² among consecutive years. The equilibrium run is followed by a 100-yr spin up using climate data and LCLUC distribution in 1900 to eliminate system fluctuations caused by simulation mode shift from equilibrium to transient mode. Finally, the 100-yr spin up is followed by a transient simulation, where the carbon and nitrogen stocks and fluxes were driven by changes in climate, atmospheric chemistry (nitrogen deposition, tropospheric ozone, and increasing atmospheric CO2 concentration), and land use and land cover. We started our simulation from 1901 to capture the legacy effects of land-use and land-cover change, climate, nitrogen deposition, tropospheric ozone, and atmospheric CO2, but this study focused on the terrestrial NPP in Africa during the period 1980–2009.

To quantify drought impacts on NPP, we identified 1999, 2006, and 2007 as the wet years and 1983, 1987, and 1992 as the dry years. We then used 1999 as the wettest year and 1983 as the driest year during the 30-yr period. In the wet years, most areas across Africa experienced precipitation increases, except parts of northern Africa, the south of southern Africa, and Indian Ocean islands. During the dry year, most areas in western Africa, central Africa, and southern Africa had significant increases (>100 mm) in precipitation. We then compared the changes in precipitation with the changes in NPP for the wet (1999) and dry (1983) years based on results from the climate-only effect analysis.

Model evaluation

In this study, we compared the DLEM-simulated terrestrial NPP in Africa with Moderate Resolution Imaging Spectroradiometer (MODIS) NPP to evaluate model performance during 2000–2009 (Fig. 4A, B). We first evaluated the spatial pattern of Africa NPP between MODIS and DLEM. Then, we carried out a grid-to-grid comparison of the DLEM-simulated NPP with MODIS product for all available grid cells in Africa. The spatial pattern of MODIS estimates and DLEM-simulated NPP are generally consistent with each other, with the highest NPP in central Africa dominated by tropical forests, which decline to the north and south toward increasingly arid and semiarid environmental conditions. We also found a good agreement between MODIS and DLEM-simulated NPP at the grid cell level (Fig. 4C). The fitted line between DLEM and MODIS estimates has a slope of 0.95 and R² of 0.68 (P < 0.001). We also performed a time-series analysis of DLEM-simulated NPP vs. MODIS NPP during 2000–2009 (Fig. 4D). Our evaluation indicates that the DLEM-simulated interannual variation in terrestrial NPP is similar to interannual variation in MODIS NPP product during 2000–2009 (R² = 0.62, P < 0.005). Additionally, we also carried out a grid-to-grid comparison of DLEM-simulated NPP with MODIS product for two dominant plant functional types (forests and shrublands). At the regional scale, DLEM-simulated NPP is closer to MODIS NPP product, with R² of 0.51 and 0.61 for forests and shrublands, respectively (Fig. 5).

Results

Changes in climate and other environmental factors in Africa during 1980–2009

Africa experienced an increase in both temperature and precipitation with substantial temporal and spatial variations during 1980–2009. Air temperature shows an overall increasing trend (temperature, 0.03°C/yr; P < 0.001). The highest temperature occurred in 2005 and 2009, which exceeded the 30-yr mean by 0.54°C and 0.59°C, respectively. Similarly, precipitation shows an increasing trend (precipitation, 1.95 mm/yr; P < 0.001). Precipitation in Africa shows substantial interannual variations, with the highest precipitation years (1999, 2006, and 2007) occurring in the latter 15 years. Across Africa, relatively higher precipitation occurred mainly in southwestern Africa, central Africa, and the Indian Ocean islands, while lower precipitation mainly occurred in northern Africa, particularly in the Sahara desert during the study period. Similarly, temperature changes show that most of northern Africa, western Africa, and the north of central Africa had higher annual temperatures (>28°C) compared to other regions. Compared to the 1980–2009 mean, spatial variations in temperature during the 2000s indicate that temperature
increased by 0.5–1°C across the African continent. Similarly, atmospheric CO2 concentration has increased remarkably from 339 ppm in 1980 to 387 ppm in 2009, with an overall increase of 48 ppm or 14%. In addition to climate factors, Africa has also experienced substantial changes in land cover and other environmental factors during 1980–2009 (Klein Goldewijk et al. 2011). Crop-land area has increased by 27% since 1980, while nitrogen deposition and nitrogen fertilization have increased by 67% and 57%, respectively in the study period.

