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Multiple drivers of seasonal change in PRI: Implications for photosynthesis 2. Stand level

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ABSTRACT

The goal of this study was to explore the relationships between stand-level photochemical reflectance index (PRI) and canopy structure/pigment pools, as well as light use efficiency (LUE) of photosynthetically active vegetation focusing on seasonal or ontogenetic time frames. PRI was originally designed as a means of assessing the xanthophyll cycle and LUE over short (e.g. diurnal) time frames, and few studies have explored the drivers of PRI over longer, seasonal time frames, particularly in crops having different photosynthetic pathways or canopy structures. Consequently, our purpose was to understand and quantify the drivers of PRI responses over seasonal time scales for two crops, maize (C_4) and soybean (C_3), contrasting in photosynthetic pathway, leaf structure and canopy architecture. In both crops, PRI was very closely related to green LAI ($R^2 > 0.90$) and stand chlorophyll (Chl) content ($R^2 > 0.93$). The slopes of the relationships in different phenological stages, vegetative and reproductive, were substantially different (3-fold smaller in the vegetative stage). The main cause of this disparity was the high PRI value of soil/residue background. While PRI was a sensitive indicator of the changes in stand green LAI and stand Chl content over the full growing season, it was not sensitive to LUE; LUE explained below 12% of PRI variation in maize and 19% in soybean. Unlike leaf-level PRI, stand-level PRI was not clearly related to the Car/Chl ratio, presumably because the large changes in canopy structure (affecting stand Chl and green LAI) had a dominant influence on PRI over this time frame. The strong relationship between PRI and stand Chl content as well as between PRI and Chl-related vegetation index over a growing cycle allowed us to subtract the stand Chl content effect from measured PRI to reveal the component of PRI most likely related to periods of stress. However, for accurate subtraction of the Chl effect from long-term PRI records, thoughtful study of uncertainties related to "natural" variation of PRI-stand Chl relationships, and stand Chl content estimation for different varieties of the same species and for different species is required. The findings of a strong link between stand-level PRI and stand green LAI and Chl content and the lack of a clear relationship between PRI and LUE over seasonal and ontogenetic time spans suggest the need for a more careful evaluation of the relationship between PRI and either LUE or photosynthetic activity. In particular, studies that contrast short-term (e.g. diurnal) vs. long-term (e.g. seasonal) pigment, PRI, and photosynthetic responses in contrasting vegetation types are needed to clarify the different mechanisms involved at different temporal and spatial scales. These findings have important implications for attempts to monitor photosynthetic phenology from remote sensing, many of which have relied on PRI as an indicator of photosynthetic activity.

1. Introduction

Much of the foundational work on the photochemical reflectance index (PRI) was done on leaves and closed-canopy stands, demonstrating a strong link between PRI, xanthophyll cycle activity, and photosynthetic light-use efficiency (LUE) over diurnal time scales (Gamon et al., 1992, Peñuelas et al., 1995, Gamon et al., 1997). Expanding this interpretation of PRI to larger spatial scales and longer temporal scales has been a challenge. Several studies have compared leaf-level to canopy-level PRI and have found a close relationship between the two for dense monocultural stands suggesting that a closed-canopy stand approximates a "big leaf" in terms of the PRI signal (e.g. Stylinski et al., 2002, Gamon and Qiu, 1999, Wong and Gamon, 2015b, Gamon, 2015). However, when expanding to the full seasonal time scale, the interpretation of PRI often remains unclear because few long-term studies explicitly compare PRI to many factors that can affect this signal (see Barton and North (2001) for examples of these potentially confounding factors). Over seasonal time scales, especially for annual vegetation that undergoes large changes in canopy structure, greening and senescence,

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the seasonal change in green canopy display can have a dominant influence on the PRI signal. While relatively few long-term remote sensing studies of PRI explicitly link this index to xanthophyll cycle activity, many studies have reported a correlation between PRI and LUE (Nichol et al., 2002, Rahman et al., 2004, Drolet et al., 2005, Goerner et al., 2011, Garbulsky et al., 2011), but the exact reasons remain obscure due to the many factors that affect the PRI signal at these scales (Barton and North, 2001) and due to the different operational definitions of LUE (Gitelson and Gamon, 2015). Understanding the underlying reasons for these correlations between LUE and PRI from aircraft or satellite data is critical to implementing defensible LUE models from remote sensing that incorporate PRI.

Modeling studies (Barton and North, 2001) suggests many potentially complicating factors when trying to apply PRI to whole stands in a remote sensing context. Among them, the effects of canopy structure, including green leaf area index (LAI), the degree of canopy closure and soil background contribution to the reflectance signal are known to strongly affect PRI. Additionally, angular effects, including leaf angle distribution and sun-target-sensor sampling geometry can have a significant influence on the PRI signal and its interpretation (Barton and North, 2001, Drolet et al., 2005, Gamon, 2015). As predicted by modeling (Barton and North, 2001), previous empirical studies have found a strong correlation between PRI and green canopy cover as measured by NDVI (Gamon et al., 1995), indicating a strong influence of green canopy structure on the PRI signal. Because these structural effects also influence the overall stand photosynthetic rate, they can potentially influence the PRI-photosynthesis relationship independently of the xanthophyll cycle activity, creating an ill-conditioned situation when interpreting PRI. There are few published, long-term studies examining how PRI is affected by canopy structure over the annual growth cycle of a vegetation stand, leaving this topic relatively unexplored.

