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Global pattern of NPP to GPP ratio derived from MODIS data: effects of ecosystem type, geographical location and climate

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ABSTRACT

Aim To examine the global pattern of the net primary production (NPP)/gross primary production (GPP) ratio of the Earth's land area along geographical and climatic gradients.

Location The global planetary ecosystem.

Methods The 4-year average annual NPP/GPP ratio of the Earth's land area was calculated using 2000–03 Moderate Resolution Imaging Spectroradiometer (MODIS) data. The global pattern of the NPP/GPP ratio was investigated by comparing it among each typical terrestrial ecosystem and plotting it along a geographical and climatic gradient, including latitude, altitude, temperature and precipitation.

Results The global terrestrial ecosystem had an average NPP/GPP ratio value of 0.52 with minor variation from 2000 to 2003. However, the NPP/GPP ratio showed considerable spatial variation associated with ecosystem type, geographical location and climate. Densely vegetated ecosystems had a lower NPP/GPP ratio than sparsely vegetated ecosystems. Forest ecosystems had a lower NPP/GPP ratio than shrub and herbaceous ecosystems. Geographically, the NPP/GPP ratio increased with altitude. In the Southern Hemisphere, the NPP/GPP ratio decreased along latitude from 30° to 10° and it exhibited high fluctuation in the Northern Hemisphere. Climatologically, the NPP/GPP ratio exhibited a decreasing trend along enhanced precipitation when it was less than 2300 mm year⁻¹ and a static trend when the annual precipitation was over 2300 mm. The NPP/GPP ratio showed a decreasing trend along temperature when it was between –20 °C and 10 °C, and showed an increasing trend along rising temperature when it was between –10 °C and 20 °C. Within each ecosystem, the NPP/GPP ratio revealed a similar trend to the global trend along temperature and precipitation.

Conclusions The NPP/GPP ratio exhibited a pattern depending on the main climatic characteristics such as temperature and precipitation and geographical factors such as latitude and altitude. The findings of this research challenge the widely held assumption that the NPP/GPP ratio is consistent regardless of ecosystem type.

Keywords

Altitude, ecosystem, latitude, MODIS, NPP/GPP ratio, precipitation, temperature.

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INTRODUCTION

Gross primary production (GPP) represents the capacity of the plants in an ecosystem to capture energy and carbon. Net primary production (NPP), the reduction of GPP after autotrophic respiration, is the net carbon stored as new plant material in an ecosystem which supplies humans with various

foods, fuels, fibres and construction materials (Chapin *et al.*, 2002). As fundamental indicators of ecosystem health and productivity, GPP and NPP have been drawing mounting attention from academics and governmental agencies (IPCC, 2001).

Among GPP, NPP and respiration, respiration is the most complex to measure because it involves various components

such as growth respiration and maintenance respiration, or above- and below-ground respiration (Waring *et al.*, 1998). Though the technique of measuring growth respiration and above-ground respiration has been much improved recently, the challenge of quantifying maintenance respiration and below-ground respiration, especially at regional and global scales, is still formidable. In terms of calculation of GPP and NPP, GPP can usually be well estimated from simulation models such as FOREST-BGC (Running & Gower, 1991) and MBL/CSA (Williams *et al.*, 1997). However, some research has suggested that estimates of NPP for ecosystems are direct and robust in the field since NPP can be equated to the annual carbon increment in wood and foliage litter (DeLucia *et al.*, 2005), while GPP estimation involves more complexity (Kerckhoff *et al.*, 2005). Regardless of the difficulties involved in calculating NPP or GPP, all researchers can benefit from calculating NPP directly from GPP or vice versa (Waring *et al.*, 1998; DeLucia *et al.*, 2007).

A method that utilizes the NPP/GPP ratio to infer NPP from GPP has significant implications for environmental and global change research (DeLucia *et al.*, 2007) and would be helpful in determining whether the terrestrial ecosystem is a carbon source or sink (Lindroth *et al.*, 1998). To make progress, the way in which the NPP/GPP ratio responds to exterior determinants, including climate, geographical location and topography needs to be assessed. These controls on the NPP/GPP ratio have broad intercorrelations with one another due to their interactions. Understanding such controls on the NPP/GPP ratio may allow for a more accurate prediction of the changing behaviour of carbon sinks under the influence of both anthropogenic and natural climate changes. Integrating the key processes regulating material and energy flows across spatial and temporal scales is an integral part of understanding ecosystem responses to global change (Mooney, 1991).

Several researchers have found that the NPP/GPP ratio is relatively stable and independent of ecosystem type (Gifford, 1994, 1995; Ryan *et al.*, 1994; Landsberg & Gower, 1997; Landsberg & Waring, 1997; Dewar *et al.*, 1998). In addition, the NPP/GPP ratio was found to be constant across a range of CO₂ levels and temperatures for herbaceous and woody plants (Gifford, 1994, 1995; Tjoelker *et al.*, 1999; Chen *et al.*, 2000). Waring *et al.* (1998) suggested that a universal value of 0.47 is appropriate for most forests based on results drawn from field data collected from 12 forest sites globally. Many models, including CASA (Potter *et al.*, 1993), have assumed a fixed value for the NPP/GPP ratio in quantifying plant respiration.

However, the assumption that the NPP/GPP ratio is independent of ecosystem type has been tested only in a limited way and it is doubtful that this principle is globally applicable (Chapin *et al.*, 2002; Xiao *et al.*, 2003; DeLucia *et al.*, 2007). DeLucia *et al.* (2007) conducted a metadata analysis and found that the NPP/GPP ratio ranged from 0.23 to 0.83 for different forest types. They suggested that it may be inappropriate to assume that respiration is a constant fraction of GPP. Xiao *et al.* (2003) found that the NPP/GPP ratio of a coniferous forest is only 0.32, much lower than that found in other studies. Chapin *et al.* (2002)

raised the concern that unstable maintenance respiration may add to the complexity of productivity conversion efficiency, and the paucity of effort addressing this efficiency in detail may be too coarse to generate the conclusion of a constant NPP/GPP ratio across different ecosystem types.

