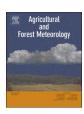
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## Global patterns of vegetation carbon use efficiency and their climate drivers deduced from MODIS satellite data and process-based models



Yue He<sup>a</sup>, Shilong Piao<sup>a,\*</sup>, Xiangyi Li<sup>a</sup>, Anping Chen<sup>b</sup>, Dahe Qin<sup>c,d</sup>

- <sup>a</sup> Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China
- <sup>b</sup> Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 46907, USA
- <sup>c</sup> State Key Laboratory of Cryospheric Sciences, Northwest Institute of Eco-environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China
- <sup>d</sup> National Climate Center, China Meteorological Administration, Beijing 100081, China

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#### ABSTRACT

Carbon use efficiency (CUE), defined as the ratio of net primary production (NPP) to gross primary production (GPP), represents the capacity of plants in converting assimilated atmospheric carbon dioxide to ecosystem carbon storage. Process-based models are important tools for simulating NPP and GPP; yet the model performance in simulating vegetation CUE has not been fully explored. The goal of this paper is thus to investigate the spatial variations in CUE from different process-based carbon cycle models in comparison with that from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data, and to analyze their linkage with climate factors. The global average CUE derived from the five process-based models is 0.45 ± 0.05 (range from 0.38 to 0.52), slightly lower than the value of 0.48 obtained from MODIS data. A strong latitudinal gradient of CUE, with greater CUE at high latitudes, is well agreed by these different datasets. However, there also exist considerable discrepancies in CUE estimations among those products, especially in temperate Northern Hemisphere. Furthermore, for both the satellite-based dataset and results from process-based models, vegetation CUE declines non-linearly with increase in temperature, but remains relatively stable with enhanced precipitation. Our results also indicate that the differences in global patterns of CUE estimated by different approaches could be primarily resulted from their systematic differences in autotrophic respiration (R<sub>a</sub>) rather than in GPP. Understanding mechanisms behind spatio-temporal changes in Ra is therefore a critical step towards better quantifying global CUE.

#### 1. Introduction

Carbon use efficiency (CUE), which is defined as the proportion of gross primary production (GPP, g C m<sup>-2</sup> yr<sup>-1</sup>) converted into net primary production (NPP, g C m<sup>-2</sup> yr<sup>-1</sup>), represents the efficiency of plants to sequester carbon from the atmosphere and is increasingly recognized as an important parameter shaping ecosystem carbon storage (Gifford, 2003; Chambers et al., 2004; De Lucia et al., 2007; Zhang et al., 2009; Piao et al., 2010; Vicca et al., 2012; Bradford & Crowther, 2013; Campioli et al., 2015). In practice, GPP usually represents the total amount of carbon captured through photosynthesis, and NPP is the net carbon stored in plant as new material after the reduction of GPP through autotrophic respiration (Ra, g C m<sup>-2</sup> yr<sup>-1</sup>) (Chapin et al., 2002). Therefore, this dimensionless parameter is also a measure of how GPP is partitioned into NPP and Ra, which could have a deep impact on vegetation structure and functioning (Ise et al., 2010). In particular, quantifying the responses of vegetation CUE to its climatic

drivers could improve our understanding of the dynamics of biosphereatmosphere carbon exchange under current and future climate change (Ise et al., 2010; Bloom et al., 2016).

Earlier terrestrial carbon-cycle models like CASA (Potter et al., 1993) and FOREST-BGC (Running & Coughlan, 1988) often assumed a fixed value of CUE to quantify  $R_a$  (De Lucia et al., 2007). However, there is increasing evidence suggesting that CUE actually varies with many factors, including vegetation type, climate conditions, management status, site fertility and forest stand age (Ryan et al., 1997; Amthor, 2000; Mäkelä & Valentine, 2001; Giardina et al., 2003; De Lucia et al., 2007; Piao et al., 2010; Vicca et al., 2012; Campioli et al., 2015). As an example, forest ecosystem CUE, according to a meta-analysis of 60 observations, ranged from 0.23 to 0.83 among different forest types (De Lucia et al., 2007).

The spatial variation of vegetation CUE across the global land and its association with environmental factors, however, remain poorly understood; although there have been many measurements of

E-mail address: slpiao@pku.edu.cn (S. Piao).

<sup>\*</sup> Corresponding author.

vegetation CUE at stand or site level (Ryan et al., 1997; Giardina et al., 2003; Van Iersel, 2003; Law et al., 2004; Metcalfe et al., 2010). The challenge comes from both the lack of sufficient observations and the large uncertainty generated in direct up-scaling from site measurements to larger spatial scale estimates. Recently, Zhang et al. (2009) used GPP and NPP products derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) to estimate the global distribution of vegetation CUE. Yet, the conclusion drawn from a single dataset is sensitive to its systematic biases and errors, making it critical to compare global patterns of vegetation CUE among different datasets. On the other hand, newly-emerged process-based carbon cycle models have been widely used to simulate major physiological and ecological processes (e.g., photosynthesis, respiration, carbon allocation and phenology) and ecosystem structures (Moorcroft, 2006; Huntingford et al., 2011; Wang et al., 2014a,b; Prentice et al., 2015; Wang et al., 2016; Piao et al., 2017; Liu et al., 2018; Wu et al., 2018). These process-based models may provide us a new approach to estimate vegetation CUE at the global scale.

Currently there are a variety of approaches available in obtaining CUE at the global scale (Ise et al., 2010; Zhang et al., 2009, 2014). But none of them are solely based on observations but rely upon certain assumptions and simplifications about model structures and parameters in simulating photosynthesis and autotrophic respiration. Hence, there is no consensus on the spatial variation of vegetation CUE and its drivers among different data streams. It is necessary to identify the sources of variation in CUE simulated by different models and/or dataset (MODIS), which could inform us of the potential uncertainties in the simulation of CUE and provide guidance on the future model development.

