



Spatial variation of canopy PRI with shadow fraction caused by leaf-level irradiation conditions



Tuure L.H. Takala, Matti Mõttus *

Department of Geosciences and Geography, University of Helsinki, P.O. Box 68, FI-00014, Finland

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ABSTRACT

Photochemical reflectance index (PRI) is one of the best proxies to estimate the light use efficiency and photosynthetic activity of vegetation from remote sensing observations, especially if diurnal variations can be monitored. The calculation of PRI from leaf-level spectral reflectance measurements is unambiguous. Interpretation of the value of this index is more complicated, as it is affected by leaf structure and its carotenoid and chlorophyll content. Generally, a change in leaf-level PRI indicates a change in its photosynthetic capacity. At the scales of the canopy and beyond, various non-physiological factors modulate the leaf-level PRI signal inducing large angular and spatial variations in PRI. Specifically, previous studies have shown that within-canopy illumination variations and shadowing effects directly affect the PRI of a canopy. When observing a forest with a resolution finer than the size of a tree crown, large areas of shaded and sunlit foliage become visible. The spectral distribution of irradiance in these canopy regions is different from the average top-of-canopy irradiance used in the calculation of the canopy PRI. Thus, the leaf and canopy PRI can become decoupled. To date, no thorough analytical and empirical analysis of how the spectrally variable within-canopy light conditions cause apparent, non-physiological variation in canopy PRI has been published. In this study, we propose a new method to assess these PRI variations in structured vegetation from high spatial resolution (pixel size smaller than 1 m) imaging spectroscopy data. We used airborne imaging spectroscopy of boreal forest stands to evaluate the spectral irradiance in different locations inside the canopy and calculated a correction term for the canopy PRI estimates defined using top-of-canopy irradiance. We determined the maximum value of the correction term by sampling the most sunlit and shaded road surface locations adjacent to tree crowns. Results indicated that under the particular illumination-view geometry, irradiance variations decreased the canopy PRI by as much as 0.06 (relative change > 100%). The correction depended only slightly on atmospheric correction parameters. Finally, we reduced the illumination-related apparent variation in canopy PRI using the two-leaf canopy photosynthesis modeling scheme, canopy shadow fraction and the maximum correction term. In a test scene, the average illumination-corrected PRI was 0.027 smaller than non-corrected canopy PRI and showed no correlation with the shadow fraction, indicating a lack of down-regulation at the time of measurement. In theory, approach can be applied to all canopy level PRI measurements from towers, aircrafts and satellites under any observation geometry. However, further validation, preferably using in situ leaf reflectance data from different biomes, would be required before the algorithm can be routinely applied.

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1. Introduction

1.1. Variations in canopy photosynthesis

Photosynthesis has an important role in many ecosystem processes, such the exchange of energy, carbon and water between the biosphere and the atmosphere (Baldocchi, 2008). In general, the rate at which carbon dioxide is assimilated from the atmosphere (i.e., productivity) is proportional to numerous biophysical and environmental variables,

such as to the flux of photosynthetically active radiation (PAR), amount of photosynthesizing foliage, air temperature, carbon dioxide and water vapour concentration, leaf nitrogen content, and water and nutrient availability (e.g., Demmig-Adams & Adams, 1996; Gamon, Field, Fredeen, & Thayer, 2001; Farquhar, von Caemmerer, & Berry, 1980; Mäkelä et al., 2008; Monteith, 1977). The efficiency with which absorbed light is converted to fixed carbon is known as the light use efficiency (LUE, Gitelson & Gamon, 2015) and is an essential variable to determine vegetation productivity (Monteith, 1977). Photosynthetic rate and efficiency vary significantly over space – from leaves on a single plant to different plant species and plant functional types, stands and ecosystems – and time, from seconds to seasons (Gamon et al., 2001;

* Corresponding author.

E-mail address: matti.mottus@helsinki.fi (M. Mõttus).

Garbulsky et al., 2010; Hilker et al., 2012; Peñuelas, Filella, & Gamon, 1995; Rascher, Nichol, Small, & Hendricks, 2007).