NPP and GPP have been shown to have a strong pattern along environmental gradients. Water balance has been shown to be a strong driver of the pattern of GPP in Europe (Beer *et al.*, 2007). In warmer and relatively water-limited southern European sites, water availability is a significant factor limiting GPP, while mean annual air temperature can explain more variation in GPP in the cold northern European sites (Reichstein *et al.*, 2007). The EURO-FLUX study indicated that annual ecosystem respiration increased with latitude in northern Europe, while GPP was constant along the rising latitudes (Valentini *et al.*, 2000).

All of the above research findings were obtained from discontinuous monitoring of individual plants or small plots of vegetation in a greenhouse or at a landscape scale, which can only provide a point value, often in a short time-scale. Such patchy data are not well suited to scaling up to a regional or global level (Mooney, 1991) and a long time-scale (Luo & Reynolds, 1999). An assessment of global patterns in the NPP/GPP ratio can enhance knowledge about features of the NPP/GPP ratio and benefit global change research.

Remote sensing has been used to monitor GPP and NPP dynamics at the regional and global scale (Nemani *et al.*, 2003; Zhao *et al.*, 2006). The Moderate Resolution Imaging Spectroradiometer (MODIS) is one of the most reliable data sources at the global scale. MODIS data have been available since 2000, but these products have only recently been validated in terms of GPP and NPP. The MODIS dataset provides the first operational, near real-time calculation of global GPP and NPP at a 250-m spatial resolution with daily coverage (Zhao *et al.*, 2005). The resulting MODIS GPP and NPP product has been validated as being able to capture spatial and temporal GPP and NPP patterns across various biomes and climate regimes, and it is consistent with the ground flux tower-based GPP and field-observed NPP estimation (Zhao *et al.*, 2005; Heinsch *et al.*, 2006). Direct comparison with site measurement has also confirmed the accuracy of the MODIS GPP ($r = 0.859$) (Heinsch *et al.*, 2006). The availability of GPP and NPP calculated from the MODIS data provides a unique opportunity for examining the spatial patterns of the global NPP/GPP ratio and its relationships with climate. Specifically, we used 4-year averaged MODIS NPP and GPP data in the current study to explore the spatial pattern of the NPP/GPP ratio and its relationship with precipitation, temperature, altitude and latitude.

The objectives of the current study were to: (1) map the global NPP/GPP ratio pattern; (2) compare the NPP/GPP ratio among different terrestrial ecosystems; and (3) examine trends in NPP/GPP ratio along climatic gradients including temperature and precipitation and along geographical factors including latitude and altitude. Such findings should improve knowledge about changes in global primary productivity under rapid land-use change and global warming.

METHODS

GPP and NPP data

The MODIS GPP was calculated as $GPP = \epsilon \times FPAR \times PAR$, where ϵ is the radiation use conversion efficiency of the vegetation as determined by biome type, temperature and vapour pressure deficit (VPD) limitation inferred from a biome properties look-up table; PAR (photosynthetically active radiation) was specifically the PAR attendant on the canopy and FPAR was the fraction of incident PAR that was absorbed by the canopy. The FPAR and ϵ_{\max} were determined using remote sensing MODIS. PAR was determined from meteorological data. The meteorological data used in calculating GPP and deriving VPD for the following NPP calculations were from the NASA's Data Assimilation Office (DAO). The DAO has a resolution of $1.00^\circ \times 1.25^\circ$ (DAO, 2002) and a daily interval. The coarse-resolution DAO data were interpolated to 1-km resolution (Zhao *et al.*, 2005). The interpolated fine-scale meteorological data were proved to remove DAO footprints even in regions with abrupt climatic gradients. The daily meteorological data used in NPP and GPP calculations ensured the accuracy of NPP and GPP products. NPP was calculated as

$$NPP = \sum_{i=1}^{365} PsnNet - (R_{mo} + R_g)$$

where $PsnNet = GPP - R_{ml} - R_{mr}$; R_{mo} is the maintenance respiration by all other living parts except leaves and fine roots, and R_g is the growth respiration; R_{ml} and R_{mr} are maintenance respiration by leaves and fine roots, respectively. The growth and maintenance respirations were determined by remotely sensed leaf and root mass and their maintenance respiration rate was based on biological properties for each biome (Heinsch *et al.*, 2003).

MODIS17A3 GPP and NPP data are formatted as a HDF EOS (Hierarchical Data Format – Earth Observing System) tile and have a resolution of 1 km (Running *et al.*, 2004). Each tile is 1200×1200 km (Zhao *et al.*, 2005). Because MODIS data after 2004 used a completely different version of meteorological data than previous data, they are not comparable with data for the other 4 years and were excluded from this study. For bare areas such as the Sahara desert in North Africa and desert in central-east Asia and western China, there are no calculated GPP data and they were ruled out from the analysis.

Annual MODIS17A3 (version 005) GPP and NPP data for 4 years (2000–03) in sinusoidal projection were downloaded tile by tile from the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana (<http://hdfeos.net/>). Each tile was converted into an image format using the HDF-EOS to GeoTIFF (HEG) tool developed by the Earth Observing System (EOS) (http://eosweb.larc.nasa.gov/PRODOCS/misr/tools/geotiff_tool.html). In ArcInfo, each image tile was converted into a grid format and merged together to obtain a global annual GPP and NPP dataset. In the whole process of converting hdf files into tiff images and converting tiff images into grids all files were kept in the equal-area projection (sinusoidal projection). Consistently

using the sinusoidal projection has two advantages: first, the sinusoidal projection is an equal-area projection and it can warrant the accuracy for each grid when calculating area; second, no projection transformation can avoid error caused by recalculation of cell values in reprojection.

