Convergence of daily light use efficiency in irrigated and rainfed C3 and C4 crops

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\textbf{Abstract}

The goal of this study is to quantify variability of daily light use efficiency (LUE) based on radiation absorbed by photosynthetically active vegetation (LUE\textsubscript{green}) in C3 and C4 crops. Data contained GPP, fAPAR, total and green leaf area index taken over 16 site years of irrigated and rainfed maize and 8 site years of soybean in 2001–2008 including years with quite strong drought events. LUE\textsubscript{green} in irrigated and rainfed sites were statistically indistinguishable showing low sensitivity to water availability. Seasonal changes of LUE\textsubscript{green} remained remarkably small over a wide range of water supply, leaf area index and weather conditions. The magnitude and composition of incident radiation affected the magnitude of the day-to-day LUE\textsubscript{green} change – increases in incident PAR caused statistically significant decreases of LUE\textsubscript{green}. Convergence of LUE\textsubscript{green} to a narrow range in irrigated and rainfed crops brought important implications for understanding mechanisms of plant response to stress and remote estimation of primary production in crops.

\section{Introduction}

The amount of photosynthesis or primary production of a plant canopy is largely determined by the amount of photosynthetically active radiation (PAR) absorbed by the vegetation; i.e., APAR = \textit{f}APAR \times PAR\textsubscript{in}, where \textit{f}APAR is the fraction of absorbed PAR and PAR\textsubscript{in} is the photosynthetically active radiation incident on the canopy. This is further modified by the efficiency with which this absorbed light is converted to fixed carbon. Light use efficiency (LUE).

There are two contrasting view points on the temporal behavior of LUE; namely,

(a) LUE is a widely variable biophysical characteristic (e.g., Turner et al., 2003; Kergoat et al., 2008),

(b) there is a functional convergence of LUE in vegetation predicted by the concept of an optimization of limited resource allocation (Field, 1991; Field et al., 1995; Goetz and Prince, 1999; Ruimy et al., 1996, 1999).

We argue that for accurate remote estimation of gross primary production (GPP), it is necessary to quantify the effect of LUE on GPP and, thus, to understand how variability in LUE affects the accuracy of remote GPP estimation.

There are many definitions of LUE. Definitions differ in the form of fixed carbon in the numerator (e.g., CO\textsubscript{2}, aboveground biomass, total biomass) and in the time frame over which LUE is determined (e.g., seconds, hours, days, years). Definitions also vary in the form the denominator takes, specifically, the radiation range over which the ‘light’ is measured. Moreover, the ‘light’ term may be based on (a) incident radiation (e.g., Nichol et al., 2000; Suyker et al., 2005; Barton and North, 2001), (b) total absorbed radiation (Monteith, 1972; Norman and Arkebauer, 1991; Lindquist et al., 2005; Kergoat et al., 2008), or (c) radiation absorbed by photosynthetically active/green vegetation (Hall et al., 1992; Viña and Gitelson, 2005; Rossiini et al., 2012). LUE based on total PAR, which is a common expression of LUE in field studies, incorporates measurements of canopy light absorption that do not distinguish the contribution of green from brown/yellow components to the overall absorption. LUE based on radiation absorbed by photosynthetically active/green vegetation (LUE\textsubscript{green}) is not confounded by changing pigmentation and canopy structure during plant growth and senescence, its properties are clearly different from the other two definitions (Gitelson and Gamon, 2015; Gitelson et al., 2017); thus, LUE\textsubscript{green} provides the most mechanistically sound definition. The uncertainty estimates for GPP using different LUE definitions is a critical...
component of the total error budget in the context of remotely sensed based estimations of GPP.

We took advantage of the Carbon Sequestration Program at the University of Nebraska-Lincoln (UNL), which presented a unique possibility for comparison of multiyear LUE at closely located irrigated and rainfed maize and soybean sites. The data sets allowed us to answer a pivotal question: is LUEgreen in irrigated and rainfed crops widely variable or conservative and how strongly does the change in LUEgreen modulate GPP? Specifically, the goal is to quantify:

- long term seasonal constitutive and short term day-to-day facultative changes in LUEgreen, of irrigated and rainfed crops having different photosynthetic pathways, physiology, phenology, leaf structure and canopy architecture,
- LUEgreen response to drought.

