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Effects of irradiance and photosynthetic downregulation on the photochemical reflectance index in Douglas-fir and ponderosa pine

John A. Gamon [a,*], Barbara Bond [b]

[a] Departments of Earth & Atmospheric Sciences and Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E3, Canada
[b] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

Using the "photochemical reflectance index" (PRI) as a measure of xanthophyll pigment activity and photosynthetic light-use efficiency, we examined physiological responses to diurnal illumination in mature forest stands. In a Douglas-fir forest in Corvallis, Oregon, PRI varied primarily with illumination, which was strongly influenced by canopy aspect and time of day. Once normalized for illumination, PRI exhibited a pattern of midday depression similar to that of leaf photosynthesis and stomatal conductance. Comparable optical responses to illumination were detected at canopy and leaf scales, demonstrating that remote spectroradiometry could be applied to monitor photosynthetic downregulation in uniform, closed stands. In similar measurements at a ponderosa pine forest in Black Butte, Oregon, an old tree exhibited more suppressed midday PRI values than a young tree, once values were normalized for illumination. Unlike the PRI response in Douglas-fir, variation in the diurnal PRI response between individual ponderosa pine trees was a predominant source of PRI variation. This contrasting age effect was consistent with other studies at this site showing reduced midday photosynthesis and stomatal conductance in old trees due to hydraulic limitations. These results indicate that diurnal and spatial patterns of photosynthetic activity in structurally complex evergreen forest stands can be characterized with narrow-band spectral reflectance, provided measurements are properly normalized by illumination. These findings also support recent studies using field and satellite remote sensing that report strong effects of illumination on the PRI signal from forest stands, and provide additional evidence that individual canopy responses can reveal contrasting degrees of photosynthetic downregulation due to varying stress effects within a single forest stand. Together, these results support the hypothesis that photosynthesis is coordinately regulated, allowing PRI to detect changing levels of stomatal activity and carboxylation. While illumination patterns and photosynthetic downregulation both influenced PRI, pigment pool sizes and enhanced PRI under prolonged low light provided additional sources of PRI variation in the canopy signal. Further understanding of these multiple PRI responses could help realize the goal of remote sensing of photosynthetic activity using PRI.

1. Introduction

Many plants experience "midday photosynthetic depression" or "downregulation," manifested as stomatal closure and reduced photosynthetic rates (Tenhunen et al., 1985). Midday stomatal closure, in turn, is associated with increasing vapor pressure deficit at the leaf surface and decreasing water availability at the root surface (e.g., Kaufmann, 1976; Lange et al., 1971; Lopushinsky & Klock, 1976; Raschke, 1975; Sandford & Jarvis, 1986). At the leaf scale, photosynthetic depression is often detected with gas exchange measurements using portable gas exchange systems. At the ecosystem scale, eddy covariance studies have demonstrated midday reductions in water vapor and carbon dioxide fluxes in conifer forests during conditions of high midday VPD (Anthoni et al., 1999; Baldocchi et al., 1997; Jarvis et al., 1997; Joiner et al., 1999). These studies suggest that stomatal control can exert a significant restriction on regional-scale fluxes of carbon dioxide and water vapor. At continental and global scales, the extent of this physiological control is unclear due to a difficulty of obtaining adequate, direct measurements of stomatal behavior over large areas; however, modeling studies indicate that downregulation has the potential to alter regional and global climate (Bonan, 2008; Sellers et al., 1996). Further, because eddy covariance techniques provide estimates of net ecosystem fluxes (rather than individual component fluxes) it is not always clear to what extent reductions in net carbon uptake by entire forest stands can be attributed to reductions in gas exchange at the leaf level.

Improved methods for detecting midday depression, or downregulation, of photosynthesis and transpiration over large landscape regions could improve our knowledge of carbon and water vapor fluxes and also increase our understanding of physiological controls on climate (Sellers et al., 1996). Remote sensing offers one way of sampling such large areas; however, conventional remote sensing instruments and methods are not able to easily detect "invisible" changes in physiological

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* Corresponding author. Tel.: +1 780 492 0345; fax: +1 780 492 2707.
E-mail address: gamon@ualberta.ca (J.A. Gamon).