Land cover, altitude, temperature, precipitation and latitude data

The 1-km resolution Global Landcover 2000 (GLC2000) data comprising 22 land-use types was retrieved from the Global Landcover 2000 web site (Bartholomé & Belward, 2005) (Appendix 1). The GLC2000 data were based on the SPOT-4 vegetation VEGA2000 dataset which provides accurate baseline landcover information. The 1-km resolution altitude data were obtained from the US Geological Survey (Hastings & Duanbar, 1999). The aim of our research was to reveal a global average pattern of NPP/GPP ratio. The relevant findings can benefit from analyses based on long-term and stable meteorological data. We utilized the 30-year average (1971–2000) precipitation and temperature data in $10'$ resolution, which were acquired as a text file from UK Meteorological Office, Hadley Centre (New *et al.*, 2002). The temperature and precipitation data were transformed into grid format from text format in ArcInfo. Half-degree resolution grid files representing latitude from poles to the equator were created in ArcInfo. Land=cover, precipitation, temperature and altitude grid files were all transformed to the sinusoidal projection to match MODIS NPP and GPP files. To examine the NPP/GPP ratio pattern along each geographical and climatic factor, the mean NPP/GPP ratio value (dependent factor) for each range of precipitation, temperature, latitude and altitude (independent factors) was calculated using [Zonalstats] of ArcInfo, where independent factors were used as zones and the dependent factor was used as a value. The resulting information table was exported into dbf format. Areas occupying an extremely small portion of the globe or non-vegetated areas, such as regions with latitude higher than 70° in the Northern Hemisphere (NH) and lower than 50° in the Southern Hemisphere (SH), regions with altitude higher than 7000 m and regions with precipitation of over 4500 mm, were eliminated from the analysis.

Analysis of global pattern of NPP/GPP ratio

The temporal fluxes of NPP, GPP and NPP/GPP ratios during the four study years were compared on their average and standard deviation after being standardized into the same absolute scale. Spatially, the NPP/GPP ratio averaged for the 4 years was presented in a world map. Further analysis was conducted to examine the difference in NPP/GPP ratio among each typical terrestrial ecosystem. The typical ecosystems examined in this study included extensively distributed and clearly defined ecosystems. For example, ecosystem type seven (regularly flooded forest) was excluded due to its small area of distribution and ecosystem type nine (forest/other natural vegetation mosaic) was excluded due to its fuzzy definition which leads to including a mixture of several life forms. In examining the differences in

NPP/GPP ratio among ecosystems, a 4-year average ratio value was used. To examine its pattern along the geographical and climatic factors at a global scale, the 4-year average NPP/GPP ratio was plotted against latitude, altitude, precipitation and temperature. The Pearson product moment correlation coefficient (R) was employed to signify the trend of the NPP/GPP ratio along each factor. A high R -value signifies a better relationship while a low R -value represents the opposite. A positive R implies that the NPP/GPP ratio has the same trend with each factor, while a negative R implies the opposite.

In addition to the analysis for the global ecosystem, the relationships between the NPP/GPP ratio and the geographical and climate variables were also examined for each individual ecosystem. In total there were 11 ecosystems and four climatic and geographical factors investigated in this study. A graph of the NPP/GPP ratio along each factor by each individual ecosystem would generate 44 figures. To simplify the description of the results for individual ecosystems, this study only listed the R -value to indicate the relationship between the NPP/GPP ratio with each factor.

Validation using field data

Previous research findings on calculating the NPP/GPP ratio using field measurement data were obtained through a thorough search of related literature. Based on the location where each field study was conducted or the targeted ecosystem type, the corresponding NPP/GPP ratio calculated from MODIS data was retrieved. The general pattern concluded from field measurement was compared with that drawn from MODIS data.

RESULTS

The pattern of the NPP/GPP ratio at the global scale

From 2000 to 2003, the global GPP and NPP and their ratio showed minor fluctuation with an average GPP, NPP and NPP/GPP ratio of 110 Pg C year⁻¹, 55 Pg C year⁻¹, and 0.5, respectively (Table 1). During the 4 years, the highest global GPP occurred in 2001 and the lowest in 2003. The difference between these 2 years was only 3 Pg C, or about 3% of the annual GPP. Similarly, NPP also saw its highest and lowest value in the same year as GPP, and the difference between 2001 and 2003 for NPP was almost the same as that of GPP. The annual NPP/GPP ratio showed higher stability than NPP or GPP during the 4 years with

a minimum of 0.512 in 2003 and a maximum of 0.522 in 2001. When the ratio was standardized into the same absolute scale with NPP and GPP, the standard deviation of the standardized ratio was 0.485, while the standard deviation of GPP and NPP was 1.4685 and 1.2504, respectively. The relatively small variation in the ratio demonstrated that the NPP/GPP ratio had a much higher stability than NPP and GPP. Interestingly, the minimum and maximum values of the NPP/GPP ratio occurred in the same year as those of GPP and NPP.

The NPP/GPP ratio featured a strong global pattern characterized by low ratios in wet, warm, low-elevation environments and high ratios in dry, cold and high-elevation zones (Fig. 1). For example, the average ratios were as low as 0.37, 0.36 and 0.35 in the Amazon plain of South America, West Africa, and Southeast Asia, respectively. The average ratios were as high as 0.7, 0.8, 0.71, 0.81 and 0.71, respectively, in the western United States, western South America, central Asia, South Africa and western Australia, which feature dry climates with low precipitation.

