DIURNAL AND SEASONAL DYNAMICS OF CANOPY-LEVEL SOLAR-INDUCED CHLOROPHYLL FLUORESCENCE AND SPECTRAL REFLECTANCE INDICES IN A CORNFIELD

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KEY WORDS: chlorophyll fluorescence, ChlF; solar induced fluorescence, SIF; light use efficiency, LUE; photochemical reflectance index, PRI; Fraunhofer Line Depth, FLD.

ABSTRACT:

A collaborative field campaign was undertaken to examine the temporal dynamics of canopy-level solar-induced fluorescence (SIF) and the Photochemical Reflectance Index (PRI) in conjunction with photosynthetic light use efficiency (LUE) obtained from fluxes measured at an instrumented tower. We conducted intensive diurnal measurements weekly from June-August (6 dates) in 2007, and from mid-July through early October 2008 (14 dates), using high resolution (0.2 - 3.0 nm) field spectroradiometers and collecting supporting leaf-level and canopy biophysical data. At the canopy level, we used a Fraunhofer Line Depth (FLD) retrieval approach to obtain SIF in the two atmospheric oxygen bands (O_2-B and O_2-A) centered on 688 and 760 nm. We found that canopy-level SIF, fluorescence yield (Fyield), and the PRI varied significantly throughout each field day. In addition, daily averages for PRI, SIF, and Fyield declined across the growing season as the cornfield progressed through vegetative and reproductive stages, and senescence. The greatest seasonal change was captured by SIF expressed in energy units (W m^{-2} sr^{-1} um^{-1}) in the O_2-B band (r^2 = 0.93) and the O_2-A band (r^2 = 0.87), and by the PRI (r^2 = 0.88), all determined from 1 nm spectral resolution data (with Ocean Optics spectroradiometer). The PRI determined at 3 nm resolution (with an ASD-FR spectroradiometer) from both years was related to LUE (r^2 = 0.67), obtaining PRI values of +0.02 (indicating little stress) in the early growth stage but late stage values of -0.075 (indicating substantial stress), as LUE declined from 0.048 mol C/mol Qa to near zero LUE. The PRI (@1 nm): LUE relationship (r^2 = 0.61) was similar, but enabled detection of a slightly greater range in LUE. The PRI (@1 nm) and Fyield were strongly correlated for daily values examined over the season: PRI: F688yield (r = 0.88) and PRI: F760yield (r=0.86). Daily trends for leaf-level photosynthesis were similar to those obtained from tower measurements, but knowledge of the green canopy fraction was necessary to model the canopy net production from leaf-level data inputs.

1. INTRODUCTION

The terrestrial ecosystem and remote sensing science communities have a common goal: to employ hyperspectral information on a global scale to improve assessments of ecosystem productivity and down-regulation of photosynthesis in vegetation due to environmental stresses. This is the rationale for the Fluorescence Explorer (FLEX) satellite mission concept under development by the European Space Agency (ESA), currently being considered for a Technology Demonstration. To provide justification for the FLEX mission and to contribute to the scientific understanding of steady state chlorophyll fluorescence under natural sunlight conditions, our Spectral Bio-Indicator Team at NASA/Goddard Space Flight Center is investigating various remote sensing approaches for retrieving and monitoring vegetation photosynthetic parameters, including light use efficiency (LUE). A major field campaign spanning several field experiments was conducted by ESA scientists in 2007 (e.g., Rascher et al., 2009) and the results demonstrated that solar induced fluorescence (SIF) could be retrieved from ground as well as from remote sensing platforms (e.g., aircraft), and that SIF is a good proxy for canopy photosynthetic efficiency. Another line of investigation for photosynthetic light use efficiency (LUE), has examined a reflectance index based on two narrow green spectral bands, the Photochemical Reflectance Index (PRI) (e.g., Gamon et al., 1992; Meroni et al., 2008, Middleton et al., 2009). Our research on SIF and the PRI contributes to studies recently published by our European colleagues (Middleton et al., 2006a,b, 2008; Rascher et al., 2009; Zarco-Tejada et al., 2009; Damm et al., 2009a,b; Meroni et al., 2009).

2. METHODS

2.1 Data Collections

The experiment was conducted by scientists at the NASA/Goddard Space Flight Center in Greenbelt, MD USA and the USDA/Agriculture Research Service (ARS) in Beltsville, MD USA on corn (*Zea mays* L.; variety, Pioneer 33A14) canopies and plants at the research cornfield managed by USDA/ARS. An instrumented tower was installed (39.03°N, 76.85°W) for continuous carbon flux and environmental measurements during the growing season. We conducted intensive diurnal measurements weekly from June-August (6 dates) in 2007 during a drought period, and from mid-July through early October 2008 (14 dates) when precipitation was normal. Canopy-level reflectance observations were collected one meter above the vegetation with a nadir view from pole-mounted fiber optic probes. These were linked to spectroradiometers carried in body-packs by investigators who traversed along 100 m transects at multiple times (4-11) per day (~hourly), sampling at ~1 m intervals, on cornrows selected to be representative of the flux tower footprint. A transect collection for canopy reflectance typically was completed in ~15 min. On field days in 2007 (June 21; July 2, 9, 31; and August 9, 14), we collected observations with a spectroradiometer (ASD-FR FieldSpec Pro, Analytical Spectral Devices, Inc., Boulder, CO, USA) having a spectral resolution of ~3 nm (sampled at 1 nm). On field days in 2008 (July 25; August 1, 6, 12, 19, 26; September 2, 8, 18, 24; and October 2, 7, 10, 11), we collected canopy-level reflectance spectra along two parallel transects ~20 m apart using two different field spectroradiometers, an ASD and an USB4000 Miniature Fiber Optic Spectrometer (Ocean Optics Inc., Dunedin, Florida, USA), having a spectral resolution of ~1.5 nm (sampled at 0.2 nm). Approximately ~60-100 spectral observations were acquired along transects at the canopy level during each hourly measurement period, which generated between 240 and 1,100 spectra per day for each instrument.