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status associated with photosynthetic downregulation, particularly in drought-tolerant evergreens (Gamon et al., 1995; Running & Nemani, 1988). This is, in part, because the wide spectral bands of most existing satellite sensors cannot resolve subtle, spectral features linked to physiological state. However, hyperspectral spectrometers – instruments with many, narrow, adjacent wavebands – have shown considerable promise for detecting subtle shifts in vegetation optical properties linked to photosynthetic downregulation (Gamon & Qiu, 1999).

Knowledge of leaf-scale physiology is needed to understand mechanisms of photosynthetic downregulation and to provide a solid foundation for interpreting larger scale studies. Historically, many studies of downregulation have focused on the "carboxylating end" of the photosynthetic system, and have emphasized stomatal closure and attendant reductions in carbon dioxide and water fluxes (Sellers et al., 1996). Another set of studies have focused on the "light-harvesting end" by emphasizing photosystem II (PSII) behavior, often using chlorophyll fluorescence, and some of these studies have noted altered PSII activity under stress, including drought and temperature extremes (Ludlow & Björkman, 1984; Powles, 1984; Valladares & Pearcy, 1997). Relatively few studies have attempted to connect these two "opposite ends" of the photosynthetic system, particularly under field conditions. Consequently, it remains unclear to what extent PSII activity is coordinately regulated with carbon fixation (Gamon et al., 1997), particularly under field conditions where combined measurements of gas exchange and optical properties are more challenging. Under some conditions, PSII and carboxylation can be disjointly regulated. For example, under conditions of stomatal closure, photorespiration or cyclic electron transport can maintain high rates of electron transport, and thus high levels of PSII activity. Under short-term experimental perturbation, it is possible to manipulate the relative activities of carbon fixation and PSII so that there is an excess electron transport capacity (Harbinson et al., 1990). However, from the perspective of economical resource use, it makes little sense for a plant to maintain a high investment in PSII if that activity cannot realize high rates of carbon fixation. Consequently, there should be selective pressure for coordinated regulation of the component photosynthetic processes. To the extent that plants coordinately regulate PSII activity, carboxylation, and stomatal behavior, it may be possible to use PSII activity as an indirect indicator of change in carbon or water vapor fluxes. This hypothesis of coordinated regulation is an implicit (and often unstated) assumption of many studies that attempt to monitor photosynthetic carbon exchange using remote sensing. Validating this hypothesis, and understanding conditions where it fails, are keys to improved application of photosynthetic models driven from remote sensing.

At the leaf scale, several methods can be used to study PSII activity. These include estimates of electron transport capacity (J_{max}) from gas exchange (Stylinski et al., 2000), and xanthophyll cycle pigments via HPLC (Thayer & Björkman, 1990). Because xanthophyll cycle pigments are photoprotective pigments closely linked to PSII light regulation (Demmig-Adams & Adams, 1996; Frank et al., 1994), they can reveal conditions of photosynthetic downregulation in foliage that is experiencing high irradiance combined with other stresses (Gamon et al., 1997). Unfortunately, traditional methods of xanthophyll pigment analysis (Thayer & Björkman, 1990) are destructive and time consuming, and are not easy to apply in the field. Optical sampling methods provide rapid and portable alternatives to these more tedious, destructive methods of leaf pigment analysis (Gamon & Surfus, 1999; Sims & Gamon, 2002) and also offer the opportunity for sampling over larger spatial scales (Gamon & Qiu, 1999).