The NPP/GPP ratio pattern along latitude exhibited higher complexity in the Northern Hemisphere (NH) than in the Southern Hemisphere (SH). In the SH the ratio increased from 0.52 in the equatorial zone to 0.6 around 6° and then fell to 0.5 around 13°. From 13° to 30°, the ratio increased from 0.5 to 0.7 and then there was a flux around 0.7 between 30° and 38°. Above 38°, the ratio decreased between 38° and 42° and then increased above 42°. In the NH the ratio increased from 0.52 around the equator to 0.65 around 13° and then it decreased to 0.53 around 21°. Between 21° and 30°, the ratio increased to 0.61. The ratio was stabilized around 0.61 between 30° and 60°, and then it decreased to 0.4 toward the pole (Fig. 2). The highest ratio occurred around 30° in the SH. The lowest ratio occurred around 70° in the NH, and the second lowest ratio value occurred in the equatorial zone. Statistically, the NPP/GPP ratio had a significant relationship with latitude in the SH, altitude and precipitation, and did not have a significant relationship with latitude in the NH or temperature (Table 2). The most apparent relationship between the NPP/GPP ratio with latitude occurred in the zone from 13° to 30° in the SH. The relationship can be fitted to a linear equation of $NPP/GPP = 0.0009 \times \text{latitude} + 0.4$ with an R^2 value of 0.79.

The overall NPP/GPP ratio trend along altitude was simpler than along latitude. The ratio followed a globally increasing trend along rising altitude except in a certain altitude range (3600–4750 m) where the ratio decreased with rising altitude. From 400 m to 1500 m, increasing slope was around 0.0013, and between 1500 and 3600 m this rate decreased to 0.0003. Above 4750 m, the ratio began to increase with rising altitude again (Fig. 3).

The NPP/GPP ratio increased with increasingly higher average annual temperatures between -10 °C and 20 °C. The increasing trend can be fitted to a linear equation $NPP/GPP = 0.0007 \times \text{temperature} + 0.59$ with an R^2 value of 0.87. Specifically, the ratio decreased between -22 and -12 °C; increasing between -12 and -4 °C; remaining stable between -4 and 1.5 °C; increasing between 1.5 and 8 °C; remaining stable between 8 and 20 °C; and decreasing between 20 and 26 °C. The highest ratio zone appeared between 8 and 20 °C. The lowest ratio zone was found

Table 1 Global NPP, GPP and the NPP/GPP ratio from 2000 to 2003.

Year	NPP (Pg C year ⁻¹)	GPP (Pg C year ⁻¹)	Ratio
2000	55.92	108.00	0.518
2001	57.57	110.33	0.522
2002	55.36	107.40	0.515
2003	54.63	107.09	0.510

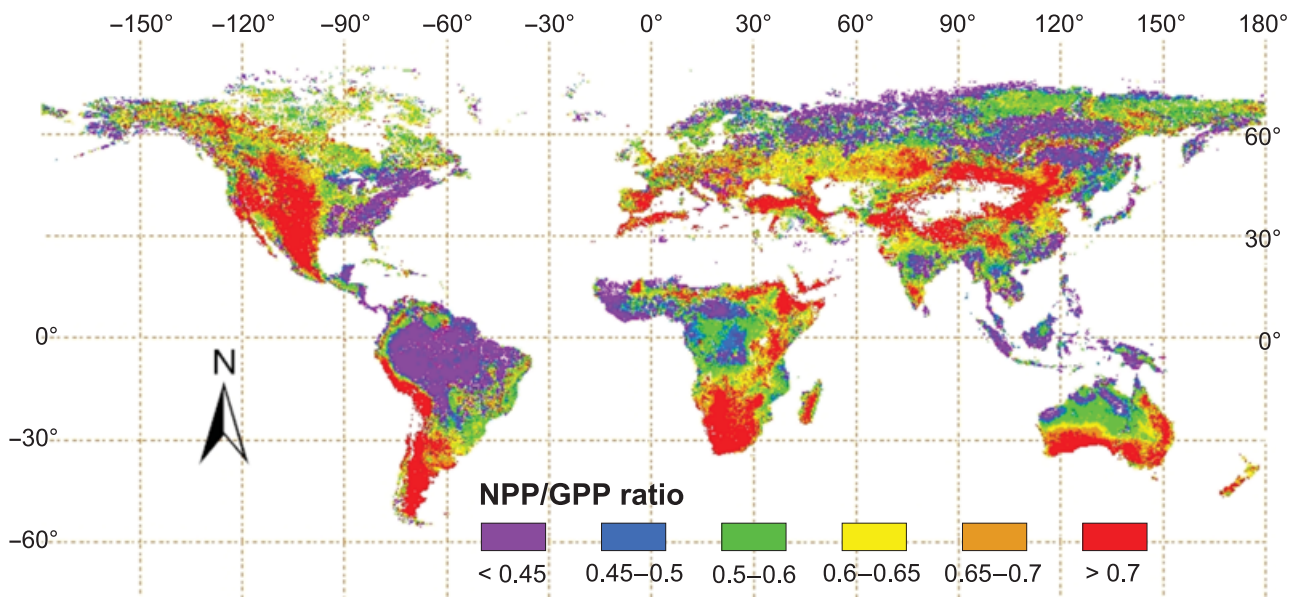


Figure 1 Global spatial pattern of the average NPP/GPP ratio.

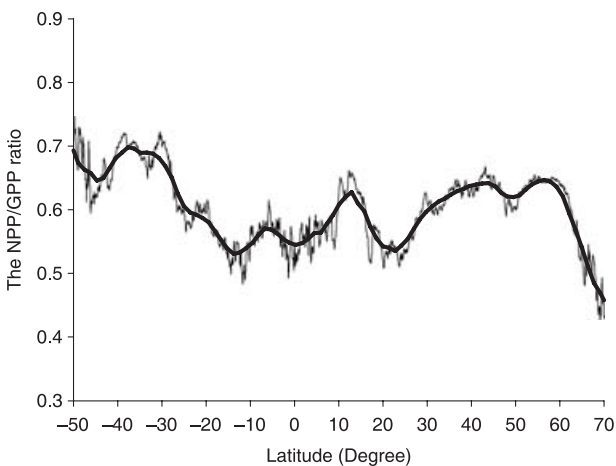


Figure 2 The latitudinal NPP/GPP ratio pattern. The thin line connects each point representing the average NPP/GPP ratio over 0.1° latitudinal bands; the bold line represents the central tendency produced by the moving average over 5° latitude.