Along a third transect located between the two used for canopy reflectance, we tagged 20 leaves each day for *in situ* measurements on either the 3rd or 4th leaf from terminal (leaf #13/14). Portable leaf chambers were supported on tripods, to obtain photosynthetic capacity (Amax, μmol CO_2 m^{-2} s^{-1}) with LI-6400 photosynthetic systems (LI-COR, Inc., Lincoln, NE, USA). Amax was determined on adaxial leaf surfaces at saturating (1000 ppm) and ambient (380 ppm) CO_2 concentrations under controlled conditions--matching available mid-day photosynthetically active radiation (PAR, 1500-2000 μmol m^{-2} s^{-1}), average daily air temperature (21-25°C), and at fixed relative humidity (~30-35%). Leaf level adaxial reflectance measurements were also made daily *in situ* on these same leaves with an ASD. On the morning following a field day, the tagged leaves were excised for laboratory measurements. Supporting biophysical field data were also collected on all field days, including leaf area index (LAI), mid-day canopy PAR transmission, soil reflectivity, and soil moisture.

2.2 Data Analysis

Fluxes: Half-hourly averages of Net Ecosystem Production (NEP, mg CO_2 $m^{-2}s^{-1}$) were determined using eddy covariance techniques (Baldocchi et al., 1988). Midday measurements of the fraction of absorbed PAR (*f*APAR) were collected along the transect using a Ceptometer (Decagon Devices, Inc., Pullman, WA, USA) on several of the observation days. For each transect, *f*APAR was estimated using the difference between the Normalized Difference Vegetation Index (NDVI) values for the vegetation (calculated from the average transect canopy reflectance) and bare soil reflectance. Light use efficiency (LUE, mol C/mol Qa) was computed as the ratio, NEP/APAR (where APAR = Qa = incident PAR x *f*APAR; Monteith, 1977; Russell et al., 1989). LUE was computed at the times corresponding to field reflectance measurements for PRI and SIF comparisons, for which NEP and incident PAR values came from averages of two half-hourly flux tower observations that coincided with the time of the transect measurements. Evaluation of nighttime NEP, when all of the carbon flux can be attributed to ecosystem respiration, indicated that respiration for this cornfield was small compared to the photosynthetic uptake.

Reflectance: A horizontal Spectralon calibration panel was continuously monitored at 10 s intervals with stationary ASD and Ocean Optics instruments. At the beginning and end of each transect reflectance collection, the calibration panel was measured with the portable instruments to cross-calibrate the field and reference panel (i.e., irradiance) measurements. Reflectance factors were calculated for each observation by matching each sample obtained along the transect with the panel measurement closest in time. The resulting spatially sampled reflectance values were averaged to obtain an average transect spectrum per measurement period (~hourly). In 2007, all transect spectral samples were averaged together, while in 2008, due to frequent intermittent cloudiness, only the first 10 observations (~15 m) for the ASD data were averaged together for this analysis. The 2008 Ocean Optics data were screened for cloud effects, but included data from the full transect.

Spectral Bio-Indicator Parameters: From both the ASD and the Ocean Optics instruments, the Photochemical Reflectance Index (PRI) was derived as (R531-R570)/(R531+R570). The solar-induced fluorescence (SIF) was calculated from the 1 nm Ocean Optics data using the Fraunhofer Line Depth (FLD) retrieval approach (Corp et al., 2006) in the two atmospheric oxygen bands centered on 688 nm (O_2-B) and 760 nm (O_2-A), designated as F@688 and F@760, respectively. The approach compares radiance from the reference panel with that obtained above the canopy to obtain steady state SIF expressed in energy units (W m^{-2} sr^{-1} nm^{-1}). The relative steady state fluorescence yield (Fyield) was calculated for the O_2-B (F688yield) and O_2-A (F760yield) bands by normalizing the SIF with the available PAR. Details of the retrieval algorithm can be found in Corp et al. (2006). The estimates for PRI, SIF, and Fyield were then averaged to provide a mean value representative of the transect (~hourly) to study their diurnal dynamics. These diurnal values were also averaged daily to examine their long-term trends across the growing season. Statistical evaluations were conducted, including regression and correlation analyses, using Systat 10 (Jandel Scientific, San Rafael, CA, USA).

