Climate-driven global changes in carbon use efficiency
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ABSTRACT
Aim Carbon use efficiency [net primary production (NPP)/gross primary production (GPP) ratio] is a parameter related to the allocation of photosynthesized products by plants and is commonly used in many biogeochemical cycling models. But how this parameter changes with climates is still unknown. Faced by an aggravated global warming, there is a heightened necessity in unravelling the dependence of the NPP/GPP ratio on climates. The objective of this study was to examine how ongoing climate change is regulating global patterns of change in the NPP/GPP ratio. The study finding would elucidate whether the global vegetation ecosystem is becoming more or less efficient in terms of carbon storage under climatic fluctuation.

Location The global planetary ecosystem.

Methods The annual NPP/GPP ratio of the global terrestrial ecosystem was calculated over a 10-year period based on Moderate Resolution Imaging Spectroradiometer data and an ecosystem productivity model. The temporal dynamics of the global NPP/GPP ratio and their dependence on climate were investigated.

Results The global NPP/GPP ratio exhibited a decreasing trend from 2000 to 2009 due to decreasing NPP and stable GPP over this period. The temporal dynamics of the NPP/GPP ratio were strongly controlled by temperature and precipitation. Increased temperature lowered the NPP/GPP ratio, and increased precipitation led to a higher NPP/GPP ratio.

Conclusions The NPP/GPP ratio exhibits a clear temporal pattern associated with climatic fluctuations at a global scale. The associations of the NPP/GPP ratio with climatic variability challenge the conventional assumption that the NPP/GPP ratio should be consistent independent of environmental conditions. More importantly, the findings of this study have fundamental significance for our understanding of ongoing global climatic change. In regions and time periods experiencing drought or increased temperatures, plant ecosystems would suffer a higher ecosystem respiration cost and their net productivity would shrink.

Keywords Climate, GPP, global scale, NPP/GPP ratio, NPP, temporal dynamics.

INTRODUCTION
Increasing atmospheric CO2 concentrations and global climate change have heightened our need to better understand ecosystem carbon cycle responses to the changing environment. Gross primary production (GPP), net primary production (NPP) and autotrophic respiration (Ra) are three basic and highly related components of carbon cycling. GPP represents the amount of photosynthesis by all plants measured at the ecosystem scale (Luo & Reynolds, 1999; Chapin et al., 2002). NPP is the balance between the carbon gained by GPP and the carbon released by plant respiration, i.e. NPP = GPP − Ra (Chapin et al., 2002; Zhang et al., 2009). Ra plus heterotrophic respiration (Rh) constitutes ecosystem respiration (Re), i.e. Re = Ra + Rh. Theoretically, when the ecosystem reaches an equilibrium status, NPP (GPP − Ra) will be equal to Rh and NPP − Rh will be zero.
In reality, however, due to their drastically different response time, NPP – Rh value of a system reaching an equilibrium status would barely be zero. Vice versa, a system with zero value of (NPP – Rh) cannot be an indicator of an equilibrium status.

The carbon fixed via photosynthesis is allocated to a variety of usages, including 50−70%, that is returned immediately to the environment through Ra (DeLucia et al., 2007; Luyssaert et al., 2007). These allocation processes are highly relevant to understanding ecosystem carbon cycles and carbon storage, as they strongly influence the residence time and location of carbon in the ecosystem. For example, the residence times of the carbon used for maintenance respiration and the carbon used for the structural biomass of organs are drastically different (Campioli et al., 2011). To date, although many studies have been conducted on carbon exchange between plants and the atmosphere, there are still fundamental unanswered questions about the fate of the carbon taken up by the ecosystem and its relationship with the environment and ecosystem types.