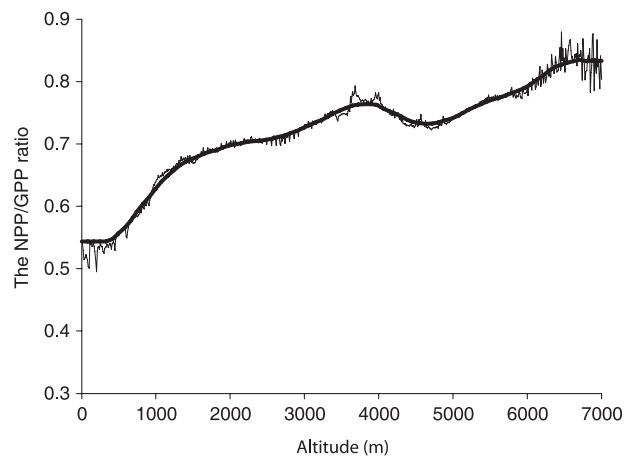


Figure 3 The altitudinal NPP/GPP ratio pattern. The thin line connects each point representing the average NPP/GPP ratio over 10 m altitude; the bold line represents the central tendency produced by the moving average over 100 m altitude.

around 26 °C (Fig. 4). Temperature was divided into ranges of -22 to -12 °C, -12 to 21 °C, 21–27 °C and 27–30 °C according to the global ecosystem trend along latitude. In these temperature ranges, the global terrestrial ecosystem had a significant trend along temperature. The relationship in ranges of -22 to -12 °C, 21–27 °C and 27–30 °C was negative and positive in the range of -12 to -21 °C.

The decreasing trend of the ratio with increasing average annual precipitation was evident from extremely dry regions (100 mm) to wet areas where precipitation reached 2300 mm. The decreasing trend can be fitted to a linear equation of NPP/

$GPP = -0.001 \times \text{precipitation} + 0.66$ with an R^2 value of 0.97. In areas with precipitation above 2300 mm, precipitation had no apparent impact on the ratio (Fig. 5).

NPP/GPP ratio pattern at each individual ecosystem scale

The NPP/GPP ratio showed a significant difference among ecosystems. Areas with a low NPP/GPP ratio were largely occupied by forest ecosystems such as broadleaved evergreen or broadleaved deciduous forests. Sparse herbaceous or shrub

Table 2 Correlation coefficients between the NPP/GPP ratio and latitude, altitude, precipitation and temperature by ecosystem type.

Ecosystem type	Latitude (SH)	Latitude (NH)	Altitude	Precipitation	Temp.
Global terrestrial ecosystem	0.616	-0.351	0.856	-0.65	0
1 Broadleaved, evergreen	0.78	0.68	0.98	-0.54	-0.80
2 Broadleaved, deciduous, closed	0.57	-0.76	0.96	0	0
3 Broadleaved, deciduous, open	0	0	0.81	-0.52	-0.86
4 Needleleaved, evergreen	0	0	0.92	-0.90	-0.46
5 Needleleaved, deciduous	0	-0.70	0.94	0	0
6 Mixed leaf type	-0.80	0	0.63	0	0
11 Shrub, closed–open, evergreen	0.89	0	0.87	-0.84	0
12 Shrub, closed–open, deciduous	0.71	0	0.89	-0.78	0
13 Herbaceous, closed–open	0	0	0.73	-0.66	0
14 Sparse Herbaceous or shrub	0	0	0.75	0	0.51
16 Cultivated and managed areas	0	0	0.86	-0.60	0

A positive *R*-value in the Southern Hemisphere (SH) represents that the ratio increases from the equator to the South Pole. A negative *R*-value in the northern hemisphere (NH) represents a decreasing ratio along rising latitude in the NH. Zero represents no significant trend.

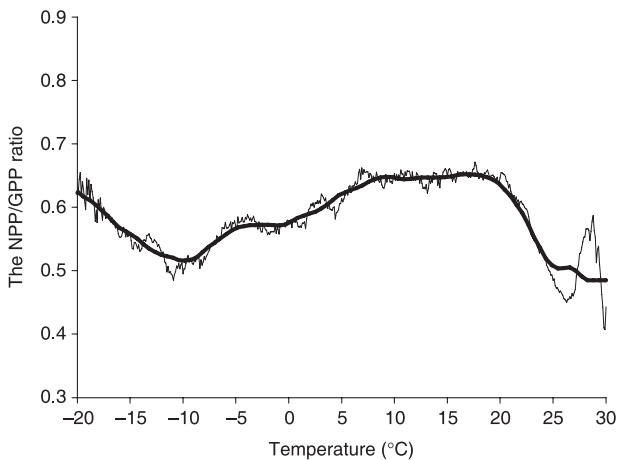


Figure 4 The NPP/GPP ratio pattern with temperature. The thin line behind connects each point representing the average NPP/GPP ratio over 0.1 °C temperature; the bold line represents the central tendency produced by moving average over 1 °C temperature.

vegetation located in high elevations or dry zones had the highest ratio, followed by needleleaved evergreen and then open broadleaved deciduous forest. Ecosystems distributed in wet and warm environments such as evergreen shrub, broadleaved evergreen and closed broadleaved deciduous had a lower NPP/GPP ratio than their counterparts distributed in relatively dry and cold environments. Dense forests had a lower ratio than open forests (Fig. 6). For example, closed broadleaved deciduous forests had a lower ratio than open broadleaved deciduous forests, and closed herbaceous vegetation had a lower ratio than sparse herbaceous or shrub. Broadleaved forests had a lower ratio than deciduous forests and evergreen forests had a lower ratio than deciduous forests. Broadleaved forests had a lower ratio than needle forests. Cultivated and managed areas had a medium ratio similar to closed-open shrub.