Biophysical Collections: Leaves previously tagged and used for *in situ* measurements, were excised the day following field measurements and taken with leaf basal portions submerged in water to the laboratory. Measurements included spectral optical properties made with an integrating sphere (LI-COR 1800, attached to an ASD spectroradiometer), total leaf chlorophyll content, leaf dry matter, leaf water thickness, fresh weight, leaf area, and specific leaf mass, made with standard procedures. These measurements were made ~weekly on 11 days through the 2008 growing season, ending on October 7. Canopy height, temperature, incident PAR and soil moisture were also collected for each day. Canopy *f*APAR was determined below the canopy with a light bar (LI-191 Line Quantum Sensor, LI-COR, Lincoln, NE, USA) and also above the canopy with pole mounted PAR sensors (LI-190SA Quantum Sensor, LI-COR, Lincoln, NE, USA), at each of the measurement locations.

Crop Production Model: *In situ* measurements of Amax (µmol CO_2 m^{-2} s^{-1}) made with the portable photosynthesis systems, at either saturating CO_2 levels (1000 ppm) or at the local ambient CO_2 concentration (380 ppm), were used as inputs to a crop production model. The saturating CO_2 levels allow diffusion across the stomatal membrane to induce photosynthesis rates comparable to those under maximum stomatal conductance. PAR, leaf temperature, and relative humidity were constrained within the chamber to achieve reproducible conditions conducive for midday maximum gas exchange rates. The plant gas exchange simulator (GCX, Kim et al., 2006), a comprehensive user-driven graphical interface to model leaf/canopy gas exchange, is based on the nested iterative solutions of three sub- models: photosynthesis, stomatal conductance, and energy balance. The GCX model was used to combine the effects of key environmental variables such as LAI, PAR, ambient CO_2, air temperature, relative humidity, wind speed, and soil properties (including moisture) in order to scale leaf observations and obtain canopy NEP estimates.

3. RESULTS

3.1 Leaf and Canopy Biophysical Measurements

Leaf and canopy biophysical measurements made in 2008 (Tables 1-3) reveal phenological changes. Photosynthetic capacities (Amax) measured at the two CO_2 levels (Tab. 1) were equivalent for ~half of the days examined, but Amax at 1000 ppm was significantly higher on five days and lower on the last day than Amax at the ambient CO_2 level of 380 ppm. Amax at 380 ppm (Tab. 1) declined by more than 50%

Variable	Date	N	Mean (±SE)	Date	N	Mean (±SE)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 1000 ppm CO_2	7/25/2008	29	59.55 (2.22)	9/2/2008	21	31.77 (1.84)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 380 ppm CO_2			50.36 (3.66)			25.55 (1.58)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 1000 ppm CO_2	8/1/2008	20	49.28 (1.61)	9/8/2008	20	44.19 (1.42)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 380 ppm CO_2			48.56 (1.01)			36.21 (0.72)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 1000 ppm CO_2	8/7/2008	18	48.51 (1.56)	9/18/2008	20	31.21 (1.88)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 380 ppm CO_2			46.68 (1.77)			28.95 (1.55)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 1000 ppm CO_2	8/12/2008	22	39.10 (1.98)	9/24/2008	20	29.43 (1.62)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 380 ppm CO_2			42.02 (1.39)			22.95 (0.85)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 1000 ppm CO_2	8/19/2008	20	43.17 (1.53)	10/2/2008	20	17.30 (2.43)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 380 ppm CO_2			37.29 (1.05)			22.03 (0.78)
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 1000 ppm CO_2	8/26/2008	20	38.82 (1.16)			
Amax (mmol CO_2 $m^{-2}s^{-1}$) at 380 ppm CO_2			36.48 (1.21)			

Table 1. The average photosynthesis values obtained on each field day are shown for photosynthetic capacity, Amax, at the saturating CO_2 level (1000 ppm) and the ambient CO_2 level (380 ppm). Amax was determined *in situ* on twelve of the days that canopy reflectances were acquired.

Variable	Date	N	Mean (±SE)	Date	N	Mean (±SE)
total chlorophyll (mg/cm^2)	7/25/2008	29	45.62 (0.72)	9/2/2008	21	50.00 (1.03)
C_m (g/cm^2)			0.0050 (0.0001)			0.0057 (0.0001)
C_w (g/cm^2)			0.0223 (0.0005)			0.0176 (0.0004)
specific leaf mass (g/cm^2)			0.0272 (0.0006)			0.0233 (0.0004)
FW (g)			14.55 (0.32)			12.31 (0.32)
leaf area (cm^2)			536.4 (10.3)			527.7 (9.5)
total chlorophyll (mg/cm^2)	8/1/2008	20	51.77 (1.41)	9/8/2008	20	50.14 (0.83)
C_m (g/cm^2)			0.0054 (0.0001)			0.0059 (0.0001)
C_w (g/cm^2)			0.0217 (0.0006)			0.0170 (0.0003)
specific leaf mass (g/cm^2)			0.0271 (0.0006)			0.0229 (0.0004)
FW (g)			16.89 (0.48)			12.08 (0.31)
leaf area (cm^2)			624.2 (12.4)			528.3 (10.4)
total chlorophyll (mg/cm^2)	8/7/2008	18	52.79 (0.98)	9/18/2008	20	53.27 (1.35)
C_m (g/cm^2)			0.0054 (0.0001)			0.0057 (0.0001)
C_w (g/cm^2)			0.0194 (0.0004)			0.0179 (0.0003)
specific leaf mass (g/cm^2)			0.0248 (0.0004)			0.0236 (0.0003)
FW (g)			15.14 (0.37)			12.28 (0.31)
leaf area (cm^2)			612.3 (11.8)			520.6 (10.1)
total chlorophyll (mg/cm^2)	8/12/2008	22	50.34 (1.2)	9/24/2008	20	45.07 (1.62)
C_m (g/cm^2)			0.0054 (0.0001)			0.0053 (0.0001)
C_w (g/cm^2)			0.0171 (0.0002)			0.0162 (0.0002)
specific leaf mass (g/cm^2)			0.0225 (0.0003)			0.0215 (0.0003)
FW (g)			13.15 (0.34)			10.82 (0.33)
leaf area (cm^2)			582.3 (10.2)			504.4 (14.8)
total chlorophyll (mg/cm^2)	8/19/2008	20	53.45 (1.16)	10/2/2008	20	42.81 (1.76)
C_m (g/cm^2)			0.0057 (0.001)			0.0057 (0.0001)
C_w (g/cm^2)			0.0174 (0.0003)			0.0163 (0.0005)
specific leaf mass (g/cm^2)			0.0229 (0.0004)			0.0220 (0.0006)
FW (g)			13.45 (0.32)			10.72 (0.30)
leaf area (cm^2)			588.2 (12.5)			497.7 (11.7)
total chlorophyll (mg/cm^2)	8/26/2008	20	50.18 (1.64)			
C_m (g/cm^2)			0.0061 (0.0001)			
C_w (g/cm^2)			0.0169 (0.0004)			
specific leaf mass (g/cm^2)			0.0230 (0.0005)			
FW (g)			12.70 (0.38)			
leaf area (cm^2)			550.5 (8.4)			

