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Linking stand architecture with canopy reflectance to estimate vertical patterns of light-use efficiency

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ABSTRACT

Remote sensing of plant carbon uptake, or gross primary production (GPP), in a repeatable and consistent manner remains a key element of a comprehensive understanding of the role of vegetation within the global carbon cycle. To further this understanding at a landscape level or global scale, accurate remote sensing of photosynthetic light-use efficiency (LUE) is required to understand photosynthetic down-regulation and environmental constraints to plant photosynthesis. The past decade has seen advances in detecting both leaf- and canopy-level physiological stress behaviours using the photochemical reflectance index (PRI), a narrow-waveband normalized difference index that relates LUE to a xanthophyll-induced absorption feature at 531 nm. To date, however, much of this research has occurred using top of canopy measurements, while our understanding of the vertical distribution of LUE within the crown is limited. In this study, we demonstrate an approach which could be used to scale photosynthetic behaviour of vegetation vertically and horizontally using estimates of vertical canopy structure obtained from terrestrial Light Detection and Ranging (LiDAR) data to predict proportions of shaded and sunlit canopy which are then linked to predictions of LUE. We apply the approach over a mature Aspen study site located in central Saskatchewan, Canada utilising full-waveform LiDAR data provided by the ground-based laser scanner system and canopy spectra obtained by the AMSPEC II spectro-radiometer. Agreement between predictions of Gross Primary Productivity (GPP) using the developed approach compared to independent observations was highly significant at hourly intervals ($R^2 = 0.80$, $p < 0.01$) under clear sky conditions. A range of LUE vertical profiles for different stand structures across the growing season were developed providing estimations of how crown structure can impact LUE vertically in the crown. We conclude with a recommendation for ongoing research to verify these types of trends using concurrently acquired, independently derived leaf LUE from photosynthesis light-response curves, and forest structure variation from LiDAR, to provide a more exact quantification of these patterns.

1. Introduction

Remote sensing of plant photosynthesis, or gross primary production (GPP), in a repeatable and consistent manner remains a key goal of assessing the role of vegetation in the terrestrial carbon cycle (Hall et al., 2011). Remote sensing of photosynthesis typically involves measurements of the amount of energy absorbed by vegetation and its photosynthetic light use efficiency (LUE), the efficiency with which plants can use absorbed radiation energy to produce biomass (Hilker et al., 2010b). This efficiency is determined by a series of limiting environmental stresses (here defined as any factors that temporarily reduce a plants ability to assimilate carbon as a result of a shortage of photosynthesis-required resources other than light; Demmig-Adams, 1990).

The past decade has seen research into both leaf- and canopy- level physiological stress behaviour. Plants absorb radiation energy principally through chlorophyll but also through carotenoid pigments contained in green plant tissue. A range of approaches exist to balance light availability and light use by plants, which can principally be classified into mechanisms that regulate light absorption, thus affecting absorbed photosynthetically active radiation (PAR), and mechanisms that govern energy dissipation, once radiation has been absorbed by the photosynthetic apparatus. In remote sensing, measures of absorbed PAR are typically acquired from vegetation indices quantifying the amount of radiation absorbed in the visible (red) vs near infrared part of the spectrum. Once absorbed, light harvested energy can be directed mainly along three competing pathways (Coops et al., 2011). The first energy

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pathway, photochemical quenching, refers to the transfer of energy to the reaction center of photosystem II providing energy for the photosynthetic dark reaction. Alternatively, non-photochemical quenching, results from a lack of available resources to support photochemical quenching. Thought to be initiated mainly through de-epoxidation of the xanthophyll pigment complex that has the ability to safely dissipate absorbed radiation energy as heat in order to prevent damage to the photosynthetic apparatus (Björkman and Demmig, 1987, Demmig-Adams, 1990). This process is also referred to as photoprotection. Finally, the amount of energy temporarily resident within the photosynthetic apparatus, regulates a third energy pathway, which describes the re-emittance of photons into space, also known as chlorophyll fluorescence. Not actively controlled through physiological mechanisms, fluorescence can provide some indication of photosynthetic activity, although disentanglement of stress related dissipation and actual increases in vegetation productivity is not straightforward (Porcar-Castell et al., 2014).

One of the most successful methods to quantifying changes in the amount of non-chemical quenching (and by inference LUE) is through the photochemical reflectance index (PRI) (Gamon et al., 1993; Gamon et al., 1992; Hilker et al., 2008b; Hilker et al., 2012a, 2012b; Hilker et al., 2008a; Hilker et al., 2008c, Middleton et al., 2009), which is a narrow-waveband normalized difference index that relates changes in LUE to a xanthophyll-induced absorption feature at 531 nm. Numerous studies have demonstrated the relationship between PRI and LUE at the leaf scale where reflectance is acquired close to the target (Hilker et al., 2008a) across a wide range of vegetation types (Schickling et al., 2016, Zhang et al., 2015) and compared to flux estimates of photosynthetic photon flux density (Wong and Gamon, 2015b) and other indicators of photosynthesis (Schickling et al., 2016). Studies have demonstrated that PRI is closely timed with photosynthetic reactivation measured by gas exchange and these relationships with non-chemical quenching are strongest over diurnal and daily timescales where plants adjust their internal energy distribution (Wong and Gamon, 2015a). Changes in PRI have also been associated with longer term physiological patterns associated for example with the changing pigment pools of the vegetation such as the carotenoid: chlorophyll pigment ratios.