**Magnitude and interannual variations of terrestrial NPP in Africa during 1980–2009**

The DLEM simulations show a terrestrial NPP of about 10.22 (minimum–maximum range of 8.9–11.3) Pg C/yr during 1980–2009 driven by multiple environmental factors including climate, atmospheric CO2 concentration, nitrogen deposition, tropospheric ozone, LCLUC, and nitrogen fertilizer use. The simulation results further indicate substantial interannual variations in terrestrial NPP, which positively correlate with changes in total precipitation ($R^2 = 0.74$, $P < 0.001$; Fig. 6). Temperature, in particular, shows a positive association with NPP in Africa; however, the effect was not
significant ($P = 0.36$). Increasing CO$_2$ concentration also had a significant positive effect on NPP, accounting for 29% of the variations in NPP ($P < 0.01$). Comparison of interannual variations in NPP with changes in environmental factors show that increasing nitrogen deposition had a significant positive association, accounting for 28% of the variations in NPP ($P < 0.01$).

The temporal changes in NPP show that combinations of climate variability, increasing atmospheric CO$_2$, nitrogen deposition, tropospheric ozone concentration, and LCLUC resulted in an overall increasing trend in terrestrial NPP. Africa experienced an increase in terrestrial NPP of 0.03 Pg C/yr, which is equivalent to a total increase of 0.9 Pg C over the 30-yr period. The DLEM-simulated NPP for each decade shows that the 1980s were a period of high interannual variations due to large climatic variability compared to the 1990s and the 2000s (Fig. 7). The drought events, due to below-average precipitation in 1983, 1984, and 1987, resulted in a low magnitude of NPP in the 1980s compared to the 1990s and the 2000s. The average NPP for the 1980s, the 1990s, and the 2000s were 9.97 Pg C/yr, 10.21 Pg C/yr, and 10.49 Pg C/yr, respectively.

Spatial variations of terrestrial NPP in Africa during 2000–2009

Our results show substantial variation in terrestrial NPP induced by climate and other environmental factors. Regions, such as northern and southern Africa, dominated by desert and shrubs were least productive, with an NPP of 0–200 g C·m$^{-2}$·yr$^{-1}$, while central Africa, dominated by forests, was the most productive region, with an NPP of $>900$ g C·m$^{-2}$·yr$^{-1}$ (Fig. 4A). Analysis of specific climatic factors across the region show that both precipitation and temperature had a positive influence on terrestrial NPP; however, the effect of temperature was insignificant ($P = 0.93$). Dry regions, such as southern Africa, were highly sensitive to changes in precipitation, explaining 88% of the variations in NPP. Northern Africa, however, was less sensitive to changes in precipitation because increasing temperature resulted in substantial NPP decline (10.6%), explaining 40% of the variation in NPP. In central Africa, however, both temperature and precipitation show a positive association with terrestrial NPP.

Across Africa, spatial patterns of NPP for each decade show that the 1980s were a period with relatively lower NPP, primarily due to drought (driven by reduced precipitation) inducing reduction in NPP in year 1983. The drought period of the 1980s was followed by an NPP recovery during the 1990s, when increased precipitation resulted in larger increases in NPP in most parts of the continent. In addition, above-average precipitation across all years during the 2000s resulted in the largest increase in NPP across Africa. The 2000s was a period where most of the African regions experienced the largest increase in NPP, about $>50$ g C·m$^{-2}$·yr$^{-1}$.