Table 2. Leaf level measurements were made weekly on 11 days at the USDA/ARS research cornfield during the 2008 growing season. The same leaves used for Amax measurements (Tab. 1) were excised and the following variables were determined on fresh material in the laboratory the following day: total chlorophyll; C_m, dry matter; C_w, water thickness; specific leaf mass; SLM; fresh weight, FW; and leaf area.

from ~50 µmol CO_2 m^{-2} s^{-1} in the maturing July canopy to ~22 µmol CO_2 m^{-2} s^{-1} in the senescent October crop. However, Amax at 1000 ppm declined even more (72%) over the season, from ~60 to ~17 µmol CO_2 m^{-2} s^{-1}. In addition to the pattern of steady decline through the growing season, Amax at both CO_2 concentrations declined during drier periods. For example, a drop in Amax was observed on September 2, 2008, following the lowest soil moisture measurement (2.8%)

Variable	Date	Mean	Date	Mean
canopy height (cm)	7/25/2008	90	9/2/2008	291
average incident PAR (mmol/m^2/s)		1186.5		1172.0
temperature (^{0}C)		27.8		28.0
soil moisture (%)		18.9		4.4
canopy height (cm)	8/1/2008	154	9/8/2008	291
average incident PAR (mmol/m^2/s)		1192.3		1058.2
temperature (^{0}C)		29.4		26.2
soil moisture (%)		11.6		10.4
canopy height (cm)	8/7/2008	215	9/18/2008	291
average incident PAR (mmol/m^2/s)		1126.5		888.9
temperature (^{0}C)		28.9		23.5
soil moisture (%)		8.7		5.7
canopy height (cm)	8/12/2008	248	9/24/2008	291
average incident PAR (mmol/m^2/s)		1175.9		836.1
temperature (^{0}C)		24.2		19.3
soil moisture (%)		8.7		
canopy height (cm)	8/19/2008	270	10/2/2008	291
average incident PAR (mmol/m^2/s)		1150.1		792.8
temperature (^{0}C)		29.4		15.3
soil moisture (%)		4		20.1
canopy height (cm)	8/26/2008	291		
average incident PAR (mmol/m^2/s)		1094.0		
temperature (^{0}C)		21.4		
soil moisture (%)		2.8		

Table 3. Canopy height and environmental variables (incident PAR, air temperature, and soil moisture) are summarized for our field days at the USDA/ARS research cornfield during the 2008 growing season.

made on Aug 26, and increased again by ³10 µmol CO_2 m^{-2} s^{-1} following a rain event just before Sept 8, when the soil moisture recovered to 10%. Leaf chlorophyll content (Tab. 2) increased from July to August, was stable during August, then declined through the remaining growing season. Seasonal change in dry matter (Cm) (Tab. 2) for green leaves was minor (0.0056 ± 0.0002 g cm^{-2}). Leaf water thickness (Cw) (Tab. 2) was highest in late July - early August (~0.02 g cm^{-2}) and again during early September (~0.0175 g cm^{-2}), after which it declined along with soil moisture (Tab. 3). Full canopy height (2.91 m) was achieved by mid-August (Tab. 3). Mid-day PAR and air temperature (Tab. 3) ranged from 1187 µmol m^{-2} s^{-1} and 27.8^o C (in late July) to 703 µmol m^{-2} s^{-1} and 15^o C (in early October), respectively.