LUE is defined a posteriori over a certain time interval as the ratio of gross primary production (GPP) to photosynthetically active radiation absorbed by green canopy elements (APAR) (Gitelson & Gamon, 2015; Monteith, 1977) and is widely utilized in modeling contexts. Both PAR and APAR can vary significantly within a forest canopy and are proportional to, for example, canopy structural parameters (e.g., the distribution of leaf area density) and the angle of illumination (e.g., Gamon et al., 2001; Hall, Hilker & Coops, 2012; Oliphant, Susan, Grimmond, Schmid, & Wayson, 2006). Gamon et al. (2001) demonstrated that APAR alone can explain a significant part of the photosynthetic variation within plant canopies. On the other hand, LUE aggregates a number of biophysical and environmental factors. In photosynthesis models, these factors are often considered as constraints to a certain maximum (potential) LUE value characteristic to the vegetation. Some of these constraints (e.g., soil water availability) are often known with considerable uncertainty (Goerner et al., 2011).

The most important drivers of daily LUE across various biomes are light and water availability, and temperature (Schwalm et al., 2006; Yuan et al., 2007). Light conditions have been found to affect the photosynthetic efficiency in several different ways which are mostly associated with plants' photoprotective mechanisms. Firstly, under excess incident radiation (the amount of PAR absorbed by a leaf exceeds the energy used in the photosynthesis), de-epoxidation of xanthophyll cycle pigments occur and result in the downregulation of the photosynthetic apparatus. As a consequence, LUE is decreased while the excess energy is re-directed toward non-photosynthetic pathways and primarily dissipated as heat (Demmig-Adams & Adams, 1996; Müller, Li, & Niyogi, 2001). Shaded leaves do not experience this downregulation. Secondly, over longer timescales plants and their leaves typically acclimate and adapt to the prevailing illumination conditions by developing different biochemical, biophysical or morphological characteristics. Differences have been reported in, for example, leaf pigment content, structure and dimensions, surface properties, and even selective light use efficiency of direct over diffuse light, which can result in different functional relationships between incident irradiance, photosynthetic capacity and efficiency (Brodersen, Vogelmann, Williams, & Gorton, 2008; Demmig-Adams, 1998; Lichtenthaler, Ač, Marek, Kalina, & Urban, 2007; Špunda et al., 1998). Hence, the contribution of diffusely irradiated leaves to total canopy photosynthesis is larger than their fraction of APAR. Gu et al. (2002) stated that accurate biophysical modeling of vegetation canopies demands consideration of both the diffuse and direct irradiance components as well as the sunlit and shaded foliage fractions. Separate treatment of sunlit and shaded parts of the foliage has been successfully used for canopy photosynthesis modeling with reasonable accuracy (Chen, Liu, Cihlar, & Goulden, 1999; De Pury & Farquhar, 1997; Wang & Leuning, 1998). Within this context, it is clear that illumination and its spatial variation are among the most crucial factors in estimating accurately the photosynthetic rate and efficiency.

1.2. Photochemical reflectance index

The photochemical reflectance index (PRI) is a narrow-band spectral index that was developed for direct estimation of LUE of plant leaves and canopies, particularly on a diurnal timescale (Gamon, Peñuelas, & Field, 1992; Peñuelas et al., 1995). It is also one of the few available remote sensing avenues that allow direct estimation of LUE in various spatial scales from leaf to ecosystems (Garbulsky, Filella, Verger, & Peñuelas, 2014). Photochemical reflectance index is most commonly defined as:

$$\text{PRI} = \frac{r_{531} - r_{570}}{r_{531} + r_{570}}, \quad (1)$$

where r_λ denotes the reflectance factor of a leaf or a canopy at the

wavelength λ given in nanometers. The sensitivity of PRI to LUE is based on reversible biochemical reactions in xanthophyll cycle pigments in response to excess light. The de-epoxidation of xanthophyll pigments results in a decrease in leaf reflectance centred at 531 nm, which can be optically measured with a spectroradiometer with sufficient spectral resolution at either leaf or canopy level (Gamon et al., 1992). Meanwhile, the reflectance at the reference wavelength, r_{570} , remains unaffected by the xanthophyll cycle. Hence, for healthy photosynthesizing foliage, the PRI of shaded leaves is higher than of sunlit leaves (Cheng et al., 2012; Gamon et al., 1992; Middleton et al., 2009; Peñuelas et al., 1995). On the other hand, under light-limited (e.g., cloudy or overcast) conditions, leaf-level PRI and LUE remain relatively constant between leaves with similar biochemical and biophysical properties since no downregulation occurs (Hilker, Gitelson, Coops, Hall, & Black, 2011; Middleton et al., 2009).

In a boreal forest biome PRI has been found to correlate well with many variables such as LUE, PAR, productivity and net CO₂ assimilation, in a number of studies (Drolet et al., 2008; Louis et al., 2005; Nichol et al., 2002; Porcar-Castell et al., 2012; Rahman, Gamon, Fuentes, Roberts, & Prentiss, 2001). On a broader scale, PRI has been found to be sensitive to numerous physiological factors and physical quantities related to vegetation status and characteristics. While these factors may extend the applicability of the index, they also potentially complicate LUE estimation and hence are often considered as confounding. In the long term, from seasonal to inter-annual timescales, physiological changes such as sizes of chlorophyll and carotenoid pigment pools, but potentially also structural and morphological changes occurring in plants, can significantly affect PRI and PRI–LUE relationships in leaves (Filella et al., 2009; Porcar-Castell et al., 2012; Sims et al., 2006; Stylinski, Gamon, & Oechel, 2002). The underlying drivers for such changes include the seasonal growth cycle, senescence, water stress or drought, and ambient temperature (Filella et al., 2009; Nakaji et al., 2008; Rascher et al., 2007; Sims et al., 2006; Suárez, Zarco-Tejada, Berni, González-Dugo, & Fereres, 2009). On a short timescale, up to a few days, the xanthophyll cycle alone primarily drives the PRI (Filella et al., 2009; Sims & Gamon, 2002). Recent studies have further indicated that PRI–LUE relationships become stronger on shorter timescales and PRI is mainly controlled by APAR, the ratio of direct to total PAR, temperature and water vapour deficit (Soudani et al., 2014; Wong & Gamon, 2015) – largely the same factors which are driving LUE. The physical factors affecting the PRI signal contribute significantly also in the spatial domain. These factors include canopy structure, most notably the leaf area index (LAI) and leaf angle distribution (LAD) (Barton & North, 2001; Hernández-Clemente, Navarro-Cerrillo, Suárez, Morales, & Zarco-Tejada, 2011; Suárez et al., 2009), view and illumination angles (e.g., Cheng et al., 2012; Drolet et al., 2008; Galvão, Breunig, dos Santos, & de Moura, 2013; Middleton et al., 2009; Sims, Rahman, Vermote, & Jiang, 2011; Verrelst, Schaepman, Koetz, & Kneubühler, 2008), stand density (Hernández-Clemente et al., 2011), fraction of non-photosynthetic vegetation (NPV, e.g., trunks and branches) (Hilker et al., 2010; Verrelst et al., 2008), background or soil reflectance (Barton & North, 2001; Filella, Peñuelas, Llorens, & Estiarte, 2004; Suárez et al., 2008), and atmospheric effects (Barton & North, 2001; Hall, Hilker, & Coops, 2011; Hilker et al., 2009; Möttöus et al., 2015).

We can expect that canopy-level PRI shows a large variation across the canopy arising from the fine-scale spatial changes in apparent reflectance. While some of the causes for reflectance variation may be attributed to the within-canopy changes in biochemical, biophysical, and structural characteristics within and between different plant species and vegetation types (Asner, 1998; Jacquemoud et al., 1996), the inhomogeneous structure of real canopies induces also a spatial variability in the radiation field inside a stand (Ross, 1981). This type of spatial variability is most evident for woody plants with large patches of sunlit and shaded foliage. However, it is also encountered in structurally and biochemically homogeneous stands whose phytoelements have constant optical properties. The variation can be expected to become

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