Based on this understanding of light harvesting complexes within a leaf recent advances in the estimation of LUE have focused on the use of PRI to predict canopy-level physiological stress behaviour. Canopy-level LUE provides an average of the photosynthetic efficiency of individual leaves within the crown and is primarily a function of the radiation regime to which the leaves are exposed. (Hall et al., 2008). The crucial role illumination plays in determining canopy-level LUE has resulted in an increased focus on the role of direct and diffuse sky radiation and between- and within-crown shading effects (Hilker et al., 2008a; Hilker et al., 2008c). These studies have amplified the role of tree and crown structure in the photosynthesis process and resulted in the need to more comprehensively link structural conditions with physiological processes. For instance, while downregulation may always occur as a function of light intensity, in situations where photosynthesis is limited by factors other than light, the sunlit components of a canopy are exposed to more excessive radiative energy than shaded elements of the vegetation. As a result, canopy-level PRI is strongly dependent on shading – the shadow fraction – with directional changes in PRI at near-simultaneous time intervals almost entirely attributable to changes in levels of excess radiation (Hall et al., 2008). Consequently, the slope of the relationship between shadow fraction and PRI changes as a function of vegetation stress. Under low stress conditions, differences between sunlit and shaded PRI are relatively smaller, because absorbed radiation in both parts of the canopy can mostly be used for photosynthesis. However, under high stress conditions, sunlit canopies are unable to take advantage of higher light levels compared to shaded canopies, thus the amount of excess light dissipated as heat is relatively higher. Variations in energy dissipation of sunlit and shaded canopy parts may be assessed from multi-angle observations of PRI and by modelling the index at the reflectance hotspot (100% sunlit) and reflectance darkspot (100% shaded) (Hall et al., 2008, Hall et al., 2011, Hilker et al., 2012a, 2012b). While these results are encouraging, as they potentially allow us to observe canopy LUE from multi-angle satellite sources, airborne and satellite passive remote sensing observations are limited to the top of the canopy, potentially ignoring much of the below-canopy architecture that may significantly contribute to photosynthesis. The contribution to the overall carbon budget of these lower, and more shaded, canopy elements is understood but required for scaling flux tower estimates to landscape and global levels using remote sensing techniques.

A range of factors may limit shade photosynthesis such as competition with the overstorey vegetation for resources especially in stands with poorer soils and limited nutrient pools (Coomes and Grubb, 2000). Arguably two of the key factors determining the contribution of understorey photosynthesis in forested ecosystems are the below-canopy architecture and vertical structure of vegetation. Traditionally assessed through only a few inventory parameters, technologies such as Light Detection and Ranging (LiDAR) have allowed us to obtain accurate information on the vertical structure of a forest canopy using remote sensing devices (Næsset, 1997). Airborne LiDAR is able to provide detailed characteristics of the top-of-tree and upper-crown structure (Aschoff and Spiecker, 2004; Baltsavias, 1999; Lefsky et al., 1999; Van Leeuwen et al., 2010) while ground-based LiDAR can represent the internal structure of a forest stand using three-dimensional mesh approaches with similar precision (Hopkinson et al., 2004; Maas et al., 2008; Tansey et al., 2009; Thies et al., 2004). These approaches can be used to accurately model the shadow regimens and the fraction of absorbed radiation at any location in the canopy at a very high level of detail (Danson et al., 2007; Huang and Pretzsch, 2010; Vaccari et al., 2013). Combined, these sets of studies have confirmed both the role of tree and crown structure in the photosynthesis process, as well as capacity of remote sensing technology to both assesses the physiological state of vegetation as well as estimate forest stand structure. The objective of this paper is therefore to combine ground-based, full-waveform LiDAR with tower-based remote sensing measurements to predict canopy spectral estimates of LUE derived from the proportions of shaded and sunlit components within a forest canopy. We develop our approach over a mature Aspen study site located in central Saskatchewan, Canada utilising full-waveform LiDAR data provided by a ground-based laser scanner system and canopy spectra obtained by the AMSPEC II spectro-radiometer (Hilker et al., 2010a). We compare the estimates to independent eddy-flux covariance (EC) estimates of Gross Primary Productivity (GPP) to provide an initial validation of the approach.

2. Methods

2.1. Site description

The study was undertaken in a mature Aspen study site, hereafter referred to as Southern Old Aspen (SOA), established as part of the Boreal Ecosystem-Atmosphere Study (BOREAS) carried out between 1994 and 1996. Located in the center of Saskatchewan, Canada (53.62889° N, 106.19779° W) at an elevation of 600 m, the study site is in the southern ecotone of the Western boreal forest and has a mean annual temperature of about 0.5 °C. The 86-year old stand comprises about 10% balsam poplar (*Populus balsamifera* L.), a thick, 2–3 m hazelnut understory (*Corylus cornuta* Marsh) with sparse alder (*Alnus crispa* (*Alt.*) Pursch), and is otherwise dominated by trembling aspen (*Populus tremuloides* Michx). Stem density is 830 stems ha^{-1}, with a mean overstorey tree height of about 22 m and a mean LAI of 2.1 m^2 m^{-2} (Barr et al., 2007). LAI of the understory was estimated to be 1.07 m^2 m^{-2} (Chasmer et al., 2011).