3.2 Tower Measurements for NEP, PAR, and LUE

Diurnal courses for NEP, PAR, and LUE are shown in Figure 1, obtained from half-hourly measurements on the days when our 2008 intensive field measurements were undertaken. There was considerable within-day as well as day to day variation for each of these parameters (NEP, PAR, and LUE), and all declined over the growing season. LUE exhibited the greatest seasonal decrease (because PAR changed less than NEP) and the most variation in within-day diurnal trends (Fig. 1). As the corn matured, LUE reached a peak in early August and then decreased as the growing season continued. However, the highest mid-day PAR occurred earlier (on day 207), and the highest NEP

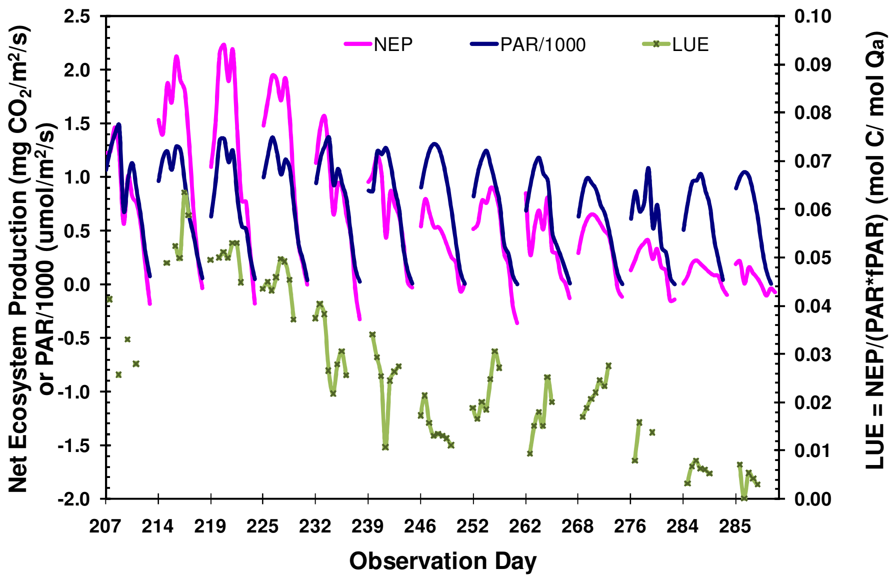

Figure 1. Daily patterns of NEP (pink line, mg CO_2 m^{-2} s^{-1}) and incident PAR (dark blue line, µmol m^{-2} s^{-1}) for the 14 Intensive Study Days in 2008 at the USDA/ARS cornfield. Note: values of PAR were scaled to fit the charting area (PAR/1000).

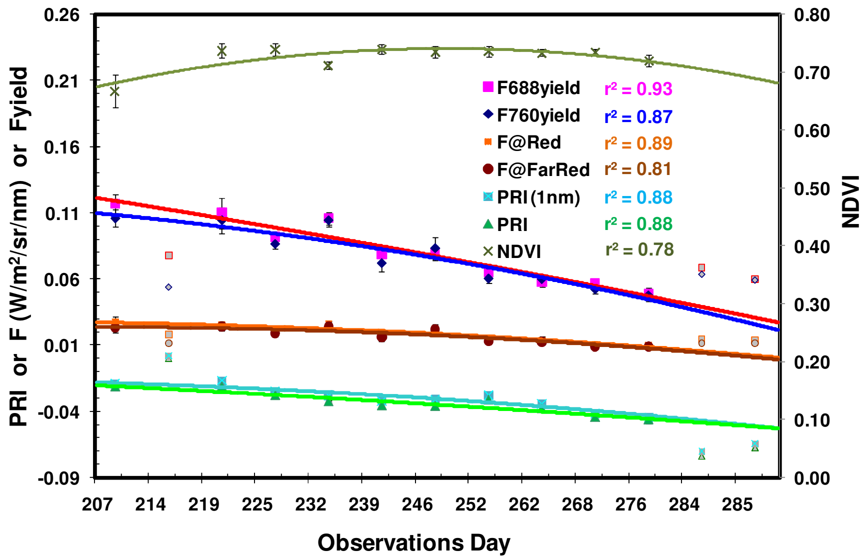

Figure 2. Daily average values for PRI, SIF, and fluorescence yield, Fyield (F688yield, F760yield), and NDVI are plotted against day of the year. Fyield exhibits the strongest seasonal change for F688yield (r^2 = 0.93) and for F760yield (r^2 = 0.87). The original SIF values (F@Red, F@FarRed) changed less seasonally. PRI values also showed strong seasonal declines over the season (r^2 = 0.88).

later (on day 219), than the peak LUE (on day 214). Early season measurements (e.g., days 214, 219 = August 1, 6) indicate low-stress conditions where incident PAR and NEP were closely linked compared to the other days where stress conditions caused NEP to decouple from incident PAR. In the LUE model, this decoupling of NEP from incident PAR in the absence of changes in *f*APAR is described by variations in the LUE term (e). 2008 was a wetter year and the maximum LUE was significantly higher, than in 2007.

3.3 Spectral Bio-Indicators

The PRI and fluorescence parameter values, determined with measurements acquired at 1 nm spectral resolution (with an Ocean Optics spectroradiometer, tracked daily as well as seasonal changes in canopy level physiological stress. All of the physiologically active spectral indicators (PRI, SIF, and Fyield) showed seasonal declines over the entire 2008 field campaign (Figure 2). The greatest seasonal change was captured by SIF expressed as Fyield: F688yield (r^2 = 0.93) and F760yield (r^2 = 0.87). SIF expressed in energy units (W m^{-2} sr^{-1} nm^{-1}) also showed significant, but less strongly expressed, seasonal change: the O_2-B band, F@Red (r^2 = 0.89); and F@Far-red for the O_2-A band (r^2 = 0.81). Over the season, Fyield dropped from ~11% to 2%, while SIF (F@Red and F@Far-red) decreased from 0.025 to 0.0095 W m^{-2} sr^{-1} um^{-1}. The PRI also exhibited a strong linear decline across the season (r^2 = 0.88), from -0.02 to -0.06. For PRI and fluorescence, the higher values that occurred early in the growing season indicate less stressful conditions, whereas the progressively lower values seen later in the season occurred during the physiological changes for reproductive stages and senescence. However, the Normalized Difference Vegetation Index (NDVI) was almost constant seasonally, ~0.73 ± 0.02 (Fig. 2).