The NPP/GPP ratio, or carbon use efficiency, is a commonly used parameter that reflects the carbon allocated to NPP and to Ra, the two basic components of GPP. This parameter indicates the fraction of total assimilated carbon being incorporated into new tissues and represents the efficiency with which ecosystems sequester carbon from the atmosphere in terrestrial biomass (Valentini et al., 2000; DeLucia et al., 2007). The NPP/GPP ratio is a critical ecosystem property for carbon cycle research because it is often used to calculated GPP from NPP, or likewise to estimate Ra as the difference between GPP and NPP (Waring et al., 1998; Zhang et al., 2009; Macinnis-Ng et al., 2011). For many carbon cycle or productivity models such as Carnegie-Ames-Stanford approach and marine biological laboratory/soil-plant-atmosphere canopy model, the NPP/GPP ratio acts as a fundamental ecosystem model parameter (Potter et al., 1993; Williams et al., 1997). A minor modification of the parameter’s value can result in a drastic change in model predictions. For example, when scaling up landscape model results to a terrestrial biosphere scale, a 25% increase of this parameter value is equivalent to enhancing the ecosystem NPP by >37%, which could have considerable impacts on estimates of global C sequestration (DeLucia et al., 2007).

To date, many empirical and field monitoring studies have been conducted to determine the environmental and biological controls on the NPP/GPP ratio, including temperature, precipitation, CO₂ level and plant age (Ryan, 1991; Cheng et al., 2000; Van Iersel, 2003; Reich et al., 2006; Metcalfe et al., 2010). Most studies have concluded that the NPP/GPP ratio is a fixed value independent of ecosystem type (Gifford, 1994, 1995, 2003; Ryan et al., 1994; Landsberg & Gower, 1997; Dewar et al., 1998; Waring et al., 1998) and is constant across various CO₂ and temperature levels for herbaceous and woody plants (Gifford, 1994, 1995; Dewar et al., 1999; Tjoelker et al., 1999; Cheng et al., 2000). Treating Ra/GPP as constant is a simple and practical way to incorporate respiration CO₂ release into long-term vegetation productivity models despite the considerable complexity of Ra and its environmental influences (Gifford, 2003). Many models, such as CASA (Potter et al., 1993) and FOREST-biogeochemical cycles (Running & Coughlan, 1988), use a fixed value for the NPP/GPP ratio across different ecosystems for quantifying Ra.

In other research, the assumption of a constant NPP/GPP ratio value has been challenged by field observations and modelling studies (Medlyn & Dewar, 1999; Chapin et al., 2002; Xiao et al., 2005; Heinsch et al., 2002; Xiao et al., 2007; DeLucia et al., 2007; Zhang et al., 2009). A number of studies have found that the NPP/GPP ratio varies with ecosystem type, climate, soil nutrients and geographic locations (Lammers, 1982; Xiao et al., 2003; DeLucia et al., 2007; Maseyk et al., 2008). A recent study found that forests in high-nutrient-availability areas allocate more photosynthesis to plant biomass production than forests in low-nutrient-availability areas (Vicca et al., 2012). Previous findings that the NPP/GPP ratio is independent of biotic and environmental factors have been criticized for lacking data consistency and continuity over time and space. These findings have primarily been either based on discrete measurements of individual plants or small plots of vegetation in a green house or conducted at a landscape scale over short time periods (Ryan et al., 1997; Piao et al., 2010). Studies conducted at a single site have limited relevance for other ecosystems, and considerable errors can arise when such patchy data are scaled up to regional or global levels over long time scales (Mooney, 1991; Luo & Reynolds, 1999).

New studies utilizing data over broad areas and relatively long time periods are needed to disentangle the issues related to the relationship between respiration cost and biotic and environmental factors and to determine how photosynthesis and respiration acclimate to a changing climate. Identifying the ecological factors controlling the NPP/GPP ratio can significantly improve our understanding of the carbon cycle, including its interannual variability and long-term trends under climate change. The newly developed Moderate Resolution Imaging Spectroradiometer (MODIS) NPP and GPP products provide a rare opportunity to study the dependence of the NPP/GPP ratio on the environment and climate. These products have the strengths of global coverage, high geolocation accuracy and high radiometric resolution (Wan et al., 2004), and have been validated as being consistent with ground flux tower-based GPP and field-observed NPP (Zhao et al., 2005; Heinsch et al., 2006). The MODIS products can capture the spatial and temporal patterns in GPP and NPP across various biomes and climate regimes and have been successfully utilized to explore temporal trends in global NPP (Zhao & Running, 2010, 2011) and the spatial pattern of the global NPP/GPP ratio (Zhang et al., 2009).