2. Methods

Three AmeriFlux sites (Mead Irrigated/US - Ne1, Mead Irrigated Rotation/US - Ne2, and Mead Rainfed Rotation/US - Ne3), located at the UNL Eastern Nebraska Research and Extension Center near Mead, Nebraska, USA, were studied during growing seasons from 2001 to 2008 as part of the Carbon Sequestration Project at UNL. Each field is approximately 50 ha and all are within 4 km of each other. Two sites, site 1 and site 2, were equipped with center pivot irrigation systems, while site 3 was a rainfed that did not receive supplemental water. Site 1 was planted in continuous maize; site 2 and site 3 were both planted in a maize-soybean rotation with contents (VWC) in the root zone were monitored continuously at four depths (0.10, 0.25, 0.5, and 1.0 m) using dielectric permittivity sensors (Theta probe ML2x, Delta-T Devices, Cambridge, UK).

Multiple quantum sensors were placed at each study site to collect hourly incoming PAR (PARin), PAR reflected by the canopy and soil (PARcan), PAR transmitted through the canopy (PARtransm) and PAR reflected by the soil (PARs). PARin was measured using point quantum sensors (LI-190, Li-Cor Inc., Lincoln, Nebraska) placed 5 m above the surface pointing toward the sky at each site. Daytime PARun values were calculated by integrating the hourly measurements during a day from sunrise to sunset (period when PARin exceeded 1 μmol m\(^{-2}\) s\(^{-1}\)). Daytime PARin values are reported in MJ m\(^{-2}\) d\(^{-1}\) (Suyker and Verma, 2012). Daytime potential PAR (PARpot) was the maximal value of daytime PARun that is possible at a site when the concentrations of atmospheric gases and aerosols are minimal. PARpot thus incorporates the seasonal changes in hours of sunshine (i.e., day length) and it varies gradually throughout the growing season (Gitelson et al., 2012). At each site, daytime PARun was calculated as a maximal value of daytime PARun for each day of year (DOY) for each of the eight years of observation. The difference, ΔPAR = PARpot − PARun, reveals the influence of daily weather fluctuations. Low values of PARun (cloudy and/or hazy days) correspond to high ΔPAR, while high PARun values (sunny days) correspond to low differences. Thus, the ΔPAR differences reflect day-to-day weather variations that are not affected by the seasonal change of day length.

There are two facets of LUE: the first reflects the rapidly changing, day-to-day and the second reflects the slowly changing, seasonal or ontogenetic changes. These two have been termed the "facultative" and "constitutive" responses, respectively (Gamon and Berry, 2012). In this study, following Gamon and Berry (2012), we define "facultative LUE" as those that change on a daily time scale, and "constitutive LUE" as those that change over much longer seasonal time scale.

For the facultative component of LUE, irradiance is particularly critical due to the asymptotic shape of the photosynthetic light response relationship that results in a progressive lowering of LUE as a plant is exposed to higher irradiance (e.g., Gamon and Berry, 2012). An understanding of the effects of incident irradiance on the GPP vs. PARAP relationship and LUE is essential for remote estimation of GPP using LUE models. We used a PARun constraint criterion to select days when sites were under "clear skies" conditions and PARin was greater than the 80% of PARpot required for optical remote sensing. It has been shown that PARun above 80% of PARpot corresponds to clear sky conditions for TM, ETM and daily MODIS images collected over the US Corn Belt (Gitelson et al., 2012; Peng et al., 2013).

Within each of three study sites were six small plot areas (20 m × 20 m) representing all major occurrences of soil and crop production zones at the site (Verma et al., 2005). For each of these plots, leaf area index (LAI) was estimated from destructive samples taken at 10–14 day intervals during the growing season from 2001 through 2008. On each sampling date, plants from a one meter length of each of two rows within each plot were collected and the total number of plants recorded. Plants were kept on ice and transported to the laboratory where they were separated into green leaves, senesced (yellow or brown) leaves, stems, and reproductive components. Green and senesced leaves were run through an area meter (LI-3100, Li-Cor, Inc., Lincoln, Nebraska, USA) and the total leaf area per plant was determined. For each plot, the total leaf area per plant was multiplied by the plant population (determined by counting plants in each plot) to obtain a total LAI. Total LAI for the six plots were then averaged as a site-level value (additional details in Viña et al., 2011). Green leaves were handled in the same way to obtain the green LAI (LAIgreen). Since LAI values change gradually during the growing season, daily total LAI and LAIgreen values were interpolated based on measurements on sampling dates for each site in each year.

In three small plots (four at the rainfed Site 3), soil volumetric water contents (VWC) in the root zone were monitored continuously at four depths (0.10, 0.25, 0.5, and 1.0 m) using dielectric permittivity sensors (Theta probe ML2x, Delta-T Devices, Cambridge, UK).