In addition to canopy structure, leaf pigmentation, which can change gradually with leaf development and senescence, clearly affects PRI (Gamon et al., 2001, Sims and Gamon, 2002, Garrity et al., 2011, Gitelson et al. – the companion paper in review). In an attempt to discern the short-term effects from the longer-term effects, Gamon and Berry (2012) classified PRI responses to pigmentation in evergreens into “facultative” (xanthophyll cycle-driven effects operating over the diurnal time scale) and “constitutive” (changing pigment pool sizes over seasonal time scales, e.g. due to ontogeny and senescence and/or in response to resource levels). Several studies have now confirmed that long-term (seasonal) PRI responses at the leaf level are primarily driven by constitutive pigment pool size changes, and not facultative xanthophyll cycle activity (Stylinski et al., 2002, Sims and Gamon, 2002, Filella et al., 2009, Gamon and Berry, 2012, Wong and Gamon, 2015a, 2015b). These studies have primarily considered evergreen responses, leaving long-term PRI responses less-well characterized for deciduous and annual vegetation (e.g. crops). Because pigment content can also be tied to photosynthetic capacity and LUE, there may be multiple reasons why PRI often correlates with photosynthetic activity (Garbulsky et al., 2011, Gamon, 2015), creating an overdetermined situation that easily leads to misunderstanding of mechanism. Further clarification of these different pigment effects against a background of changing canopy structure is an essential step toward understanding PRI responses in a long-term monitoring campaign, particularly for deciduous and annual plants (e.g. crops) where long-term responses have been less-well studied.

Given the potential for PRI to provide a useful metric of LUE, a full understanding of multiple confounding variables is needed. In a companion paper, we established relationships between PRI and foliar pigment content and composition (Gitelson et al., 2017). The goal of this current study at a larger scale was to explore the relationships between stand-level PRI and canopy structure/pigment pools, as well as LUE of photosynthetically active vegetation focusing on seasonal or ontogenetic time frames. The purpose was to understand and quantify the drivers of PRI responses over seasonal time scales for two crops (C_3 and C_4), contrasting in photosynthetic pathway, leaf structure and canopy architecture. A key point was to evaluate how the PRI signal over the growing cycle is influenced by changes in canopy structure and pigment pools associated with changing crop phenology and physiology and compare it with seasonal change in LUE.

2. Methods

The study site was located at the University of Nebraska-Lincoln Agricultural Research and Development Center near Mead, Nebraska. This study site consists of three 65-ha fields. Each field was managed as either continuous irrigated maize, irrigated maize/soybean rotation, or rainfed maize (*Zea mays*)/soybean (*Glycine* max) rotation following the best management practices (e.g. fertilization, herbicide/pesticide treatment) for eastern Nebraska for its respective planting cycle. There were a total of 24 field-years for maize and soybean. Maximal green LAI values ranged from 4.3 to 6.5 $m^2\ m^{-2}$ for maize and 3.0 to 5.5 $m^2\ m^{-2}$ for soybean (details are in Verma et al., 2005 and Viña et al., 2011).

2.1. Incoming PAR and fraction of radiation absorbed by photosynthetically active vegetation

In each study site quantum sensors were placed to collect hourly incoming PAR (PAR_{in}), PAR reflected by the canopy and soil (PAR_{out}), PAR transmitted through the canopy (PAR_{transm}) and PAR reflected by the soil (PAR_{soil}). PAR_{in} was measured 6 m above the surface by point quantum sensors (Model LI-190, Li-Cor Inc., Lincoln, Nebraska) pointing toward the sky. Daytime PAR_{in} were calculated by integrating the hourly measurements during a day from sunrise to sunset (period when PAR_{in} exceeding 1 μmol $m^{-2}\ s^{-1}$).

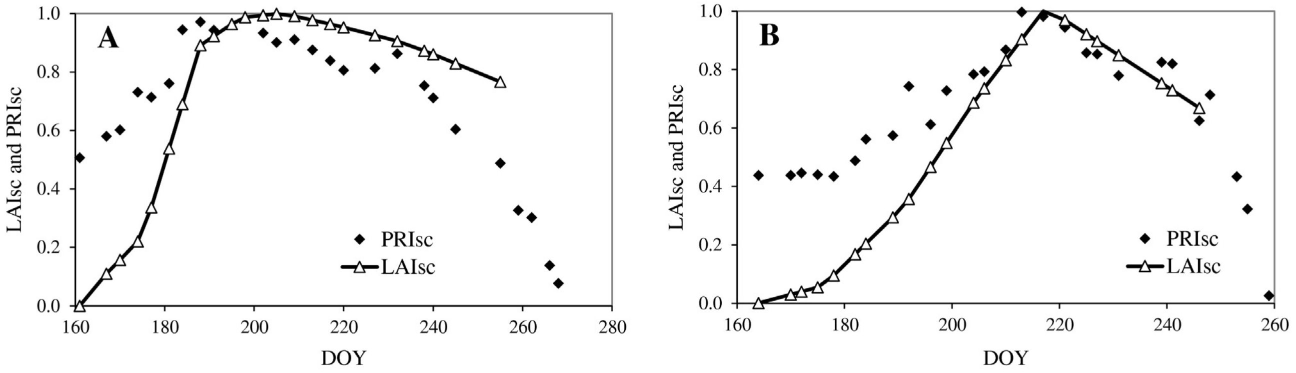

Fig. 1. Temporal behavior of scaled (between 0 and 1) green LAI and PRI of maize (A) and soybean (B).