In a particular year, wet or dry climatic conditions resulted in substantial change in the magnitude and spatial variations in terrestrial NPP in Africa. Climate effects on NPP (Fig. 8B–D) indicated that the wet year of 1999 shows the highest increase in NPP of $>75$ g C/m$^2$ in central Africa. However, southern Africa experienced the largest reduction in NPP of $>100$ g C/m$^2$ during both wet and dry years as a result of decreasing precipitation in these regions. At the continental scale, our results of climate effect on NPP show a difference in NPP of 1.6 Pg C/yr between wet and dry years, indicating that climatic conditions play an important role in determining the magnitude of terrestrial NPP in Africa.
Variations in NPP at the biome level during 1980–2009

The DLEM estimates a biome NPP that generally increases from dry to moist biomes. Area-weighted mean biome NPP varied considerably among major biomes in Africa. Forests and wetlands were the most productive biomes, with a terrestrial NPP of 596.72 g C m⁻² yr⁻¹ and 726.13 g C m⁻² yr⁻¹, respectively (Table 1). In particular, tropical evergreen forests and woody wetlands had a mean annual NPP of 1203.7 and 1158.3 g C m⁻², respectively, that correlated with changes in annual precipitation explaining 75% and 56% of the variations, respectively. Desert and deciduous shrubs were the least productive biomes, where interannual variation in NPP was primarily controlled by water availability. The area-weighted mean biome NPP of desert and deciduous shrubs was 7.5 and 156.0 g C m⁻², where annual precipitation was only 69 and 354 mm, respectively. Precipitation explained the largest variations in mean annual NPP of desert (57%) and deciduous shrubs (25%). Similarly, cropland had a mean annual NPP of 323.5 g C m⁻², where precipitation explained 44% of the variation while an increase in temperature had a negative association. Interestingly, although area-weighted mean biome NPP shows that deciduous shrubs was among the least productive biomes, the relative percentage change suggests that

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**Fig. 6.** Effect of interannual variation in precipitation and temperature on African NPP during 1980–2009. (A) Scatterplot of precipitation vs. NPP and (B) temperature vs. NPP, and (C) time series of NPP anomaly during 1980–2009; mean NPP is presented as a horizontal line, with the magnitude of the anomalies (points) shown by distance from the mean.
deciduous shrubs experienced the largest percentage of increase (14.4%) in NPP during the 2000s compared to the 1980s. Similarly, C₃ grass, C₄ grass, and desert experienced an increase in NPP of 11.7%, 11.6%, and 10.4%, respectively during the 2000s, indicating that biomes with relatively lower precipitation had the potential to increase NPP by increasing water use efficiency.

Our results further show that spatial variation in NPP differs among the 14 major biomes. Dry biomes such as desert, grasslands, and shrublands had the largest spatial variation in NPP, with a coefficient of variation of 9–14%. In contrast, tropical evergreen forest had the smallest spatial variation, with a coefficient of variation of 3.9%. Our results suggest that spatial variation of NPP within a biome is driven by spatial variations in climate. Spatial variations in temperature and precipitation within and between biomes were large, which resulted in the differences in coefficient of variation in NPP among biomes. The coefficient of variation in precipitation was large in desert, shrubs, and grasslands, but small in tropical forest.

Discussion

Comparison of DLEM-simulated terrestrial NPP with other estimates in Africa

Africa is a continent highly vulnerable to climate change (Tadesse 2010, IPCC 2014); however, few studies have been done to estimate the magnitude and interannual variations of carbon dynamics (Cao et al. 2001, Ciais et al. 2009, Weber et al. 2009). Using the DLEM, we estimated a terrestrial NPP of ~10.22 Pg C/yr during 1980–2009, which is comparable with other regional studies based on remote sensing and process-based ecosystem models. Remote sensing product (MODIS 17) estimates a terrestrial NPP of 11.42 Pg C/yr as compared to our estimate of 10.49 Pg C/yr during 2000–2009. The difference in NPP estimates based on MODIS and the DLEM is likely due to an inherent difference in the approach of NPP estimation. The MODIS-estimated NPP is based on the light-use efficiency approach, which is a function of the fraction of incident photosynthetically active solar radiation (PAR) absorbed by terrestrial surface (Running et al. 2004). MODIS NPP is particularly sensitive to radiation conversion efficiency (ε), a parameter that determines the fraction of solar radiation that can be used by plants to make carbon product. The radiation conversion efficiency is also a function of climatic variables, such as vapor pressure deficit and air temperature. While the use of meteorological data and fraction of solar radiation to estimate radiation use efficiency can provide reasonable estimates of NPP at global and continental scales, other factors such as nutrient availability, soil type, and soil water content are more important at local to regional scales, which are not fully expressed in the remote sensing algorithm (Pan et al. 2006). For example, Pan et al. (2006) found that MODIS overestimated NPP for coniferous forest and therefore developed the available soil water index for adjusting the MODIS NPP estimates, which resulted in remarkable improvements in NPP for coniferous forests. It is possible that in regions like Africa, where NPP is highly sensitive to changes in soil moisture (Weber et al. 2009), a MODIS algorithm based on meteorological data and PAR may not be sufficient to estimate the terrestrial NPP.

