



Original Articles

Water use efficiency in response to interannual variations in flux-based photosynthetic onset in temperate deciduous broadleaf forests



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ABSTRACT

Climate change has significantly influenced the productivity of terrestrial ecosystems through water cycles. Water use efficiency (WUE) is an important indicator for understanding how water couples with the carbon cycle. Abiotic factors such as climatic factors and CO₂ concentration have been investigated to understand the mechanisms involved in the coupled carbon-water cycle of terrestrial ecosystems in response to climate change. However, the effects of biotic factors on WUE are less clear. By analyzing 66 site-years of flux and meteorological data obtained from 8 temperate deciduous broadleaf forest sites across North America and Europe, we found that ecosystem-scale WUE (defined here as the ratio of gross primary production (GPP) to evapotranspiration (ET)) in the spring significantly increased with the advance of the flux-based photosynthetic onset (FPO), mainly because an earlier FPO could lead to a steeper increase in GPP than in ET. However, the advance of FPO probably reduced summer WUE as a result of the enhancement of water stress by ET in the spring in temperate deciduous broadleaf forest. Our results also implied that spring warming had an indirectly positive effect on WUE through advancing spring phenology, but such a positive effect will likely weaken once the sensitivity of spring phenology to warming decreases as reported. Here, we argue that phenology, which exerts critical biotic control over most ecological processes, plays a larger role than expected in the regulation of the seasonal WUE and cannot be ignored in earth system models.

1. Introduction

Global warming, changes in precipitation patterns and frequent drought events have already significantly influenced the carbon uptake and cycles of terrestrial ecosystems through water cycles (Liu et al., 2015; Hufkens et al., 2016; Wolf et al., 2016). Water use efficiency (WUE)—the rate of carbon uptake per unit of water lost—is an important indicator of ecological functions and the coupled carbon-water cycle of terrestrial ecosystems (Keenan et al., 2013; Tang et al., 2014). Researchers have investigated temporal-spatial variations in WUE and their correlations with abiotic controls to understand the coupled carbon-water cycle of terrestrial ecosystems in response to climate change (Li et al., 2008; Yu et al., 2008; Dong et al., 2011; Niu et al., 2011; Zhu et al., 2011; Keenan et al., 2013; Sun et al., 2015; Huang et al., 2015, 2016). However, the variations in WUE in response to biotic controls remain little understood.

As an important plant trait, phenology is directly or indirectly

associated with many physiological and ecological processes in plants (Noormets, 2009). From a broad perspective, phenology is not restricted solely to the timing of life cycle events or phenomena (e.g., the sprouting and coloring of plants) but also includes the transitions of annual cycles of ecosystem processes (e.g., the seasonality of photosynthesis in winter-dormant/summer-active ecosystems) (Morissette et al., 2009; Tang et al., 2016). It is well established that plant phenology significantly regulates carbon uptake and water loss across diverse plant functional types (Piao et al., 2007; Noormets, 2009; Richardson et al., 2010; Schwartz, 2013; Wu et al., 2013; Keenan et al., 2014; Shen et al., 2015). Due to these diverse sensitivities of carbon and water fluxes to interannual fluctuations of phenology, the variations in WUE with phenology can potentially be quite dynamic, depending on the strength of the coupling between carbon assimilation and water consumption (Richardson et al., 2013).

Attempts and exploitations on WUE response to variations in phenology have been carried out. For example, previous studies have

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shown that mature leaves exhibit a lower WUE than new leaves (Sobrado, 1994; Muthuri et al., 2009), and the seasonal WUE is closely associated with variations in the leaf area index (LAI) in plant communities (Werner and Máguas, 2010; Singh et al., 2014). However, studies at the scale of leaves or individual plants are insufficient to explain the relationship between the ecosystem WUE and phenology at regional and global scales. Moreover, these studies have only examined the variation in the transient WUE associated with a successive phenological process within a yearly cycle, but they could not explain the seasonal or annual WUE in response to the interannual variability of a certain phenological transition.

Current climatic changes have affected the spring phenology of plants to a great extent in the middle and high latitudes of the Northern Hemisphere, particularly in temperate deciduous broadleaf forests (Peñuelas and Filella, 2001; Fu et al., 2015a, 2015b; Piao et al., 2015), which in turn affect ecosystem processes related to carbon and water cycles, with consequences for WUE (Peñuelas et al., 2009; Richardson et al., 2010, 2013). To account for the warming and extreme drought events predicted in the future, awareness of the responses and sensitivities of WUE to interannual variations in critical phenological transitions in temperate forest ecosystems is critical.

Fortunately, the rich data contained in the FLUXNET database can be used to explore the relationship between variability in phenology and WUE across plant function types. Continuous measurements of carbon and water exchange can be obtained using the eddy-covariance (EC) technique. Thus, carbon flux phenology, as a more robust indicator related to the transitions of photosynthetic cycle compared with satellite- or ground-observation phenology (Garrity et al., 2011; Wu et al., 2012), can be linked to carbon flux and latent heat flux (evapotranspiration) simultaneously (Richardson et al., 2010). Using 66 site-years of flux data obtained from 8 temperate forest sites across North America and Europe (with a median time period of 7 years), this study investigated the response of seasonal and annual WUE to the interannual variability of the flux-based photosynthetic onset and examined the roles of phenological and climatic factors in regulating WUE.