The relationship of PRI to canopy LUE is shown in Figures 3 and 4. PRI values determined with the ASD-FR (at ~3 nm resolution) were combined for measurements made in 2007 and 2008 (r^2 = 0.67), and yielded similar trends in both years (Fig. 3). The relatively high, positive PRI values (+0.02) in the early growth stage indicate low environmental stress, whereas late stage values of -0.075 indicate substantial stress effects, associated with LUE values that declined from 0.048 mol C/mol Qa to near zero LUE. A nearly identical result for the PRI:LUE relationship was obtained with the observations acquired at 1 nm spectral resolution (with the Ocean Optics) in 2008 (r^2 = 0.61), but the narrower resolution enabled detection of a slightly greater range in LUE (zero to +0.65 mol C/mol Qa) (Fig. 4). Although the linear pattern of change in PRI with LUE was apparent over the growing season, there was considerable variation within each day (Figs. 3, 4).

The PRI (@ 1 nm) and the Fyield spectral parameters were strongly correlated for daily values examined over the season (Figure 5): F688yield (r = 0.88) and F760yield (r=0.86).

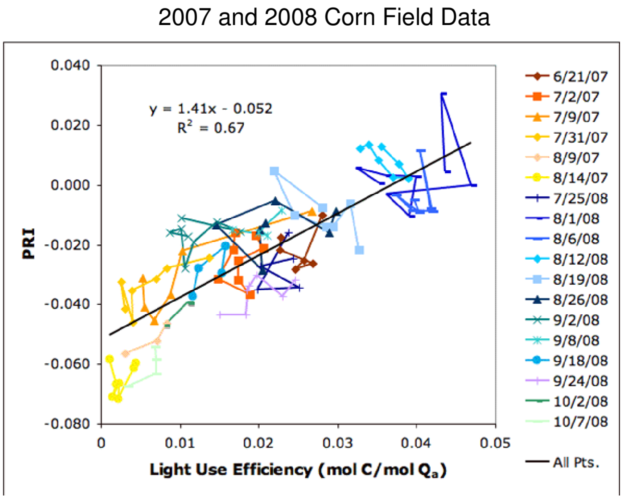

Figure 3. The PRI was determined from average transect reflectances measured with the ASD (~3 nm resolution) versus LUE (mol C/mol Qa) from observations at the UDSA/ARS cornfield in 2007 and 2008. Colored lines connect observations collected over the same day (2007: browns to yellows; 2008 in blues to greens). Regression line (r^2 = 0.67, n = 109).

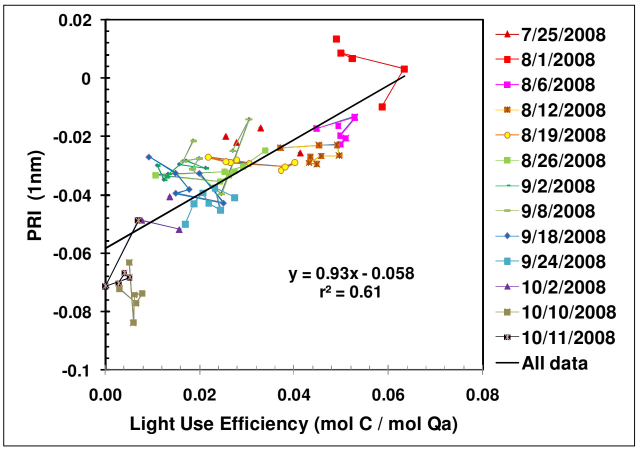

Figure 4. The PRI was determined from average transect reflectances measured with the Ocean Optics (1 nm resolution) versus LUE (mol C/mol Qa) from observations at the UDSA/ARS cornfield in 2008. Colored lines/symbols connect observations collected over the same day. Regression line (r^2 = 0.61, n = 81).

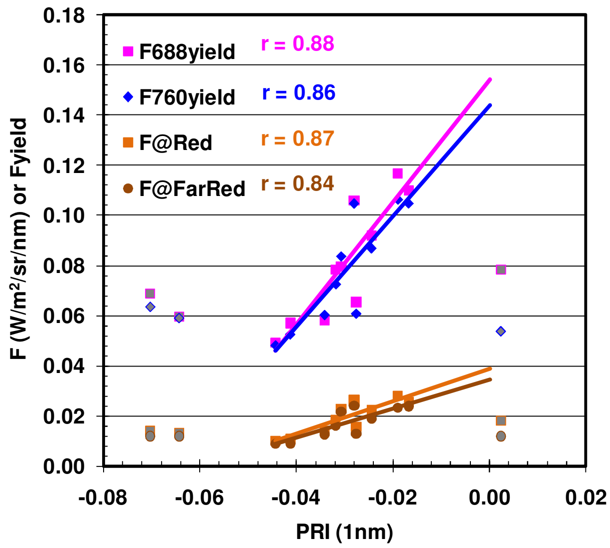

Figure 5. Correlations between PRI and Fyield (F688yield, r = 0.88; F760yield, r = 0.86) and SIF (F@Red, r = 0.87; F@Far-red, r = 0.84).