We further compared the DLEM-simulated NPP with several model-based estimates across Africa. Our NPP estimates of 10.22 Pg C/yr during 1980–2009 are comparable with published model estimates that range from 7 to 13 Pg C/yr (Cramer et al. 1999, McGuire et al. 2001, Valentini et al. 2013). In a recent study of the full greenhouse gas budget of Africa, Valentini et al. (2013) estimated a terrestrial NPP of 13.27 ± 3.25 Pg C/yr based on nine dynamic global vegetation models (DGVMs). The large standard deviation from the mean indicates that DGVMs vary substantially in realistically representing various ecosystem processes. For example, modeling tree–grass coexistence in savannas is still a major challenge for many DGVMs (Cramer et al. 1999, Scheiter and Higgins 2009), which vary across models, resulting in large differences in NPP estimates among DGVMs. In a model intercomparison study, Weber et al. (2009) estimated a terrestrial NPP of 9.16–17.28 Pg C/yr using four different models (ORCHIDEE, LPJ-DGVM, LPG-Guess, and JULES) across Africa. While LPJ-Guess-estimated and JULES-estimated NPP were closer to DLEM, LPJ-DGVM and ORCHIDEE overestimated terrestrial NPP by 7.06 and 5.16 Pg C/yr, respectively, compared to the DLEM-simulated NPP. This overestimation based on LPJ-DGVM and ORCHIDEE is likely because savannah ecosystems are not realistically represented in the model (Weber et al. 2009). Similarly, Williams et al. (2008) estimated an annual NPP of 16.6
Pg C/yr for Africa, which is much higher than the DLEM-simulated NPP and other published model estimates. This is primarily because Williams et al. (2008) changed the monthly climate data to match with the Tropical Rainfall Measuring Mission (TRMM) and CRU patterns. In addition, Williams et al. (2008) increased the normalized difference vegetation index (NDVI) to partially correct for aerosol contamination, resulting in a larger magnitude of NPP in Africa compared to other studies.

**Interannual variations in NPP during 1980–2009**

Our results indicate that interannual variations of NPP are mainly driven by changes in precipitation rather...
than temperature at the continental scale. The relationship between NPP and precipitation during 1980–2009 was positive and statistically significant, accounting for 74% of the variations in NPP. The annual pattern of NPP estimated by the DLEM shows a progressive increase in NPP from 9.97 Pg C/yr during the 1980s to 10.21 Pg C/yr and 10.49 Pg C/yr during the 1990s and 2000s, respectively. The decadal changes in NPP are consistent with extensive hydro-climatic fluctuations, which show progressively warmer and wetter climatic conditions resulting in larger variations of decadal NPP in Africa.

We further found that Africa’s terrestrial NPP has been increasing since the 1980s, as a result of multiple environmental changes. This trend is consistent with the GPP and net biome production (NBP) trend as simulated using an ORCHIDEE model (Ciais et al. 2009). The upward trend in NPP is a result of a combination of increasing precipitation, elevated atmospheric CO2 concentration, and nitrogen deposition. Our results indicate that Africa has experienced a significant increase in terrestrial NPP over the last 30 years at a rate of 0.03 Pg C/yr ($P < 0.05$). Interestingly, this increasing trend of 0.03 Pg C/yr is similar to the annual GPP trend based on Ciais et al. (2009) during 1901–2002. Ciais et al. (2009) reported that an increase in terrestrial GPP is primarily driven by elevated atmospheric CO2 concentration and recently increasing precipitation. Our result is also consistent with these findings, but in addition to elevated atmospheric CO2 concentration and increasing precipitation, nitrogen deposition had a significant positive influence on terrestrial NPP ($R^2 = 0.28$, $P = 0.01$).