Here we conducted a systematic study of spatial patterns of vegetation CUE and their climatic drivers based upon MODIS satellite data and five process-based models. Moreover, we also examined the discrepancies in modelled CUE among different datasets and explored the potential reasons.

#### 2. Material and methods

#### 2.1. MODIS satellite data

Similar to the studies of Zhang et al. (2009; 2014), we used the MODIS GPP and NPP products (collection-055) over the period 2000-2012 (downloaded from http://files.ntsg.umt.edu/data/ NTSG\_Products/MOD17/GeoTIFF/MOD17A3/GeoTIFF\_30arcsec/) to calculate vegetation CUE. The MODIS algorithm integrates a light use efficiency logic using satellite observed LAI/FPAR to estimate GPP with an autotrophic respiration module to derive NPP (Running et al., 2004; Zhao et al., 2006; Zhao & Running, 2010). Both GPP and NPP in MODIS are driven by the NCEP/DOE II reanalysis climatic dataset (http:// www.esrl.noaa.gov). In addition to using satellite and climate data as inputs, it also requires biophysical parameters of biomes that are stored in the biome parameter look-up table (BPLUT). The uncertainties in the MODIS algorithm and its input data could lead to the biased estimation of NPP and GPP compared to in-situ measurements (e.g. Zhang et al., 2009, 2014; Sjöström et al., 2013). Note that the latest collection-6 MODIS NPP/GPP products (ftp://ladsweb.nascom.nasa.gov/allData/6/ ) were not used in our study because of large data gaps in this version. For example, in MODIS NPP product, there are some missing tiles in western Africa, most of Europe and the regions north of 60 °N (Fig. A.1 in Supplementary materials). We found that the estimated MODIS CUE from the collection-6 show higher values in the temperate zone of the two hemispheres and lower values in African sub-Sahel areas than those from collection-55 over the common region and periods (Fig. A.1 in Supplementary materials), suggesting the uncertainty of MODIS product in characterizing productivity. We therefore do not contend that MODIS CUE is necessarily more accurate than any of the five process model simulations.

#### 2.2. Process-based carbon cycle models

This study used global annual GPP and NPP simulated by five process-based carbon cycle models: the CSIRO Atmosphere Biosphere Land Exchange-3.5 (CABLE) (Wang et al., 2010, 2011); Community Land Model-4.0 (CLM4CN) (Thornton et al., 2007); Lund-Potsdam-Jena (LPJ) (Sitch et al., 2003); Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE) (Krinner et al., 2005); and Vegetation Integrative Simulator for Trace gases (VISIT) (Ito, 2010). All these models were run at a spatial resolution of 0.5° (Huang et al., 2015; Piao et al., 2015). Here, we focus on the model simulations which were driven by observed climate change based on CRU-NCEP v.4 (http:// dods. extra.cea.fr /data/ p529viov/ cruncep/) and the observed increasing atmospheric CO2 concentrations. Note that CLM4CN and CABLE have taken nitrogen cycle into account; therefore effects of nitrogen-limitation in photosynthesis could be assessed. Further information about the characteristics of each model is listed in Supplementary Table A.1, and the main processes and parameters of photosynthesis and autotrophic respiration in Supplementary Table

#### 2.3. Analyses

Because MODIS satellite data start in 2000, we used the simulations of the five process-based models from 2000 to the latest year available (different datasets have different time series, see Table A.1 in Supplementary materials). GPP and NPP outputs from MODIS data were re-gridded to  $0.5^{\circ}$  spatial resolution to be consistent with those of the process-based model outputs. Then, the monthly outputs of GPP and NPP from process-based models were combined to give annual values. To rule out areas with negligible vegetation, those pixels with mean annual normalized difference vegetation index (NDVI) lower than 0.1 were excluded from the analysis (Piao et al., 2014; Zhu et al., 2016; Wang et al., 2017). The vegetation CUE at the pixel scale was calculated as:

$$CUE = \frac{NPP}{GPP} \tag{1}$$

where NPP refers to annual net primary productivity (g C m $^{-2}$  yr $^{-1}$ ) and GPP to annual gross primary productivity (g C m $^{-2}$  yr $^{-1}$ ). Then, the yearly CUE was further averaged across the full study period to obtain multi-year mean value at the pixel scale. On the other hand, we calculated the yearly global mean CUE based on the average of CUE from all pixels. In addition to the area, the CUE in each pixel is also weighted by its GPP, which ensures that the regions with higher productivity will contribute more to the global mean CUE.

To compare the spatial patterns of vegetation CUE in the MODIS data with that produced by the process-based models, we applied the comparison map profile (CMP) method — a statistic-based new way in comparing two spatially explicit datasets (Gaucherel et al., 2008). This method estimates similarity indices between the two datasets using moving windows to compare their relationships at multiple spatial scales simultaneously. Firstly, the absolute value of the distance (D) between the means of dataset  $\boldsymbol{x}$  and dataset  $\boldsymbol{y}$  is computed according to the equation:

$$D = |\overline{x} - \overline{y}| \tag{2}$$

where both  $\overline{x}$  and  $\overline{y}$  are sample means of their moving windows respectively. Secondly, another similarity is obtained by the cross-correlation coefficient (CC) to compare the spatial data structures:

$$CC = \frac{1}{N^2} \sum_{i=1}^{N} \sum_{j=1}^{N} \frac{(x_{ij} - \bar{x})(y_{ij} - \bar{y})}{\sigma_x \sigma_y}$$
(3)

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