



Explaining inter-annual variability of gross primary productivity from plant phenology and physiology



Sha Zhou^{a,b,*}, Yao Zhang^c, Kelly K. Caylor^b, Yiqi Luo^{d,e}, Xiangming Xiao^{c,f}, Philippe Ciais^g, Yuefei Huang^{a,h,*}, Guangqian Wang^a

^a State Key Laboratory of Hydrosience and Engineering, Department of Hydraulic Engineering, Tsinghua University, Beijing 100084, China

^b Department of Civil and Environmental Engineering, Princeton University, Princeton, NJ 08544, USA

^c Department of Microbiology and Plant Biology, Center for Spatial Analysis, University of Oklahoma, Norman, OK 73019, USA

^d Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA

^e Center for Earth System Science, Tsinghua University, Beijing 100084, China

^f Institute of Biodiversity Science, Fudan University, Shanghai 200433, China

^g Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, Gif-sur-Yvette 91190, France

^h College of Ecological and Environmental Engineering, Qinghai University, Xining 810086 Qinghai, China

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ABSTRACT

Climate variability influences both plant phenology and physiology, resulting in inter-annual variation in terrestrial gross primary productivity (GPP). However, it is still difficult to explain the inter-annual variability of GPP. In this study, we propose a Statistical Model of Integrated Phenology and Physiology (SMIPP) to explain the contributions of maximum daily GPP (GPP_{max}), and start and end of the growing season (GS_{start} and GS_{end}) to the inter-annual variability of GPP observed at 27 sites across North America and Europe. Strong relationships are found between the anomalies of GS_{start} and spring GPP ($r = 0.82 \pm 0.10$), GPP_{max} and summer GPP ($r = 0.90 \pm 0.14$), and GS_{end} and autumn GPP ($r = 0.75 \pm 0.18$) within each site. Partial correlation analysis further supports strong correlations of annual GPP with GS_{start} (partial r value being 0.72 ± 0.20), GPP_{max} (0.87 ± 0.15), and GS_{end} (0.59 ± 0.26), respectively. In addition, the three indicators are found independent from each other to influence annual GPP at most of the 27 sites. Overall, the site-calibrated SMIPP explains $90 \pm 11\%$ of the annual GPP variability among the 27 sites. In general, GPP_{max} contributes to annual GPP variation more than the two phenological indicators. These results indicate that the inter-annual variability of GPP can be effectively estimated using the three indicators. Investigating plant physiology, and spring and autumn phenology to environmental changes can improve the prediction of the annual GPP trajectory under future climate change.

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1. Introduction

Global carbon cycle exhibits strong inter-annual variability, most of which has been inferred to be caused by changes in carbon sequestration in terrestrial ecosystems (Ballantyne et al., 2012). Indeed, the inter-annual variability is one of the least understood carbon cycle processes (Luo et al., 2015). Past researches have been focused on the timings of spring emergence and autumn senescence under global warming, which were found to shift in

the Northern Hemisphere, and the length of growing season has changed (Cleland et al., 2007; Ibáñez et al., 2010). Growing season length has substantial effects on annual carbon uptake; both gross primary productivity (GPP) and net ecosystem productivity (NEP) are enhanced by longer growing seasons caused by warming climate (Churkina et al., 2005; Dragoni et al., 2011; Keenan et al., 2014; Piao et al., 2007; Richardson et al., 2010). In addition, warming-induced drought stress limits plant photosynthesis in summer and leads to great decline in peak summer productivity and even annual GPP (Angert et al., 2005; Buermann et al., 2013; Ciais et al., 2005; Schwalm et al., 2012). Since both phenology dates and photosynthetic physiology greatly affect annual GPP, it is necessary to explain annual GPP variability from both plant phenology and physiology yet to partition their respective contributions.

Recently, Xia et al. (2015) proposed that annual GPP is jointly controlled by plant phenology and physiology and can be diag-

* Corresponding authors at: State Key Laboratory of Hydrosience and Engineering, Department of Hydraulic Engineering, Tsinghua University, Beijing 100084, China

E-mail addresses: zhous13@mails.tsinghua.edu.cn (S. Zhou), yuefeihuang@tsinghua.edu.cn (Y. Huang).

nosed by the product of the length of CO₂ uptake period (CUP) and the maximum capacity of CO₂ uptake (GPP_{max}). The product of CUP and GPP_{max}, i.e., CUP × GPP_{max}, can explain more than 90% of the temporal GPP variability in most areas of North America during 2000–2010 and more than 95% of the spatial GPP variation among 213 flux tower sites. Although CUP is a good phenological indicator, it does not allow us to separately evaluate the influence of spring and autumn phenology on annual GPP variability. While CUP does not change, spring emergence and autumn senescence may shift and affect annual GPP in different ways (Richardson et al., 2010). In addition, the respective contributions of spring emergence and autumn senescence to growing season change and hence annual GPP variability have not been separated, and their contributions seem to vary across different ecosystems (Garonna et al., 2014; Jeong et al., 2011; Menzel and Fabian, 1999; Zhu et al., 2012). Thus, the effects of both spring emergence and autumn senescence on annual GPP should be considered separately to investigate the contributions of spring and autumn phenological changes to the inter-annual variability of GPP.