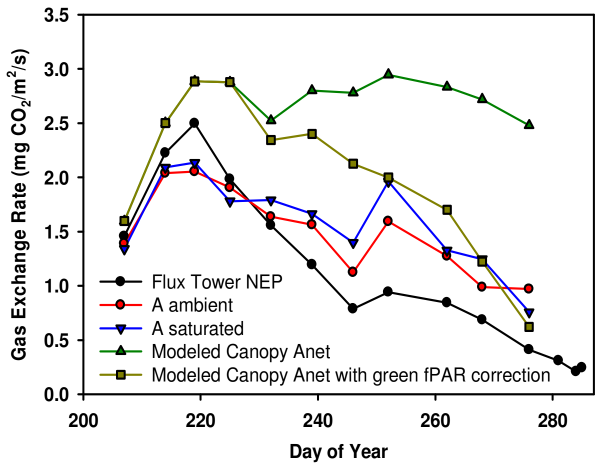

Figure 6. Seasonal corn canopy net ecosystem productivity (NEP) along with measured and GCX modeled leaf photosysnthetic gas exchange rates under ambient and saturated CO_2 concentrations.

The comparable correlations were slightly lower for the original SIF (F@Red, r = 0.87; F@Far-Red, r = 0.84) (Fig. 5). In addition to demonstrating strong correlations on a daily basis to PRI (Fig. 5), the normalized Fyield (F688yield, F760yield) outperformed the SIF (F@Red, F@Far-red) in capturing seasonal change (Fig. 2), most likely because variations in Qa were taken into account (by definition). In general, PRI showed greater values (less stressed) during early morning or late afternoon and more negative values (increased stressed)during midday. On the other hand, SIF showed the exact opposite diurnal pattern (higher values during midday and lower values in the morning or afternoon). For instance, during the most active growth phase, the PRI changed from -0.012 to -0.022, whereas the values during senescence indicated greater stress, changing from -0.038 and -0.052. On those two days, the early and mid-day red SIF values (expressed as % irradiance) varied between 0.118 and 0.093 (growth phase) and between 0.063 and 0.041 (senescence).

In a separate study of a coniferous forest, we found that the PRI was linearly related to the SZA (Middleton et al., 2009). Therefore, we examined the correlation between spectral parameters and solar zenith angle (SZA) for this corn dataset (Table 4). The average daily values on each field date (e.g., July 25) for each spectral parameter are shown in the top section of Tab. 4, whereas the responses at a given local time (e.g., 11 am) averaged across all dates appear in the lower section (Tab. 4). The highest associations between a spectral variable and SZA were observed with the SIFs (F@Red, F@Far-Red), especially in the O_2-A band, for diurnals on most field days when correlations exceeded 0.80. In contrast, SZA was only a significant factor ($r \geq 0.85$) influencing PRI when examined seasonally at each daylight hour, especially for the wider band PRI (10 nm, as for Hyperion satellite bands = Hyp), as might be expected from light-intensity driven pigment biochemistry (Middleton et al., 2009). However, the Fyields were weakly affected by SZA, especially for diurnals (top section), although early morning and late afternoon time periods showed some moderately high correlations (r~0.82-0.84).

3.4 Modeling Canopy Production

Seasonal dynamics of field corn photosynthetic gas exchange during mid-day (typically when the maximum rates are observed) are shown in Figure 6. These