2. Material and methods

2.1. Study sites

In this study, the flux and meteorological dataset was derived from the “Fair Use” La Thuile FLUXNET data set (V4) (<http://www.fluxdata.org>). Here, the study sites were identified using the following criteria for inclusion: at least 5 years of continuous and complete data records; less than 20% gap-filled records in each year; availability of site-level meteorological data; a lack of recent disturbances or heavy managements. In addition, only temperate deciduous broadleaf forest sites were selected, where temperature and day length are considered the main drivers of the seasonal variation in phenology (Richardson et al., 2010). Finally, the 8 sites and 66 site-years were included in our analysis. Additional details regarding these sites are provided in Fig. 1 and Table 1.

2.2. Flux and meteorological measurements

WUE represents the rate of carbon uptake per unit of water loss and is calculated using various methods at different scales (Keenan et al., 2013). In this study, we defined WUE at the ecosystem scale as follows:

$$WUE = \frac{GPP}{ET} \quad (1)$$

where GPP refers to the seasonal/annual mean gross primary productivity (g Cm^{-2}) and ET to the seasonal/annual mean evapotranspiration (mm) in a forest site (Sun et al., 2016; Huang et al., 2015, 2016). Spring and summer, the target seasons in this study, were defined as

March–May and June–August, respectively (Huang et al., 2016).

The GPP fluxes that we used were derived from 30-min eddy covariance measurements (net ecosystem exchange of CO_2 , NEE) that were standardized and gap-filled using a set of common algorithms (Papale et al., 2006; Moffat et al., 2007). The measured latent heat (LE, W m^{-2}) fluxes were used to obtain the water loss (ET, mm/day) by multiplying a factor of 0.035 which was converted by the formula $ET = LE/\lambda$ (where λ represents amount of energy needed to evaporate one unit weight of water: $2,454,000 \text{ J kg}^{-1}$) (Tang et al., 2014).

We also calculated the corresponding spring, summer and yearly means of the principal climatic variables affecting WUE, including the mean air temperature (T_a , $^{\circ}\text{C}$), total precipitation (Prec, mm), daily shortwave global radiation (R_g , $\text{MJ m}^{-2} \text{ day}^{-1}$) and atmospheric carbon dioxide concentration (CO_2 , ppm), at each site. Due to data access restrictions, the CO_2 concentration for each site was replaced by that measured at Mauna Loa (Hawaii).

2.3. Photosynthetic onset based on GPP flux

The following procedures were used to calculate the spring phenological transition dates of the photosynthesis cycle based on the daily GPP for each year for each studied site, which is referred to as the flux-based photosynthetic onset (FPO). Notably, we examined the timing of changes from one state to the other in this study, referred to as state-transition dates, rather than the instantaneous phenological states of the plants (Moulin et al., 2010).

A seven-parameter logistic function (Gonsamo et al., 2013) was adopted to derive smoothed curves for the daily GPP observations, as follows:

$$f(x) = \alpha_1 + \frac{\alpha_2}{1 + e^{-\partial_1(x-\beta_1)}} - \frac{\alpha_3}{1 + e^{-\partial_2(x-\beta_2)}} \quad (2)$$

where x is a day of the year, and $f(x)$ is the observed GPP at x . α_1 is background GPP; α_2 is the amplitude from the background to the spring and early summer plateau; and α_3 is the amplitude from the background to the late summer and autumn plateau. ∂_1 and ∂_2 are the normalized slope coefficients, and β_1 and β_2 are the midpoints in the DOYs of the greenup and browndown periods, respectively. The smoothed GPP values were used to define the FPO, with the dates on which the smoothed daily GPP reached 10% of the seasonal maximum in spring used to represent the onset of significant photosynthesis. This 10% GPP threshold was determined because dynamic thresholds are more beneficial for capturing and comparing interannual variations in phenological events (Wu et al., 2012, 2013) (Fig. 2).

2.4. Statistical analysis strategy

Linear regression analysis was used to examine the relationships between WUE and phenological factors with respect to local and regional patterns in this study. Additionally, panel (data) analysis, a robust statistical method widely used in social science and econometrics (Debarsy et al., 2012), was used in this study. In the panel analysis, a random-effects generalized least squares (GLS) regression model (Schmidheiny and Basel, 2011) was applied to identify the independent effect of each selected variable (e.g., spring phenology, meteorological variables and CO_2 concentration) on seasonal and annual WUE and its components after controlling the others across all study sites.

3. Results

First, we quantified the response of WUE in the spring to interannual variations in photosynthetic onset. The linear regression analysis showed that spring WUE was negatively correlated with FPO at each forest site over the measurement period (Fig. 3a). The change in spring WUE associated with FPO was significant ($P < 0.05$) at four of the

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