The sole previous global study of the NPP/GPP ratio focused only on its spatial patterns, and the validity of the conclusions might be sensitive to the simplified parameters used in the MODIS NPP and GPP product algorithms (Zhang et al., 2009). In particular, several basic biome-specific physiological parameters such as the maximum radiation conversion efficiency, the respiration rate per unit of leaf and livewood biomass were set at constant values within each biome, limiting the spatial heterogeneity within each biome (Heinsch et al., 2003). Aside from being constrained by simplified parameters, the previous findings regarding the pattern of the NPP/GPP ratio at a regional scale relied on only 4 years of data. A longer temporal analysis,
which is achievable using recently generated data, would more comprehensively consider the inter-annual variability of the NPP/GPP ratio and its relationship with climate.

The objective of this study was to examine how ongoing climate change is regulating global NPP/GPP ratio dynamics. Specifically, we investigated how the changing climate is driving the NPP/GPP ratio of global plant ecosystems by exploring its temporal dynamics using 10 years of remotely sensed model data. The findings will shed light on the changes in global plant ecosystem carbon use efficiency and respiration costs in response to a changing environment and have the potential to improve global carbon sequestration accounting and advance global change research.

MATERIALS AND METHODS

MODIS GPP data

Annual 1-km-resolution GPP and NPP data from 2000 to 2009 in TIF format and the WGS84 geographic coordinate system were downloaded from the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana (http://www.ntsg.umt.edu/) and converted into a grid format in ArcGIS software (http://www.esri.com/software/arcgis/index.html). Non-vegetated areas, including water bodies, barren land and built-up areas for which there are no calculated GPP data, were eliminated from the analysis.

The latest Collection 5 (MOD17) MODIS GPP values are calculated as follows:

\[
GPP = \varepsilon_{\text{max}} \times 0.45 \times S W_r a d \times F P A R \times f V P D \times f T_{\text{min}}
\]

where \(\varepsilon_{\text{max}}\) is the max radiation use conversion efficiency of the vegetation; \(S W_r a d\) is short-wave downward solar radiation, of which 45% is photosynthetically active radiation (PAR); \(F P A R\) is the fraction of incident PAR that is absorbed by the plant canopy; and \(f V P D\) and \(f T_{\text{min}}\) are the reduction scalars from water stresses (high daily vapour pressure deficit) and low temperature (low daily minimum temperature \(T_{\text{min}}\)), respectively. Each parameter value is obtained from the Biome Parameter Look-Up Table (BPLUT), which contains parameters for specific leaf area (SLA) and respiration coefficients for representative vegetation in each biome type (Running et al., 2000; White et al., 2000). Among the parameters used in calculating GPP, FPAR is estimated via satellite remote sensing; PAR, SWrad, fVPD and fTmin are derived from meteorological field data; and \(\varepsilon_{\text{max}}\) is determined based on the theory of Monteith (1972) for each biome. The GPP product has been validated by comparison with data from 250 global eddy flux towers, and the results showed strong correlations between the modelled GPP and the site-derived GPP data (Heinsch et al., 2006).

MODIS NPP data

NPP is calculated as the difference between GPP and respiration, which includes both maintenance and growth components. To model respiration, leaf mass is first estimated from the leaf area index (LAI) and SLA as Leaf_Mass = LAI/SLA, where LAI is obtained from the MOD15 product and SLA is obtained from the BPLUT. Then, root biomass is calculated as Root_Mass = Leaf_Mass \times \text{root_leaf_ratio}, where root_leaf_ratio is the ratio of root to leaf biomass obtained from the BPLUT.

Maintenance respiration is calculated on a daily basis based on the parameters for maintenance respiration per unit of leaf and root biomass obtained from the BPLUT. Live woody tissue is obtained from the difference between the annual maximum leaf mass and the mass of livewood, and the associated livewood maintenance respiration is then calculated based on the respiration rate per unit of live wood carbon per day obtained from the BPLUT.

Growth respiration (GR) is calculated on an annual basis. The annual leaf GR is calculated as Leaf_GR = (annual maximum leaf mass) \times (annual turnover proportion of leaves) \times (leaf base GR). The annual respiration values for root, livewood and deadwood growth are calculated as ratios of leaf GR. These parameters are obtained from the BPLUT.