Chlorophyll fluorescence is a widely used optical assay of PSII behavior that can be related to the activity of PSII and the xanthophyll cycle pigments. In particular, the fluorescence parameter $\Delta F/Fm'$ provides a rapid measure of PSII light-use efficiency (LUE) (Genty et al., 1989). While the interpretation of leaf fluorescence has long been well-established (Baker, 2008; Bolhar-Nordenkampf & Oquist, 1993; Maxwell & Johnson, 2000; Schreiber et al., 1994; van Kooten & Snel, 1990), fluorescence assessment of PSII activity requires a modulated light source and saturating light pulses that necessitates that the observer be in close proximity (<1 cm) to the leaf.

Spectral reflectance provides an alternate optical sampling method that can be used to monitor declines in PSII light use efficiency across spatial and temporal scales (Gamon & Qiu, 1999). Many laboratory and field studies, at both leaf and canopy scales, have demonstrated that the photochemical reflectance index (PRI) can provide a potent index of xanthophyll cycle pigment activity and photosynthetic light-use efficiency in a large variety of species, particularly over diurnal time scales (Gamon et al., 1992; Gamon et al., 1997; Garbulsky et al., 2010; Peñuelas et al., 1995). Because PRI can be sampled at multiple spatial scales and can be linked to photosynthetic physiology, it provides a useful, non-invasive tool for exploring photosynthetic downregulation at a range of levels from leaf to ecosystem. While often inferred, direct validation of photosynthetic downregulation detected by reflectance is rare, largely due to the differences in sampling scale for most remote sensing and physiological measurements and the challenges of matching field measurements to aircraft or satellite overpasses. However, experimental studies employing leaf- or canopy-scale measurements ("proximal remote sensing") often show strong relationships between PRI and photosynthetic activity. For example, a survey of top-canopy leaves from 20 species grown in a common garden (Gamon et al., 1997) concluded that there was a strong correlation between carbon fixation (measured by gas exchange as midday photosynthetic rates and photosynthetic light use efficiency), PSII activity (determined by chlorophyll fluorescence and xanthophyll pigment levels) and the photochemical reflectance index (PRI, sampled with spectral reflectance). A recent meta-analysis of published literature provided further evidence for significant correlations between PRI and photosynthetic light-use efficiency across many species (Garbulsky et al., 2010). Additional studies have demonstrated strong parallels between leaf- and stand-level PRI diurnal patterns across a range of vegetation types, indicating this signal is "scalable" at least for homogenous, closed stands (Gamon & Qiu, 1999; Stylinski et al., 2002). These and other studies have provided a strong foundation for interpreting PRI measurements of canopies and stands from airborne and satellite platforms, and have provided support for the hypothesis of coordinated regulation.

Studies of boreal forest stands have indicated significant correlations between PRI detectable by aircraft sensors and whole-stand photosynthetic activity determined by eddy covariance (Nichol et al., 2000; Rahman et al., 2001). More recent forest studies have confirmed that a coherent PRI signal can be detected from the MODIS satellite sensor, but that this signal is strongly affected by illumination and sensor view angle (Drolet et al., 2005, 2008). Reports from a Douglas-fir stand in British Columbia, Canada, confirm a strong influence of illumination and view angle on PRI (Cheng et al., 2009; Hall et al., 2008; Hilker et al., 2008a,b; Middleton et al., 2009). Together, these results suggest that periods of photosynthetic depression in evergreen forests may be observable at a range of scales using spectral reflectance if illumination and angular effects are properly considered. This conclusion is generally supported by comparisons with whole-stand LUE derived from eddy covariance (Drolet et al., 2005, 2008; Garbulsky et al., 2010; Garbulsky et al., 2008; Goerner et al., 2011; Nichol et al., 2000; Rahman et al., 2001). However, eddy covariance cannot resolve individual canopy responses and total ecosystem fluxes are not always easily resolved into photosynthetic and respiratory components. So, while we often see broad correlations between PRI and photosynthetic LUE at the scale of whole stands, most stand-level studies have not linked the PRI signal to any independent measure of pigment activity or photosynthetic physiology at the leaf or canopy scale, so the exact physiological interpretation of PRI variation at the stand scale remains uncertain. Although the xanthophyll cycle has been implicated in these studies, it