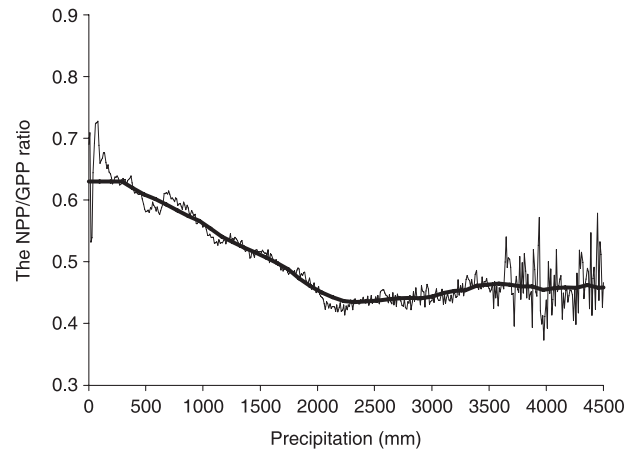


Figure 5 The NPP/GPP ratio pattern with precipitation. The thin line connects each point representing the average NPP/GPP ratio over 10 mm precipitation; the bold line represents the central tendency produced by the moving average over 100 mm precipitation.

For latitude in the SH, some ecosystems (i.e. broadleaved evergreen, closed broadleaved deciduous and shrub) had trends similar to the global ecosystem; mixed forest showed the opposite trend than the global ecosystem; others exhibited no significant trend. In the NH, closed deciduous broadleaved and deciduous needleleaved followed the same trend while broadleaved evergreen had a reversed trend from the global ecosystem.

Each individual ecosystem had almost the same trend as the global ecosystem along altitude. The ratio had a negative correlation with precipitation for ecosystems of broadleaved evergreen, open broadleaved deciduous, needleleaved evergreen, all shrub and grassland. Other ecosystems exhibited no significant trend along precipitation (Table 2).

Forest ecosystems showed a stronger trend along temperature than shrub or grassland. Temperature failed to exert significant

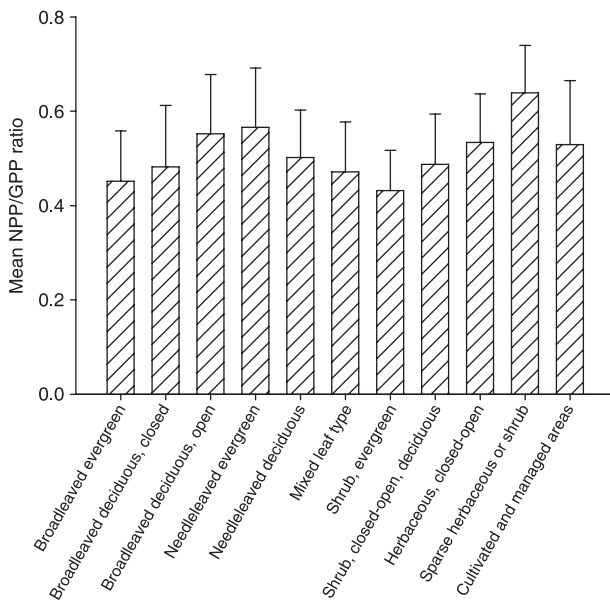


Figure 6 The mean NPP/GPP ratio for each ecosystem. Error bars represent standard errors within each ecosystem.

control on individual ecosystems except broadleaved evergreen, open broadleaved deciduous and evergreen needleleaved forests, which had an evident negative relationship with temperature, as well as sparse herb and shrub ecosystems which had a positive relationship with temperature.

Validation results

The result that NPP/GPP ratio was variable among ecosystems (Fig. 6) is consistent with several studies (Amthor, 2000; Van Iersel, 2003; Delucia *et al.*, 2007). Experimental studies in a tropical forest revealed that variation in climate, forest type or edaphic factors might impose a significant effect on the NPP/GPP ratio (Giardina *et al.*, 2003). Amthor (2000) reported a higher NPP/GPP ratio (0.46) for temperate forest than moist tropical forest (0.26) by compiling *c.* 20 studies. DeLucia *et al.* (2007) conducted a meta-analysis after compiling 60 data points obtained from 26 papers published since 1975 and indicated that the NPP/GPP ratio ranged from 0.23 to 0.83 for different forest types. The average value of the NPP/GPP ratio for old boreal forests was 0.32, the lowest among forest ecosystems. In contrast, temperate deciduous forests had the highest average value of 0.59. The average NPP/GPP ratios for temperate coniferous forests, temperate mixed forests and tropical forests were in between. Moreover, the NPP/GPP ratio decreased with increasing forest age. The ranking order of the NPP/GPP ratio for each ecosystem matched findings inferred from the MODIS NPP/GPP ratio in our study. The only empirical study relating growth and maintenance respiration and the NPP/GPP ratio showed that changes in growth and maintenance respiration related to plant age resulted in substantial variation in NPP/GPP ratio ranging from 0.2 to 0.7

(van Iersel, 2003). Based on theoretical calculations of growth efficiency and respiratory costs associated with maintenance, nutrient acquisition and transport, Amthor (2000) concluded that the NPP/GPP ratio should vary between 0.2 and 0.65. Our study provided a range between 0.4 and 0.65 (Fig. 6).

DISCUSSION

Knowledge of the global spatial NPP/GPP ratio pattern and how it is related to global geographical, topographic and climatic factors is critical for understanding carbon cycling of global ecosystems and its response to climate change (Medlyn & Dewar, 1999; Chen *et al.*, 2000; Delucia *et al.*, 2007). A well-established relationship can assist in and simplify development of NPP or GPP models used to simulate and examine global carbon cycles. A high-resolution (1 km) NPP/GPP ratio map and its pattern along geographical, topographic and climatic factors can enhance understanding of NPP/GPP ratio patterns.