Finally, NPP is calculated as follows:

\[
NPP = GPP - (R_{\text{al}} + R_{\text{lw}} + R_{\text{mw}}) - (R_{\text{gr}} + R_{\text{gw}} + R_{\text{gd}}),
\]

where \(R_{\text{al}}, R_{\text{lw}}\) and \(R_{\text{mw}}\) are maintenance respiration by leaves, fine roots and livewood, respectively, and \(R_{\text{gr}}, R_{\text{gw}}\) and \(R_{\text{gd}}\) are GR for leaves, roots, livewood and deadwood, respectively. More detailed information on the techniques used for modelling GPP and NPP can be found in related publications (Heinsch et al., 2006; Zhao et al., 2006).

The NPP product was validated using the Ecosystem Model-Data Intercomparison (EMDI) NPP data set (Olson et al., 2001). The EMDI NPP data set is composed of 2523 sites that represent the majority of global biomes. The validation process demonstrated that the modelled NPP results agree well with field NPP data.

Land cover, temperature and precipitation data

To be consistent with the GPP and NPP results, we used land cover data from the MOD12Q1 product and climate data (temperature and precipitation) from the NCEP/DOE II reanalysis climatic data sets in this study. The University of Maryland land cover classification system, which comprises 11 vegetation types and other non-vegetated land use types (Table 1), was used with the 1-km resolution MOD12Q1 product (land cover type 2 in the MOD12Q1 data sets). All tiles of landcover data were merged together and converted into TIFF format using the MODIS reprojection tool (https://lpdaac.usgs.gov/tools/modis_reprojection_tool), then converted into grid format and the Sinusoidal projection in ArcInfo to match the NPP and GPP data. NCEP/DOE II reanalysis data sets of temperature and precipitation from 2000 to 2009 were obtained from the National Oceanic and Atmospheric Administration (ftp://cdc.noaa.gov) in netCDF format and converted into grid format using FME software (http://www.safe.com/fme/fme-technology).
Table 1 The 10-year trend, 10-year mean and maximum inter-annual difference (MID) of the net primary production (NPP)/gross primary production (GPP) ratio for each ecosystem at the global and hemisphere scales from 2000 to 2009.

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<th>Trend (per year)</th>
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*Indicates that the trend is significant at a 95% confidence level.

Ecosystem type codes: 1, Evergreen needle-leaf forest; 2, Evergreen broadleaf forest; 3, Deciduous Needle-leaf forest; 4, Deciduous broadleaf forest; 5, Mixed forest; 6, Closed shrub; 7, Open shrub; 8, Woody savanna; 9, Savanna; 10, Grass; 11, Crops.

Analysis

The spatial pattern of the NPP/GPP ratio was mapped using the 10-year mean NPP/GPP ratio value. The uncertainty level of the 10-year mean NPP/GPP ratio for each pixel was calculated via bootstrapping using the 'boot' package implemented in the R statistical software environment (Mudelsee & Alkio, 2007; R Development Core Team, 2008). This method resampled the 10-year observations of NPP/GPP ratio 1000 times with replacement and calculated the mean of each sample. The 95% confidence limits were computed based on the resulting sample. The uncertainty of the global 10-year mean NPP/GPP ratio was presented as the width of the confidence interval (i.e. difference between the upper and lower bounds) at a 95% confidence level.

The temporal dynamics of NPP, GPP and the NPP/GPP ratio were explored for the global distribution of ecosystem types. In addition, the temporal dynamics of the NPP/GPP ratio were examined for each individual ecosystem type. To investigate the temporal trend in the NPP/GPP ratio from 2000 to 2009, its annual average value was plotted against time and the slope was computed to estimate the annual change rate. The statistical significance of the relationships among NPP, GPP and the NPP/GPP ratio flux and climatic variation was tested by linear regression using spss statistical software (SPSS Inc., 2010). A Maximum Inter-annual Difference (MID) index was calculated as the biggest difference between any random 2 years from 2000 to 2009 to indicate the largest annual NPP/GPP ratio variation in our studied period.

To explore the geographic variability in these trends, this study refined the analysis by classifying the global terrestrial ecosystem into multiple NPP/GPP change interval zones based on the slope sign and magnitude. The average precipitation and temperature trends for each zone from 2000 to 2009 were calculated. The increase or decrease in the NPP/GPP ratio was linked to temperature and precipitation by plotting the average change magnitude within each zone against the average changes in temperature and precipitation.