In northern temperate ecosystems, the growing season starts in spring and ends in autumn when the photosynthetic carbon assimilation is limited by temperature and solar radiation. Daily photosynthetic rate reaches its peak (GPP_{max}) in summer under favorable environmental conditions, and GPP is small or even negligible in winter (Allard et al., 2008; Hirata et al., 2007; Saigusa et al., 2008; Uehlinger, 2006). The starting and ending dates of the growing season, expressed by GS_{start} and GS_{end}, are closely correlated with spring and autumn GPP, respectively (Keenan et al., 2014). Similarly, GPP_{max} is positively correlated with summer GPP (Stoy et al., 2014). Thus, the three indicators, GS_{start}, GPP_{max}, and GS_{end}, can influence seasonal GPP and hence annual GPP. Combining the effects of these three indicators, it may have the potential to explain annual GPP variability and separate the respective contributions of both spring and autumn phenology and plant physiology to it.

Because the phenological and physiological events occur in different seasons and affect carbon assimilation in different ways, these three indicators may have independent effects on annual GPP. The spring emergence and autumn senescence dates vary temporally and spatially, and respond differently to climate change (Vitasse et al., 2009). Although there is a strong correlation between warmer temperature and earlier spring emergence, the association between temperature and autumn senescence is weaker (Menzel et al., 2006). In addition to temperature, spring emergence is also affected by other factors, such as winter chilling conditions and freeze-thaw processes (Chen et al., 2011; Fu et al., 2015; Pope et al., 2013; Yi and Zhou, 2011; Yu et al., 2010). Autumn senescence has been reported to be influenced by multiple factors, including temperature, precipitation, photoperiod, soil moisture, wind, frost events, etc. (Fracheboud et al., 2009; Panchen et al., 2015; Yang et al., 2015). In view of the different responses to climate factors, both spring emergence and autumn senescence should be included and the combination of the three indicators could provide more exhaustive explanation of annual GPP variability.

This paper proposes an integrated statistical model to explain the inter-annual variability of GPP in the Northern Hemisphere from the perspectives of both phenology and physiology and evaluates the contributions of phenological and physiological changes to annual GPP variability using data from 27 flux tower sites (283 site-years) across North America and Europe. The specific objectives are to (1) investigate the effects of variations in GS_{start}, GPP_{max} and GS_{end} on respective seasonal GPP and hence annual GPP; (2) develop a Statistical Model of Integrated Phenology and Physiology (SMIPP) involving the three indicators to explain the inter-annual variability of GPP for each site; (3) partition the contributions of

phenological and physiological changes to annual GPP variability for the 283 site-years.

2. Materials and methods

2.1. Flux tower data

GPP estimates (gC m⁻² day⁻¹) were obtained from 14 AmeriFlux sites and 13 EuroFlux sites (Table 1). A total of 283 site-years were used and the record length for each site ranged from 6 to 21 years. Generally, the 27 flux sites were classified into three plant functional types, including 8 deciduous broadleaf forests (DBF), 9 evergreen needle-leaf forests (ENF), and 10 non-forests sites (NF) (e.g., cropland, grassland, closed shrubland and wetland). The estimates of GPP were available from AmeriFlux (Level 2 products, <http://public.ornl.gov/ameriflux>) and EuroFlux (Level 4 products, <http://gaia.agraria.unitus.it/>). The half-hourly eddy covariance measurements (i.e., net ecosystem exchange) used in this study have been standardized, gap-filled using the Marginal Distribution Sampling (MDS) method, and partitioned into GPP and ecosystem respiration (Papale and Valentini, 2003; Reichstein et al., 2005).

The 27 sites were chosen according to the following four criteria. (1) The site-years with more than 80% of the GPP data which were actual measurements or gap-filled with high confidence, i.e., data marked as ‘the original’ or ‘most reliable’ according to the quality flag, were selected. Only the site-years with effective measurements covering the entire growing season (March–October) were used. (2) The sites with at least 6 site-years of data were selected in order to avoid overfitting of multiple linear regression. According to Austin and Steyerberg (2015), a minimum of two observations per variable is required to permit accurate estimation of regression coefficients (relative bias < 10%). As three variables (GS_{start}, GPP_{max} and GS_{end}) were used to build up the regression, 6 years of observations for each site is the minimum requirement. (3) Sites located in the moist tropical climate with low seasonality of daily GPP were not used because the phenology dates cannot be identified according to the given threshold. (4) Sites located in some Mediterranean climate were not used because the maximum daily GPP occurs during the winter–spring seasons.

The half-hourly data of GPP were aggregated to daily totals. The following subsequent steps were taken: (1) seasonal and annual GPP were calculated for each site-year; for seasonal analysis, spring refers to March–May, summer refers to June–August, autumn refers to September–November, and the remaining months are considered as winter; (2) the time series of daily GPP over each site-year were smoothed using singular spectrum analysis (SSA) to identify the three indicators GS_{start}, GPP_{max} and GS_{end}; (3) Pearson correlation was used to develop the relationship between the anomalies of the three indicators and their respective seasonal GPP; Pearson partial correlation was used to develop the relationship between the anomalies of annual GPP and each of the three indicators; (4) the interrelationship between each pair of the three indicators was investigated to test whether the three indicators are independent from each other; (5) a multiple regression model was established between the anomalies of annual GPP and the three indicators to explain the inter-annual variability of GPP and separate the contributions of the three indicators for each site.

2.2. Statistical model of integrated phenology and physiology

The Statistical Model of Integrated Phenology and Physiology (SMIPP) to explain the inter-annual variability of GPP is an extension of the approach of Xia et al. (2015), i.e., $GPP = \alpha \cdot CUP \cdot GPP_{max}$.

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