The NPP/GPP ratio has evident patterns along latitude, altitude and precipitation gradients. The comparison with field data revealed that the NPP/GPP ratio calculated from MODIS data followed a similar pattern with findings drawn from field data. Latitude is not a phenomenological driving variable *per se*. However, it is the combination of multiple factors, such as temperature, precipitation, length of growing season, frost events, etc. (Valentini *et al.*, 2000). The complex interactions of numerous drivers confound the relationship between the NPP/GPP ratio and latitude and result in weak global trends along latitude. The NPP/GPP ratio trend varies by region along latitude. For example, the NPP/GPP ratio decreases in Europe along rising latitude but it decreases with rising latitude in the SH such as in South America, South Africa and Australia. Similar to latitude, altitude is not a phenomenological driving factor *per se*. Its effect on the NPP/GPP ratio is a result of such direct factors as temperature, precipitation and radiation, among others. Along rising altitude, temperature decreases and precipitation increases. The net effect of decreasing temperature and enhanced precipitation along rising altitude results in increasing NPP/GPP ratio, which implies that precipitation is a stronger limiting factor on NPP/GPP ratios of the global vegetation ecosystem. The stronger effect of water availability over temperature and radiation on vegetation growth has been found in previous work (Churkina & Running, 1998; Nemani *et al.*, 2003).

The NPP/GPP ratio decreases with enhanced precipitation and remains unchanged in areas where water availability is in surplus. Previous research found that NPP increased linearly with higher mean annual precipitation and temperature in dry and cold ecosystems, but this relationship became weak in humid and warm regions (Lieth, 1975a,b; Gower, 2002). Sufficient water resources are important for plants in dry environments, but redundant precipitation can decrease or increase other sources critical for plant growth such as radiation input, nutrient leaching or soil oxygen (Schuur *et al.*, 2001). Surplus precipitation can lead to the shortage of soil oxygen, which will slow down decomposition of organic matter and subsequently nutrient supply (Schuur & Matson, 2001). Moreover, cloudiness in parallel

with rainfall can lead to less solar radiation that is necessary for high productivity.

The higher NPP/GPP ratio of vegetation in dry and cold environments is caused by several factors. First, plants have higher efficiency in storing carbon by expending less energy on sustaining living material, relative to vegetation in wet and warm environments. Second, NPP has higher resilience to dry and cold environments than GPP, and so the vegetation has higher production efficiency in extreme environments. Extreme environments generate an unequally high benefit to GPP relative to NPP. When an environment transitions from dry and cold to wet and warm, the rate of respiration increases exponentially while the rate of photosynthesis is relatively stable. As a result, the decreases in the ratio of productive to consuming tissue and maintenance respiration lead to a decline in NPP (Cannell, 1989; Ryan *et al.*, 1994; Teskey *et al.*, 1995). In the cooler period of a year, there is less biological activity and a smaller proportion of respiration relative to gross productivity, which means a higher NPP/GPP ratio. High respiratory costs caused by a warm environment and a long growing season, as well as nutrient deficiency, could be possible reasons inducing a low NPP/GPP ratio in tropical areas (DeLucia *et al.*, 2007).

Controls of climatic and geographical factors on NPP/GPP ratio pattern are realized through adapting life-forms in ecosystems to local environments. The NPP/GPP ratio is normally higher in environments characterized by a shortage of precipitation and lower temperature relative to wet and warm environments. Ecosystems normally develop life-forms characterized by short stem or sparse coverage in acclimatizing to dry or cold environments. This study found that ecosystems with sparse vegetation have a higher ratio than ecosystems with dense vegetation and that evergreen vegetation ecosystems have a lower ratio than deciduous vegetation ecosystems, which further confirms that the NPP/GPP ratio is variable for different ecosystems although the variation of the ratio is not always consistent among studies (Amthor, 2000; DeLucia *et al.*, 2007, and this study). These findings are consistent with previous studies showing that in large plant ecosystems such as old growth forests, tall trees have lower specific rates of photosynthesis and lower productivity due to higher hydraulic resistance in their stems and branches (Yoder *et al.*, 1994; Hubbard *et al.*, 1999). Similar results can also be reached from theoretical considerations. If the NPP/GPP is a constant, the autotrophic respiration (R_a) is proportional to the GPP of an ecosystem. Early work by Dewar *et al.* (1998) indicated that R_a should be constrained by or be proportional to GPP because R_a is regulated by the availability of sugars from photosynthesis and the demand for ATP by existing and developing tissue (Atkin & Tjoelker, 2003). However, more and more studies agree that R_a including both maintenance respiration and growth respiration scales with plant size and nitrogen content (Amthor, 2000; Reich *et al.*, 2006), suggesting that the NPP/GPP ratio of ecosystems is not a constant.

MODIS NPP and GPP data were obtained from model results. Factors involved in the model, including misclassified land cover, coarse resolution land cover (1 km), uncertainty inherent in meteorological data, and weakness of the algorithm used in

calculating NPP and GPP might all lead to some errors in calculating NPP and GPP (Zhao *et al.*, 2005). The comparability of NPP and GPP among these 4 years was validated because they used the same set of land-cover data, the same set of meteorological data and the same algorithm, thus ensuring that variation among NPP/GPP ratio was caused by factors other than the items used in calculating NPP and GPP. The NPP/GPP ratio shows a stable average value during 2000–03, although 2001 was a La Niña year and 2002 and 2003 were weak El Niño years (http://www.cdc.noaa.gov/ENSO/enso.mei_index.html). Global NPP decreased during those El Niño events (Nemani *et al.*, 2003) so that the NPP/GPP ratio was lower in 2002 and 2003 than in 2000 and 2001. The annual global NPP/GPP ratio was correlated with the annual global CO₂ growth rate. The NPP/GPP ratios in 2002 and 2003 were below 0.515 while the annual global CO₂ growth rate was more than 2 p.p.m. by volume (p.p.m.v.) in these 2 years (http://www.cdc.noaa.gov/ENSO/enso.mei_index.html). When the annual global NPP/GPP ratio was over 0.515 in 2000 and 2001, the atmospheric growth rate was less than 2 p.p.m.v. for the same period. During these 4 years, high GPP occurs in years of low CO₂ growth rate. In turn, high GPP occurs in the same year with high NPP/GPP ratio. The relationship between high NPP/GPP ratios and high GPP with low CO₂ growth rates indicates that higher GPP of global vegetation can lead to a lower CO₂ growth rate. In the meantime, increased GPP will cause an increase in the NPP/GPP ratio.