RESULTS

Global distribution and uncertainty of the NPP/GPP ratio

The global NPP/GPP ratio exhibited a spatial pattern closely associated with climate. In general, the NPP/GPP ratio is high in cold and dry regions and low in warm regions with abundant precipitation (Fig. 1a). In areas with low NPP/GPP ratios such as Western Australia, the Sahel and savannah regions of northern Africa, northern India and the central Amazon plains, the uncertainty is high. In contrast, the uncertainty is low in areas with high NPP/GPP ratios, such as the high latitude regions of the Northern Hemisphere (N.H.) and the Andes Mountains in South America (Fig. 1b).

Global temporal NPP/GPP ratio dynamics

Over the past 10 years, global NPP has decreased, whereas GPP has remained almost unchanged, leading to a decreasing NPP/GPP ratio under increased precipitation and temperature at a global scale (Fig. 2). Statistically, the correlations between NPP...
Figure 1 The spatial pattern of the 10-year (2000–2009) mean net primary production (NPP)/gross primary production (GPP) ratio (a) and the width of the confidence interval (difference between upper and lower bounds) of the mean NPP/GPP ratio at a 95% confidence level (b). A wider confidence interval represents a higher uncertainty.

Figure 2 Net primary production (NPP), gross primary production (GPP), NPP/GPP ratio, temperature and precipitation trends from 2000 to 2009. The sign and the P-value for NPP, GPP, NPP/GPP ratio, temperature, and precipitation are −, −, −, +, +, and 0.6, 0.946, 0.893, 0.105 and 0.082, respectively.
and temperature and precipitation are stronger than those between GPP and temperature and precipitation. The regression equation between GPP and temperature and precipitation is 

\[ GPP = 119.58 - 1.927 \times \text{[temperature]} + 0.011 \times \text{[precipitation]} \]

The \( P \)-values for the overall regression equation and for each independent variable are all non-significant at an alpha level of 0.05. The regression equation between NPP and temperature and precipitation is 

\[ NPP = 75.04 - 3.127 \times \text{[temperature]} + 0.1 \times \text{[precipitation]} \]

The \( P \)-values for the overall equation and for temperature and precipitation are 0.001, 0.004 and 0.054, respectively.

At a finer scale, the temporal trend varies with location (Table 1, Fig. 3). In the N.H., the ratio increased by 0.0007 per year. In the Southern Hemisphere (S.H.), the ratio decreased by 0.0025 per year over the time period studied, indicating a higher rate of change than in the N.H. The ratio has increased over 56% of the vegetated land areas in the N.H. (Fig. 3), mostly concentrated in North America, central Africa, India, and the middle and high latitude zones of East Asia. The areas with decreasing NPP/GPP ratios were primarily located in Eastern Europe, central Asia and high latitude zones in west Asia. The NPP/GPP ratio decreased over 68% of the vegetated land areas in the S.H., including large parts of South America, Africa, and Australia.

Each ecosystem exhibited a distinct temporal trend (Table 1). The global terrestrial plant ecosystem exhibited a decreasing NPP/GPP ratio over time, driven primarily by decreases in four ecosystems: evergreen and deciduous broadleaf forests, and open and closed shrubs. The S.H and N.H. ecosystems exhibited distinctive NPP/GPP ratio trends, as evidenced by an increasing NPP/GPP ratio for all N.H. ecosystems except evergreen broadleaf forest and decreasing NPP/GPP ratios for all S.H. ecosystems.

Climatic controls on the global temporal pattern in the NPP/GPP ratio

Temperature increases and decreases have not been consistent across the world over the past 10 years. The greatest increases (0.16°C yr\(^{-1}\)) have occurred in Western Australia and Tibet (Fig. 4a). The greatest decreases (−0.16°C yr\(^{-1}\)) have occurred in central North America and Alaska. Most parts of the Eurasian continent except India have become drier over the past 10 years. The greatest precipitation increases have occurred in the south Asian islands, central Africa and the western Brazilian Highlands. The greatest precipitation decreases have occurred in southern China, the northern part of South America and the southwestern edge of the Brazilian Highlands (Fig. 4b).