Multiple quantum sensors were placed at each study site to collect hourly incoming PAR (PARin), PAR reflected by the canopy and soil (PARcan), PAR transmitted through the canopy (PARtransm) and PAR reflected by the soil (PARs). PARin was measured using point quantum sensors (LI-190, Li-Cor Inc., Lincoln, Nebraska) 5 m above the surface pointing toward the sky. PARcan was measured with point quantum sensors aimed downward placed at 5 m above the ground. PARtransm was measured with 5 line quantum sensors (LI-191, Li-Cor Inc., Lincoln, Nebraska) placed diagonally across E-W planted rows, at about 2 cm above the ground, pointing upward and PARs was measured with a line quantum sensor placed diagonally about 12 cm above the ground, pointing downward (further details in Hanan et al., 2002; Burba, 2005). All daily values of radiation were computed by integrating the hourly measurements during a day when daily PARun exceeded 1 μmol m\(^{-2}\) s\(^{-1}\). Daily values of the fraction of PAR absorbed by the whole canopy (fAPARtotal) were then calculated as (Goward and Huemmerich, 1992; Viña and Gitelson, 2005):

$$fAPAR_{total} = \frac{PAR_{in} - PAR_{can} - PAR_{transm} + PAR_{s}}{PAR_{in}}$$

During the vegetative growth stages, when LAIgreen is equal to total LAI, fAPARtotal represents fAPAR used for photosynthesis. However, during the reproductive and senescence stages fAPARtotal remained insensitivity to decreases in crop greenness (Hatfield et al., 1984; Gallo et al., 1985; Viña and Gitelson, 2005) since both photosynthetic and non-photosynthetic components intercepted PARun with progressively less used for photosynthesis – Fig. 1 (see also Hall et al., 1992; Viña and Gitelson, 2005). To obtain a measure of the fAPAR absorbed solely by the photosynthetic component of the vegetation, fAPARgreen was estimated as (Hall et al., 1992):

$$fAPAR_{green} = fAPAR_{total} \times \frac{LAI_{green}}{total\ LAI}$$

Crop GPP was measured by the eddy covariance method. Each site was equipped with an eddy covariance tower and meteorological sensors, with which measurements of CO\(_2\) fluxes, water vapor, and energy fluxes were obtained continuously. Daytime net ecosystem exchange (NEE) values were computed by integrating hourly CO\(_2\) fluxes collected during a day when PARun exceeded 1 μmol m\(^{-2}\) s\(^{-1}\). Daytime estimates of ecosystem respiration (Re) were obtained from the night CO\(_2\)
exchange-temperature relationship (e.g., Xu and Baldocchi, 2003; Verma et al., 2005). GPP was then obtained by subtracting \( \text{Re} \) from \( \text{NEE} \): \( \text{GPP} = \text{NEE} - \text{Re} \) (note: sign convention is such that fluxes toward the surface are positive). GPP values are presented in units of g C m\(^{-2}\) d\(^{-1}\) (details in Verma et al., 2005; Suyker et al., 2004).

Daytime PAR absorbed by the whole canopy (APAR\(_{\text{total}}\)) was calculated as the product of fAPAR\(_{\text{total}}\) and daytime incoming PAR. PAR absorbed only by the photosynthetic component of the vegetation was calculated as: \( \text{APAR}_{\text{green}} = \text{fAPAR}_{\text{total}} \times \text{PAR}_{\text{in}} \). LUE of photosynthetically active green vegetation was calculated as \( \text{LUE}_{\text{green}} = \frac{\text{GPP}}{\text{APAR}_{\text{green}}} \), which is a quantitative measure of the efficiency of conversion of APAR\(_{\text{green}}\) into fixed carbon (Gitelson and Gamon, 2015) at the canopy scale.