The limitation of this study lies in that both NPP and GPP were obtained from model results. First, GPP has been overestimated in many sites and underestimated for productive sites in comparison with tower eddy flux network observations. NPP estimation had higher uncertainty for tropical forests compared with Ecosystem Model-Data Intercomparison (EMDI) data since DAO data had higher uncertainty in tropical regions and cloud-contaminated FPAR/LAI data (Zhao *et al.*, 2005). Second, some assumptions made in calculating NPP and GPP might in turn affect the NPP/GPP ratio. For example, the GPP was calculated from leaf area index (LAI) and FPAR, which are 8-day composite products. The maximum FPAR among the 8 days was selected to represent the period. So there is an assumption of non-varying LAI and FPAR among the given 8 days. Using the maximum LAI value can enhance the accuracy of estimating leaf mass which is relevant to respiration. However, in areas with frequent cloudy weather, such as tropical areas, the GPP is likely to be overestimated. Third, NPP and GPP are two related processes which have some common variables in calculation. However, NPP and GPP were calculated from independent ecological processes in MODIS. The equation used in calculating NPP and GPP illustrated that GPP was primarily determined by biome type determined by remote sensing, radiation by meteorological data and conversion efficiency inferred from the biological properties of each ecosystem. The respiration was calculated completely independently from GPP. In the whole process of calculation, no direct geometric relationship between NPP and GPP has been utilized. They were largely determined by remotely sensed information. Although remotely sensed data have many issues and cannot be the equivalent of ground measurement, only

remotely sensed data can address these ecological processes at the regional or global scale and the MODIS NPP and GPP data are the best available so far globally.

Validation by field measurement justifies the findings in this study. Direct comparison of MODIS annual GPP with field data collected from 37 Ameriflux and Fluxnet sites distributed across North America, mid-latitude zones, polar regions and a wide variety of ecosystem types bracketing forests, shrublands and grasslands resulted in an overall high consistency ($R^2 = 0.6993$ and relative error = 19%) (Zhao *et al.*, 2005). NPP data were validated by Ecosystem Model-Data Intercomparison data compiled from over 1000 ground points and resulted in overall high consistency ($R^2 = 0.77$). Through scaling and aggregating BigFoot NPP and GPP measured from nine different ecosystems around the world, Turner *et al.* (2006) validated MODIS NPP and GPP data. They found that annual GPP and NPP had a close agreement between the MODIS product and the Bigfoot product. While both NPP and GPP were simultaneously overestimated at low-productivity sites and underestimated at high-productivity sites, which would affect NPP and GPP individually, their ratio would not be biased.

CONCLUSIONS

The previous concept that the NPP/GPP ratio is constant among various ecosystems is incorrect based on calculations using MODIS NPP and GPP data. The NPP/GPP ratio has strong variability among different planetary ecosystems. Forest ecosystems have lower NPP/GPP ratios than herbaceous and shrub ecosystems; dense or open ecosystems have lower NPP/GPP ratio than sparse or closed ecosystems; evergreen ecosystems have lower NPP/GPP ratio than deciduous ecosystems. The NPP/GPP ratio has a significant trend along climatic and topographic gradients. It increases with increasing altitude, increases with growing temperature for 60% of land, decreases with enhanced precipitation and decreases with growing latitude in the SH. Identifying the factors controlling this ratio may significantly improve our understanding of the carbon cycle, including interannual variability and long-term trends under climate change.

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BIOSKETCH

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Appendix 1 Twenty-two land-use types retrieved from the Global Landcover 2000 web site (Bartholomé & Belward, 2005).

GLC global class (according to LCCS terminology)	
1	Tree cover, broadleaved, evergreen LCCS > 15% tree cover, tree height > 3 m (examples of subclasses at regional level: closed > 40% tree cover; open 15–40% tree cover)
2	Tree cover, broadleaved, deciduous, closed
3	Tree cover, broadleaved, deciduous, open (open 15–40% tree cover)
4	Tree cover, needle-leaved, evergreen
5	Tree cover, needle-leaved, deciduous
6	Tree cover, mixed leaf type
7	Tree cover, regularly flooded, fresh water (and brackish)
8	Tree cover, regularly flooded, saline water (daily variation of water level)
9	Mosaic: tree cover/other natural vegetation
10	Tree cover, burnt
11	Shrub cover, closed–open, evergreen (examples of subclasses at regional level: (i) sparse tree layer)
12	Shrub cover, closed–open, deciduous (examples of subclasses at regional level: (i) sparse tree layer)
13	Herbaceous cover, closed–open (examples of subclasses at regional level: (i) natural, (ii) pasture, (iii) sparse trees or shrubs)
14	Sparse herbaceous or sparse shrub cover
15	Regularly flooded shrub and/or herbaceous cover
16	Cultivated and managed areas (examples of subclasses at regional level: (i) terrestrial; (ii) aquatic (= flooded during cultivation), and under terrestrial: (iii) tree crop and shrubs (perennial), (iv) herbaceous crops (annual), non-irrigated, (v) herbaceous crops (annual), irrigated)
17	Mosaic: cropland/tree cover/other natural vegetation
18	Mosaic: cropland/shrub or grass cover
19	Bare areas
20	Water bodies (natural and artificial)
21	Snow and ice (natural and artificial)
22	Artificial surfaces and associated areas

LCCS, UN Food and Agriculture Organization Land Cover Classification System.