The NPP/GPP ratio exhibited a globally positive correlation with precipitation and a negative correlation with temperature in most vegetated areas from 2000 to 2009 (Fig. 4c & d). More specifically, in the S.H., the NPP/GPP ratio demonstrated a positive correlation with precipitation and a negative correlation with temperature in 74 and 90% of the vegetated areas, respectively. In the N.H., 67% of the vegetated areas had a positive correlation with precipitation, and 77% of the vegetated areas had a negative correlation with temperature. Globally, the areas with highly significantly negative (at 99% confidence level), significantly negative (at 95% confidence level, excluding areas with 99% confidence level), non-significantly, significantly positive and highly significantly positive relationships with precipitation account for 2, 2.7, 73, 9.2 and 12.2% of the vegetated areas, respectively. The areas with highly significantly negative (at 99% confidence level), significantly negative (at 95% confidence level, excluding areas with 99% confidence level), non-significant, significantly positive and highly significantly positive relationships with temperature account for 18.4, 11.2, 68.6, 1.2 and 0.6% of the vegetated areas, respectively.

The correlations between temporal NPP/GPP ratio trends and temperature and precipitation trends from 2000 to 2009 differed among ecosystem types (Table 1). The NPP/GPP ratio trend was negatively correlated with temperature for all ecosystems, whereas it had a positive relationship with precipitation for all ecosystems except global, N.H and S.H. evergreen needle-leaf forests and mixed forest ecosystems and global crop ecosystems.

Based on the direction and magnitude of the trend in the NPP/GPP ratio, eight equal-interval NPP/GPP ratio trend zones
Figure 4 The spatial pattern of the temperature (a) and precipitation (b) trends from 2000 to 2009 and the correlations between the net primary production (NPP)/gross primary production (GPP) ratio and (c) temperature and (d) precipitation. Highly significant (+), significant (+), non-significant, significant (−) and highly significant (−) represent relationships that are positive and statistically significant at a 99% confidence level, positive and significant at a 95% level, non-significant, negative and significant at a 95% level, and negative and significant at a 99% level, respectively.
The NPP/GPP ratio trend is different between the N.H and S.H., which might be related to their dissimilar climate change patterns over the past 10 years. In the S.H., large parts of Australia, South Africa and South America have simultaneously experienced decreasing precipitation and increased temperatures, which in combination are likely to lower the NPP/GPP ratio. In the N.H., a large part of Eurasia has experienced simultaneous increased temperatures and decreased precipitation, but the proportion of the area with decreasing precipitation is relatively lower than in the S.H. Zhao & Running (2010) similarly found that there are different ecosystem productivity dynamics between the S.H and N.H. due to these distinct climatic change trends.

The NPP/GPP ratio pattern along climate fluxes as revealed by this study using model NPP and GPP products is comparable with findings based on field measurement data. For example, based on results collected from approximately 100 field sites around the world, Piao et al. (2010) found a higher NPP/GPP ratio for temperate forests than for tropical forests. In another field measurement based study, temperate forests were indicated to have a higher NPP/GPP ratio than tropical forests (Delucia et al., 2007). An increasing NPP/GPP ratio with enhanced precipitation has also been found in other related model studies (Lieth, 1975) and field precipitation control experiments conducted at an Amazon forest (Metcalfe et al., 2010). On the other hand, there are some discrepancies between the present remote sensing model study and field measurement based studies. For example, Delucia et al. (2007) and Piao et al. (2010) found that boreal forests have a lower NPP/GPP ratio than temperate forests, which is opposite to the present study. The discrepancies possibly stem from two reasons. First, the present study and the field measurement based study, temperate forests were indicated to have a higher NPP/GPP ratio than tropical forests (Delucia et al., 2007). An increasing NPP/GPP ratio with enhanced precipitation has also been found in other related model studies (Lieth, 1975) and field precipitation control experiments conducted at an Amazon forest (Metcalfe et al., 2010). On the other hand, there are some discrepancies between the present remote sensing model study and field measurement based studies. For example, Delucia et al. (2007) and Piao et al. (2010) found that boreal forests have a lower NPP/GPP ratio than temperate forests, which is opposite to the present study. The discrepancies possibly stem from two reasons. First, the present study and the field measurement based studies are targeting different areas. The present study is set to summarize global continuous surface results for each ecosystem, while the field measurement-based studies only address the limited field site area. Then, the spatial distribution and the number of field sites, and site conditions would affect their representativeness. The field sites Delucia et al. (2007) and Piao et al. (2010) used are overlapped in many areas. In the two studies, there were only four boreal and five clustered boreal sites, respectively, and the study sites were fundamentally biased to temperate forests. The global NPP/GPP ratio map showed that there is a high spatial heterogeneity within each ecosystem. For example, among the boreal forest sites used in Piao et al. (2010), the Russian and Sweden sites happen to have a low NPP/GPP ratio. Another important point to note is that forest stand age and data retrieving method can significantly affect the NPP/GPP ratio on each site. The tropical forest sites included in Delucia’ studies are composed of two young forest sites and two old forest sites, and the boreal forest is composed of all old forests (stand age > 100 or at least > 50), while the temperate forests are mostly young forests. Previous studies have proved that young forests have a higher NPP/GPP ratio than mature forests (Delucia et al., 2007; Piao et al., 2010), which would boost NPP/GPP ratio value for temperate forests and change the NPP/GPP ratio trend from tropical to boreal forests.