### Spatial variations in terrestrial NPP during 1980–2009

The DLEM-simulated results indicate that annual NPP in Africa shows large spatial variations in the past three decades. The NPP was higher in central Africa and decreased to the north and south toward an increasingly arid and semiarid environment. The spatial patterns of NPP were closely related to those of climatic factors, particularly precipitation. The larger magnitude of NPP in central Africa was also related to the high vegetation density and larger area of tropical forests that have high carbon density (Malhi and Grace 2000, Lewis 2006).

However, in northern and southern Africa, the vegetation is predominantly grasses, shrubs, and croplands, which have low carbon-holding capacity compared to forests. Similarly, central Africa, which is dominated by tropical forests, was the most productive biome, which accounted for 50% of the total carbon sequestered as NPP resulting in an overall increase in terrestrial NPP by 0.013 Pg C/yr. Warmer and wetter conditions combined with elevated atmospheric CO2 concentration and nitrogen deposition might have increased NPP by alleviating climatic constraints due to increased precipitation, increasing carbon assimilation due to CO2 fertilization, and higher nitrogen uptake due to increased nitrogen deposition and mineralization. For northern Africa, however, temperature increase and precipitation decrease had resulted in an apparent decline in terrestrial NPP. While increasing air temperature has been previously thought to increase terrestrial NPP by alleviating climatic constraints to plant growth (Nemani et al. 2003), in a recent study, Pan et al. (2014) reported that NPP would start to decline after the global mean surface air temperature exceeded ~16.5°C. Soil moisture limitations and increased plant respiration due to warming may reduce carbon storage, while increasing precipitation and elevated CO2 concentration may alleviate soil moisture limitations and increase carbon assimilation (Melillo et al. 2002, Felzer et al. 2011).

### Drought-induced magnitude and spatial variation in terrestrial NPP

Climate drought due to changes in precipitation pattern has a substantial negative effect on terrestrial NPP (Tian et al. 2000, Zhao and Running 2010), resulting in large-scale vegetation dieback or mortality episodes (Bresears et al. 2005). Our study suggests that in a specific year, wet or dry climatic conditions may substantially alter terrestrial NPP. The difference in the amount of carbon sequestered as NPP between wet and dry years was 1.6 Pg C, indicating that climate-induced drought may lead to large reductions in terrestrial NPP. For example, Williams et al. (2008) reported that acute water stress was the major factor driving terrestrial photosynthetic carbon gains primarily associated with rainfall variability. Ciais et al. (2011) also found that, during an anomalously dry year (1983–1984), GPP decreased by

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### Table 1. Biome NPP response to climate and other environmental factors in Africa.

| Biome     | Precipitation (mm/yr) | Air temperature (°C) | Mean (SD) | Maximum | Minimum | CV (%) |
|-----------|-----------------------|----------------------|-----------|---------|---------|-------|
| Forests   | 999.87                | 22.33                | 596.72 (26.25) | 542.36  | 523.63  | 4.4   |
| Grasslands| 534.03                | 24.38                | 281.88 (25.70) | 331.57  | 220.37  | 9.1   |
| Shrublands| 561.86                | 23.76                | 259.61 (33.36) | 333.07  | 187.51  | 12.9  |
| Wetlands  | 1155.25               | 25.80                | 726.13 (54.28) | 891.97  | 592.31  | 7.5   |
| Croplands | 791.69                | 23.79                | 323.46 (11.38) | 341.53  | 287.33  | 3.52  |
| Desert    | 68.89                 | 24.71                | 7.54 (0.67)   | 8.84    | 5.86    | 8.82  |

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*Note: NPP (g C m^{-2} yr^{-1}).*
1.9 Pg C, primarily due to below-average precipitation. In a global study of terrestrial NPP response to climate change, Mohamed et al. (2004) found large NPP declines in tropical regions due to greater impacts of drought, and higher sensitivity and weaker physiological adjustment to changes in precipitation pattern. Therefore, projected drought stress in the future might result in NPP decline in Africa, although our results for the 30-year period suggest an increase in NPP.

