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Improving the ability of the photochemical reflectance index to track canopy light use efficiency through differentiating sunlit and shaded leaves

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A B S T R A C T

Accurate estimation of light use efficiency (LUE) of plant canopies is essential for calculating gross primary productivity (GPP) using LUE models and is also useful for calibrating process-based models for regional and global applications. A promising method for estimating LUE is through remote sensing of the photochemical reflectance index (PRI). However, there are internal (e.g. pigment concentrations) and external factors (e.g. environmental conditions and sun-target-view geometry) that affect PRI signals. Considering the reflectance difference between sunlit and shaded leaves, the ratio of observed canopy reflectance to leaf reflectance is used to represent the observed fraction of sunlit leaves, and the observed fraction of shaded leaves is calculated with a geometrical optical model. Thus, a canopy-level PRI observation is separated into sunlit and shaded PRI values, and a two-leaf canopy PRI (PRI_t) is calculated as sum of these two values weighted by their respective sunlit and shaded leaf area indices. The usefulness of PRI_t in assessing the canopy-level LUE is evaluated with automated multi-angle PRI observations acquired on a flux tower from April to September 2013 over a sub-tropical coniferous forest in southern China. In each 15-minute observation cycle, PRI is observed at four view zenith angles fixed at (37°, 47°, 57°) or (42°, 52°, 62°) and the instantaneous solar zenith angle in the azimuth angle range from 45° to 325° (from the geodetic north). In both the half-hourly and daily time steps, PRI_t can effectively improve (>50% and >35% increases in R^2, respectively) the ability as a proxy of LUE derived from the tower flux measurements over the big-leaf PRI taken as the arithmetic average of the multi-angle measurements in a given time interval. In the dry season from July to September, correlations of PRI with LUE at daily time steps are much stronger in the two-leaf case than in the big-leaf case. The correlation between PRI_t and LUE is the strongest ($R^2 = 0.785$, $p < 0.001$) in July. PRI_t is very effective in detecting the light and low-moderate drought stress on LUE at half-hourly time steps, while ineffective in detecting severe atmospheric water and heat stress, which is probably due to alternative radiative energy sink, i.e. photorespiration. Overall, the two-leaf approach well overcomes some external effects (e.g. sun-target-view geometry) that interfere with PRI signals.

1. Introduction

The gross primary production (GPP) of terrestrial ecosystems constitutes the largest global carbon flux over land and exhibits significant spatial and temporal variations (Beer et al., 2010; Frankenberg et al., 2011; Zhao and Running, 2010). Two main kinds of models, i.e. process-based models and light use efficiency (LUE) models, are widely used to estimate GPP. Due to their wide spatial coverage, remote

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sensing techniques are shown to be useful for improving the estimation of GPP in combination with LUE models (Monteith, 1972, 1977). LUE models usually express GPP as the product of the amount of absorbed photosynthetically active radiation (APAR) and the LUE (GPP = LUE × APAR) (Hilker et al., 2008a; Kumar and Monteith, 1981; Monteith, 1972).

Given accurate APAR, LUE is a critical variable in the estimation of GPP, which is determined by a large number of factors constraining photosynthetic processes (Heinsch et al., 2006; Myneni et al., 1995; Prince and Goward, 1995; Running et al., 2004; Tan et al., 2012; Turner et al., 2003; Zhao et al., 2006). In currently used LUE models, LUE is assumed to change mostly with vegetation types and also to be regulated by some environmental factors, such as temperature, water vapor pressure deficit (VPD), and soil water content (Myneni et al., 1995; Potter et al., 1993; Ruimy et al., 1994; Running et al., 2000; Tan et al., 2012; Xiao et al., 2004). However, such an assumption probably induces considerable uncertainties in determining GPP (Goetz and Prince, 1999; He et al., 2013; Lagergren et al., 2005; Oliphant et al., 2011; Zhang et al., 2011). LUE is closely related to photosynthetic parameters such as the maximum carboxylation rate and stomatal conductance (Liu et al., 2014; Santaren et al., 2007; Van Oijen et al., 2005). Therefore, proper determination of LUE is also useful for calibrating process models for regional and global applications.

A promising method for accurately estimating LUE is using the photochemical reflectance index ($PRI = (R_{531} - R_{570})/(R_{531} + R_{570})$, where R_{531} and R_{570} are spectral reflectances at wavelengths 531 and 570 nm, respectively) calculated from remote sensing data (Gamon et al., 1992; Stagakis et al., 2014). PRI is currently considered as the most representative index of the xanthophyll cycle, which is part of the leaf photoprotective mechanisms and functionally related to photosynthetic rates (Demmig-Adams and Adams, 1992, 1996; Demmig-Adams, 1998). Since PRI was developed, many studies at leaf and canopy scales use PRI to estimate LUE.