DISCUSSION

Understanding the patterns of spatial and temporal variability in the NPP/GPP ratio, the resulting impacts on carbon use efficiency, and the ways in which these are related to climatic factors at both global and biome scales is essential for advancing our knowledge of global terrestrial carbon cycling and its response to ongoing climate change (Medlyn & Dewar, 1999; Cheng et al., 2000; DeLucia et al., 2007; Zhang et al., 2009). A more accurate understanding of these relationships through time can ultimately result in more reliable estimates of global carbon storage and fluxes. Remote sensing-based NPP and GPP data that are high resolution and continuous in both the spatial and temporal dimensions, e.g. MODIS NPP and GPP, enable examination of the patterns of temporal variation in the NPP/GPP ratio at a global scale.

Figure 5 The dependency of the net primary production (NPP)/gross primary production (GPP) ratio trend on temperature and precipitation. The NPP/GPP ratio trend zones represent the slope of the NPP/GPP ratio change trend; Trend_T represents the slope of the temperature change trend, and Trend_P represents the slope of the precipitation change trend.

(<−0.009 yr⁻¹, −0.009 to −0.006 yr⁻¹, −0.006 to −0.003 yr⁻¹, −0.003 to 0 yr⁻¹, 0 to 0.003 yr⁻¹, 0.003 to 0.006 yr⁻¹, 0.006 to 0.009 yr⁻¹, >0.009 yr⁻¹) were identified (Fig. 3). There were four decreasing NPP/GPP ratio zones and four increasing NPP/GPP ratio zones. Spatially, the highest NPP/GPP increase zones were concentrated in central North America, the southern edge of the Amazon basin and central Africa. The highest NPP/GPP decrease zones were located primarily in Western Australia, southern Africa and the western Pampas region of South America. This NPP/GPP ratio trend gradient demonstrated a clear relationship with temperature and precipitation. The strongest negative NPP/GPP ratio trends occurred where positive temperature trends were the highest and precipitation trends were close to zero. Conversely, the highest positive NPP/GPP ratio trends occurred where positive precipitation trends were highest and temperature trends were negative (Fig. 5).
Plants prioritize saving temporary carbohydrates and nutrient reserves over growing new tissues, and thus they are inherently slow growing (Grime & Hunt, 1975). For example, when faced with environmental stresses such as decreased water potential or nutrient supply, the immediate actions of plants are to slow down water or nutrient supply to seedlings and decrease leaf growth rate, while the rate of photosynthesis changes occurs afterwards (Hsiao, 1973; MacDonalds et al., 1986). Under decreased precipitation, a higher proportion of energy needs to be allocated to respiratory costs, and consequently, a lower proportion is available to construct new tissues (Metcalfe et al., 2010). Under warm and dry conditions, the hot, dry atmosphere and declined soil water cause stomatal closures and decrease carbon assimilations, but Ra could still be high (Arneth et al., 1998).

During periods of low temperature, less Ra results in larger carbon reserve accumulation (Ryan, 1991; Metcalfe et al., 2010). During warmer periods, more biological activities, a longer growing season and associated nutrient deficiencies can all lead to a lower NPP/GPP ratio (Chambers et al., 2004; Delucia et al., 2007). Enhanced precipitation would reduce fine root production and fine root respiration, which can result in a less than proportionate increase in respiration and, consequently, an increased NPP/GPP ratio (Ryan et al., 1996).