Variation in biome NPP during 2000–2009

Our results indicate that the dominant driving climate factor varies among various biomes. Precipitation was found to be highly correlated with grassland ($R^2 = 0.86$) but weakly correlated with shrubs ($R^2 = 0.42$) and forest ($R^2 = 0.57$). This result may be related to the fact that different growth environments may contribute to different response of NPP to temperature and precipitation. For example, grasslands are located in more arid environments, where plant growth is often limited by soil moisture (Knapp and Smith 2001). In addition, our results indicate that grasslands and shrublands, which are located in arid and semiarid environments, have the largest coefficient of variation in NPP. This indicates that even a slight change in precipitation could substantially alter the magnitude of terrestrial NPP in a particular year. In contrast, forests are located in areas with abundant precipitation, resulting in low coefficient of variation in interannual NPP during the study period.

Warmer temperature and higher precipitation may result in greater plant productivity of forested ecosystems compared to desert, grasslands, and shrublands. Our study suggests that tropical broadleaf evergreen forests are the most productive biomes in Africa, while desert, grasslands, and shrublands are the least productive ones. Compared to the 1980s, interestingly, we found that the largest percentage of increase in NPP during the 2000s occurred in deciduous shrubs (14.4%), grasslands (11.6–11.7%), and desert (10.4%), possibly due to increased water use efficiency. Cropland NPP, in particular, shows varying responses to changes in temperature and precipitation; temperature tends to have a negative relation and precipitation tends to have a positive relation with NPP.

Uncertainty and Future Needs

There are several uncertainties associated with model assumptions, model structure, and input data sets. We did not consider the possible changes in vegetation composition and distribution during the study period, which might have an effect on terrestrial NPP in Africa. Changes in climate and elevated CO$_2$ concentration could result in variations in vegetation composition and distribution because these abiotic changes may determine which plant species can survive in a particular region (Woodward et al. 1998). Furthermore, fire is a major disturbance in the African savannah that releases substantial amounts of carbon annually; however, the magnitudes of carbon release from fire are still highly uncertain (Williams et al. 2007). In addition, biome-specific parameters were well-calibrated based on field observations, but some processes, such as response of carbon assimilation and stomatal conductance to increasing temperature and elevated CO$_2$ may change due to plant acclimation (Hui et al. 2003). Therefore, accurate quantification of the response of terrestrial NPP to climate and multiple environmental changes needs to fully consider natural disturbances such as fire and human activities such as domestic herbivory and timber harvest in future work. In addition, model representations of ecosystem processes associated with human activities require further improvement to accurately quantify terrestrial NPP in Africa.

Conclusions

This study estimates a terrestrial NPP of $\sim 10.22$ Pg C/yr during 1980–2009, resulting from the combined effects of climate change, elevated atmospheric CO$_2$ concentration, nitrogen deposition, tropospheric ozone, LCLUC, nitrogen fertilization, and irrigation. Our time-series analyses further show that African NPP had an overall increasing trend of 0.03 Pg C/yr during the study period. The overall increasing trend was primarily driven by a wetter and warmer climate, elevated CO$_2$ concentration, and nitrogen deposition. Our simulated results suggest that although Africa represents only 20% of the global landmass, it has a substantial impact on the global terrestrial primary production largely due to prevalent climatic conditions, elevated CO$_2$, and nitrogen deposition. Our results underscore the importance of dynamic responses of vegetation as influenced by multiple environmental changes in quantifying the magnitude and spatiotemporal variations of terrestrial NPP across Africa.

Across different biomes, forest was the most productive, with an average annual NPP of 596.72 g C/m$^2$, while arid and semiarid biomes such as desert and deciduous shrub were the least productive. While forest was the most productive biome, the largest percentage of increase in NPP occurred in deciduous shrubs (14.4%), grasslands (11.6–11.7%), and desert (10.4%), possibly due to increased water use efficiency. Future research needs to better understand mechanisms controlling biome sensitivity to multiple environmental changes.

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