A growing number of studies have demonstrated that PRI is an effective index to represent spatiotemporal variations of LUE for a large variety of species, at multiple scales (Drolet et al., 2005; Filella et al., 2004; Garbulsky et al., 2011, 2013; Hall et al., 2008; Hilker et al., 2008b, 2009, 2010; Nakaji et al., 2014; Peñuelas et al., 2011; Soudani et al., 2014; Stagakis et al., 2014). There is strong evidence that PRI is able to track rapid changes in photosynthetic status based on high frequency measurements (Gamon et al., 1997; Guo and Trotter, 2004; Magney et al., 2014; Magney et al., 2016). PRI is also proved to be able to capture seasonal variations of LUE in different ecosystems (Nakaji et al., 2006, 2014; Soudani et al., 2014; Zhang et al., 2015), but the relationship between PRI and LUE changes throughout the growing season due to changing pigment pool sizes that confound PRI signals (Filella et al., 2009; Sims et al., 2006; Wong and Gamon, 2015c, b). Although strong correlations are found between PRI and LUE for individual species, they are much weaker for groups of species, probably due to different light response functions among different species (Guo and Trotter, 2004, 2006). Even though PRI-LUE correlation has been examined over a large amount of ecosystems, the underlying relationship between PRI and LUE at the canopy scale is still unclear because of the confounding influence by the canopy structure at various illumination and observation geometries (Gamon et al., 1997; Garbulsky et al., 2011; Stagakis et al., 2014).

It has been documented that there are certain issues with PRI at the canopy scale. PRI is strongly influenced not only by internal physiological properties, such as species-specific configurations and adaptations of the photoprotective mechanism and pigment concentration, but also by numerous external factors, such as sun-target-view geometry, background reflectance, diffuse sky radiation, canopy structure (both leaf area index (LAI) and leaf angle distribution), and radiative signals derived from different sensors (Barton and North, 2001; Garbulsky et al., 2011). Both canopy PRI and LUE vary with the angle of illumination due to their sensitivity to the shadow/sunlit fraction (Hall et al., 2008, 2011; Hilker et al., 2008b, 2011). Nevertheless, the dependence of PRI on the shadow fraction is affected by the ratio of diffuse to total radiation, which would dampen the effect of sun-target-view geometry (Damm et al., 2015; Mõttus et al., 2015). To popularize PRI in plant physiological studies, these confounding external factors need to be considered systematically.

Multi-angle spectral observation could help separate the extraneous effects from the physiological signal. Due to the effects of sun-target-view geometry, a viewer with a given instantaneous field of view (IFOV) may see different fractions of sunlit and shaded leaves and sunlit and shaded backgrounds at different view angles above the canopy. After a semi-empirical kernel-driven bidirectional reflectance distribution function (BRDF) model is used to standardize directional observations to one common sun-target-view geometry, the correlation between canopy PRI and LUE is significantly enhanced (Hilker et al., 2008b). However, there are still some limitations in BRDF-normalized PRI. As directional PRI (observed from multiple view angles) is associated with sunlit/shaded foliage, Cheng et al. (2012) reported that various sunlit/shaded canopy ratios affected the utilization of canopy PRI over different stages of corn during a growing season. The best sunlit/shaded canopy ratio for retrieving the 'true' canopy PRI possibly changes with canopy types. Therefore, the best observation direction with an appropriate sunlit/shaded foliage ratio, a structure-based parameter, is prerequisite for using a BRDF model to interpret canopy PRI. Moreover, the contributions of understory vegetation and background to the reflectance of a forest canopy vary with changing view angles (Pisek et al., 2015; Rautiainen and Lukeš, 2015; Spanner et al., 1990). Consequently, it is not easy to eradicate the effect of the background signal using a semi-empirical kernel-driven model.

Theoretically and empirically, Hall et al. (2008, 2011) demonstrated that directional changes in observed canopy PRI in a given half hour interval can be attributed almost entirely to changes in shadow fraction (α_s). The relationship between the partial derivative of PRI with respect to α_s ($\partial PRI/\partial \alpha_s$, PRI_h) and the relative light use efficiency $\Delta\varepsilon$ (relative to an unstressed canopy) is dependent on the range of shadow fractions for which the canopy is observed. An airborne LiDAR dataset is used to derive the shadow fraction of a forest canopy using a hillshade algorithm based on a canopy height model (CHM) (Hilker et al., 2010). This work demonstrated that PRI_h is more significantly correlated with canopy LUE at both Douglas-fir and Aspen sites than PRI (Hall et al., 2011; Hilker et al., 2010). However, as the model does not account for diffuse radiation conditions, this assessment of α_s could only be used under clear sky conditions. The proportion of direct to total irradiance should certainly be featured (Mercado et al., 2009) and another measurement of sunlit/shadow fractions should be explored for LUE models.

PRI varies with different view angles within a short time period when radiation is relatively stable (Zhang et al., 2015), and variations of PRI of the whole canopy are mostly attributed to sunlit PRI. As Hall et al. (2008, 2011) demonstrated that PRI is sensitive to the shadow fraction in the canopy, while remotely sensed PRI is only from part (mainly top) of the canopy, some studies (Hilker et al., 2008b, 2009, 2010) have tried to find an effective way to extrapolate limited PRI observations to the whole canopy with an ultimate purpose of accurately estimating the whole canopy LUE. However, simple and universal methods to separate the canopy PRI into sunlit and shaded parts under variable weather conditions have not been developed yet. To better understand the ability of PRI working as an indicator of LUE at the canopy level over different temporal scales, the objectives of this study are: (1) to develop a simple two-leaf PRI approach to separate the canopy into sunlit and shaded parts, using a ratio calculated by observed canopy reflectance to leaf reflectance as the observed fraction of sunlit leaves; (2) to use this approach for estimating half-hourly average PRI of the entire canopy continuously over a growing season using in situ multi-angle spectral data acquired from a sub-tropic evergreen coniferous forest stand; and (3) to validate the two-leaf PRI against a