SZA	F688yield	F760yield	PRI	PRI (1nm)	PRI (hyp)	F@Red	F@FarRed	Red/FarRed	NDVI
overall	-0.07	-0.30	-0.26	-0.26	-0.30	-0.74	-0.74	0.35	-0.17
7/25	0.73	0.25	0.42	0.36		-0.37	-0.47	0.50	-0.43
8/1	0.52	0.49	-0.26	-0.23		**-0.88**	**-0.98**	0.30	-0.05
8/6	**0.75**	0.27	0.13	0.29	0.06	-0.72	**-0.76**	0.61	-0.21
8/12	0.42	-0.20	0.02	0.17	0.03	-0.72	**-0.83**	**0.84**	-0.46
8/19	0.71	-0.16	-0.09	0.15	0.03	**-0.90**	**-0.91**	**0.76**	-0.54
8/26	-0.10	-0.53	0.06	0.33	0.66	**-0.95**	**-0.92**	0.73	0.38
9/2	**-0.82**	**-0.91**	**0.87**	**0.83**	**0.77**	**-0.96**	**-0.96**	**0.76**	**0.84**
9/8	0.06	-0.33	0.11	0.13	0.07	**-0.84**	**-0.98**	0.38	0.16
9/18	-0.65	-0.09	**0.81**	**0.89**	**0.83**	**-1.00**	**-0.83**	-0.52	-0.35
9/24	-0.10	-0.53	0.07	0.08	-0.29	**-0.79**	**-0.89**	0.67	0.45
10/2	0.00	-0.64	-0.31	-0.38	**-0.84**	**-0.79**	**-0.93**	**0.93**	0.02
10/10	-0.32	-0.65	0.45	0.48	0.11	**-0.93**	**-0.97**	0.40	0.66
10/11	-0.31	-0.60	0.69	0.72	-0.42	**-0.96**	**-0.95**	0.57	0.66
8am	**-0.84**	-0.55	0.11	-0.20	0.36	-0.19	-0.10	-0.44	-0.22
9am	**-0.82**	**-0.77**	**-0.83**	**-0.84**	**-0.86**	**-0.85**	**-0.82**	0.06	0.25
10am	-0.60	-0.50	**-0.83**	**-0.84**	**-0.89**	**-0.76**	-0.61	-0.04	-0.60
11am	-0.74	-0.69	**-0.90**	**-0.91**	**-0.96**	**-0.92**	**-0.90**	0.29	-0.62
12pm	-0.57	-0.39	**-0.91**	**-0.92**	**-0.94**	-0.65	-0.55	0.00	-0.65
13pm	-0.47	-0.43	**-0.86**	**-0.86**	**-0.89**	-0.37	-0.35	-0.03	-0.52
14pm	-0.48	-0.27	**-0.91**	**-0.92**	**-0.93**	-0.56	-0.39	-0.44	-0.52
15pm	**-0.85**	-0.70	**-0.89**	**-0.90**	**-0.94**	**-0.83**	**-0.75**	-0.29	-0.56
16pm	-0.45	-0.50	**-0.97**	**-0.95**	**-0.88**	-0.69	-0.67	0.37	**-0.78**
17pm	**-0.84**	-0.65	**-0.81**	**-0.79**	**-0.89**	**-0.77**	-0.64	-0.33	0.24
18pm	0.20	0.10	-0.55	-0.51		0.31	0.22	**0.88**	**0.99**

Table 4. The correlation coefficient (r) between Spectral Bio-indicators and Solar Zenith Angle (SZA) are shown for diurnal sets (top section) and across the season at local time intervals (bottom section), where the gray row indicates the proposed FLEX overpass time. Correlations ≥ 0.75 are in bold fonts, ≥ 0.90 are shown in bold and underlined.

measurements span the vegetative (V8) to late reproductive growth (R6) stages. The measured canopy NEP, calculated from the eddy covariance flux data, indicates that an initial rise in maximum ecosystem CO_2 uptake occurred around day of year 220 (at the V13 vegetative growth stage), after which steady decreases in NEP were observed. Leaf-level Amax for ambient and saturated CO_2 concentrations tracked NEP below the NEP curve during the vegetative growth, but then crossed over to track NEP above the NEP curve during reproductive growth phases. The remaining variability in these photosynthetic growth response curves is associated with soil moisture. This is most likely because leaf measurements were always made on green leaves near the top of the canopy, but the bottom canopy section grew progressively more yellow through the season. Consequently, Amax for green leaves overestimates the canopy NEP when a substantial fraction of the canopy is non-green.

The canopy NEP obtained with the GCX model (topmost curve, Fig. 6), which used the green leaf Amax as an input, overestimated the peak NEP (2.8 vs. 2.0 mg CO_2 m^{-2} s^{-1}) and initially failed to show the decline in NEP that occurred after day of year ~235. However, once the LAI input to the model was adjusted to provide the fraction of green foliage, a much closer agreement between measured and modeled parameters was achieved.

4. CONCLUSIONS

We found that canopy-level SIF, Fyield, and the PRI varied significantly throughout each field day, with the available PAR (Qa) exerting a significant control on responses. Daily averages declined for each of these spectral indicators across the growing season as the cornfield progressed through vegetative and reproductive stages, and senescence. The PRI and fluorescence parameter values tracked daily as well as seasonal changes in canopy level physiological stress. All three parameters (SIF, Fyield, and PRI) successfully described seasonal declines in LUE for the cornfield, with similar regression coefficients (r^2, 0.88 – 0.93). The PRI determined with data acquired at two different spectral resolutions and spectroradiometers (3 nm, with an ASD in both 2007 and 2008; 1.5 nm with an Ocean Optics in 2008) provided similar relationships to the LUE determined from tower observations (r^2 = 0.67, 0.61). The PRI (1 nm) and the Fyield spectral parameters were strongly correlated for daily values examined over the season: F688yield (r = 0.88) and F760yield (r = 0.86). Furthermore, the normalized Fyield (F688yield, F760yield) outperformed the SIF (F@Red, F@Far-red) in capturing seasonal change, as well as for strength of relationships to LUE and PRI, most likely because variations in Qa were taken into account. Daily trends for leaf-level photosynthesis were similar to those obtained from tower measurements, but knowledge of the green canopy fraction was necessary to model the canopy net production from leaf-level data inputs. We now have a dataset that will be utilized in future research to link leaf and canopy physiological processes through model simulations.

Acknowledgments

This project was supported through a NASA Remote Sensing AO (sponsor, Dr. Diane Wickland): Spectral Bio-Indicators for Ecosystem Photosynthetic Light Use Efficiency (2006-2009). We thank the following people for assistance with field data collections: Dave Landis (Science Systems and Application, Inc., Lanham, MD USA), and members of the Laboratory for Hydrology and Remote Sensing at USDA/ARS in Beltsville, MD USA

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