Normally, it has been observed that the rate of respiration increases exponentially with temperature (Ryan et al., 1995), whereas the rate of photosynthesis tends to stabilize over a wide range of temperatures, i.e. 20–35°C (Teskey et al., 1995; Lindroth et al., 1998). As a result, plants have to incur relatively higher respiration costs with increased temperature. The present study found that NPP responded more strongly to changes in precipitation and temperature than GPP, which is in line with this general understanding of plant biology and plant growth.

The spatially explicit NPP/GPP ratio values obtained from MODIS model products are constrained by hard-coded biophysical parameters in the model (Zhang et al., 2009). Due to the various types of bias and errors associated with modelled ecosystem productivity products, their applications for addressing mechanistic issues of ecosystem response to climates are also highly constrained. Besides the biophysical input parameter errors, there are two additional main potential sources of error in the MODIS GPP products: meteorology and radiometry. Meteorological errors stem from using coarse-scale interpolated climate data. Radiometric errors arise from underlying errors in the MODIS LAI/IPAR algorithm. The meteorology data determine the climatic inputs and vapour pressure deficit, which are among the most critical factors in controlling photosynthesis. The MOD17 products utilized spatially interpolated meteorology data at a relatively coarse scale (1.00° × 1.25°) of point data, which cannot capture much of the finer-scale variability in these variables. The high uncertainty of the NPP/GPP ratio in areas with low values revealed that carbon use efficiency is not as stable in these areas as in high-value areas. Thus, climatic variability might lead to relatively larger carbon fluxes in these areas. These features of the MODIS NPP and GPP products significantly affect the accuracy of their use for exploring the dependency of the NPP/GPP ratio on spatial variability in climate. In contrast, the temporal dynamics of NPP and GPP are more likely to be driven by climatic variability than the spatial patterns. Thus, conclusions about the dependence of the NPP/GPP ratio on climatic variability over time are likely to be less biased compared with the conclusions about spatial relationships derived from MODIS products. The radiometric model logic might introduce certain degree of bias, too. The model logic stipulates each environmental constraint acts on the maximum values of productivity in a linear way. But in reality, the assumed linearity is too simple. Many ecosystems respond to elevated temperature or enhanced precipitation in a non-linear manner (Norby & Luo, 2004; Zhou et al., 2008). In addition, soil moisture was not directly included in the model, which would likely lower the model accuracy. The future model needs to incorporate soil moisture effects more comprehensively.

This study only analysed the relationship between the NPP/GPP ratio and climate over a 10-year time horizon due to the limitation imposed by data availability. Information about plant growth under longer-term dry and wet periods also needs to be examined for a more complete picture of how the NPP/GPP ratio responds to climatic flux. Phenomena taking place over longer time duration, such multi-decadal climate change trends, are beyond the detectability of this study. However, the findings of this study still have fundamental significance for our understanding of longer-term climate trends. As revealed in this study, higher precipitation can increase the NPP/GPP ratio, whereas increases in temperature can lower the NPP/GPP ratio. Along both spatial and temporal dimensions, at times and in places experiencing abnormal drought, the NPP/GPP ratio would accordingly decrease, which represents a lower net productivity for farmland and a lower net growth for forests and grasslands. Likewise, the increased evapotranspiration that resulted from higher temperatures would weaken the NPP/GPP ratio, which in turn results in similar consequences to drought. Under a projected warming climate and accompanying higher evapotranspiration, significant areas of the global terrestrial plant ecosystem would be exposed to a hotter and drier environment, under which circumstances the NPP/GPP ratio would be expected to decrease because the Re cost would increase and global terrestrial ecosystem carbon use efficiency would decrease as a result. Besides improving biogeochemical model performance, the finding about a climate regulated NPP/GPP ratio can be a useful guide for agricultural and forest management activities. For example, Land Use, Land-Use Change and Forestry, and Reducing Emissions from Deforestation and forest Degradation and other activities have been implemented to mitigate the effects of climate change. But their efficiencies would depend on the NPP/GPP ratio of the forest sites where these activities are implemented. Activities implemented in a site with higher NPP/GPP ratio will bring greater and more immediate efficiencies.

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