3. Results

3.1. GPP vs. APAR\(_{\text{green}}\) relationships

Analysis of GPP vs. APAR\(_{\text{green}}\) relationships for the two crops was the first step in understanding and quantifying variability of LUE. We compared the relationships for 16 site years of maize data (12 irrigated and 4 rainfed) and for 8 site years of soybean data (4 irrigated and 4 rainfed) taken during eight years (2001 through 2008). Nine maize hybrids and three soybean cultivars were grown during the eight years. These data allowed the study of LUE in crops under the rather harsh weather conditions of eastern Nebraska including years with very different temperature regimes and water supplies. The GPP vs. APAR\(_{\text{green}}\) relationships for very different irrigation regimes were linear and very close for both crops, although relationships for soybean have a wider scatter around the best-fit functions (Fig. 2). The relationship for irrigated maize GPP = (2.24 ± 0.011) × APAR was almost identical to that in rainfed maize GPP = (2.22 ± 0.018) × APAR. NRMSE of GPP estimation by these equations was below 13.3% for irrigated and 11.1% for rainfed maize. For irrigated soybean NRMSE of GPP estimation by the relationship GPP = (1.46 ± 0.02) × APAR\(_{\text{green}}\) was 18.6% and for rainfed soybean NRMSE by the relationship GPP = (1.42 ± 0.017) × APAR\(_{\text{green}}\) was 16%. A heteroscedastic t-test showed with 95% probability that the relationships of GPP vs. APAR\(_{\text{green}}\) were not statistically different for irrigated and rainfed sites for either crop.

3.2. Long term seasonal constitutive changes in LUE\(_{\text{green}}\)

In both crops, LUE\(_{\text{green}}\) increased in the beginning of the season and then leveled off as APAR\(_{\text{green}}\) exceeded 5 MJ m\(^{-2}\) d\(^{-1}\) in maize and 4 MJ m\(^{-2}\) d\(^{-1}\) in soybean (Fig. 3); at that time green LAI in both crops was > 2 m\(^{2}\) m\(^{-2}\). With the onset of senescence, LUE\(_{\text{green}}\) decreased. This decrease was more pronounced and occurred more quickly in soybean than in maize. Importantly, the seasonal constitutive change of LUE\(_{\text{green}}\) was alike in both irrigated and rainfed sites. LUE\(_{\text{green}}\) distributions in irrigated and rainfed sites were almost identical for both crops (Fig. 4); a t-test showed with 95% probability that the LUE distributions for irrigated and rainfed sites were not statistically different.

The standard deviation of LUE\(_{\text{green}}\) in maize across the seasons (constitutive change) was below 14.7% in rainfed sites (during four years) and below 18.4% in irrigated sites (during eight years) - Table 1A. In soybean, the standard deviation was higher than in maize - 24.9% and 28.6% in irrigated and rainfed sites, respectively (Table 1B). Significantly, mean LUE\(_{\text{green}}\) in irrigated and rainfed sites were very close; t-tests showed (95% probability) no significant difference between mean LUE\(_{\text{green}}\) in irrigated and rainfed sites for either crop.

The LUE\(_{\text{green}}\) variability early in the season may be related to uncertainties of fAPAR measurements, as crop LAI is low and leaves are clumped into rows (e.g., Burba, 2005). In senescence stages, the LUE\(_{\text{green}}\) decrease was more pronounced in soybean than in maize due to sharp decreases in leaf chlorophyll content (Mock and Pearce, 1975; Setiyono et al., 2007). In both crops, the decrease of LUE\(_{\text{green}}\) in senescence stages was likely due to overestimation of APAR\(_{\text{green}}\) as it was calculated using a subjective measure of greenness, green LAI (Gitelson et al., 2014). For the same destructively determined green LAI, leaf chlorophyll content in reproductive and senescence stages may be significantly lower than that in vegetative stages (Ciganda et al., 2009; Peng et al., 2011). To make accurate quantification of constitutive LUE\(_{\text{green}}\) changes across sites and years, GPP and APAR\(_{\text{green}}\) data for the period June 1st to August 30 were used (e.g., Turner et al., 2003, Schull et al., 2015). These criteria eliminated days early in the growing season as green LAI < 2 m\(^{2}\) m\(^{-2}\) corresponding to APAR\(_{\text{green}}\) below 5 MJ m\(^{-2}\) d\(^{-1}\) for maize and 4 MJ m\(^{-2}\) d\(^{-1}\) for soybean (Fig. 3) when uncertainties of APAR\(_{\text{green}}\) measurement were greatest. The month of September was omitted from comparisons because in late senescence stages foliage is rapidly changing from green to yellow and brown and LUE\(_{\text{green}}\) calculated using green LAI may therefore be biased. In addition, at that time green vegetation fraction drops and uncertainties in the measurement of fAPAR increased significantly.

Applying the temporal constraint criteria allowed a more accurate estimate of the variability of LUE\(_{\text{green}}\) (Table 1, June 1–August 30; Fig. 5). A t-test showed that no significant differences between LUE\(_{\text{green}}\) in rainfed and irrigated sites existed (risk level \( \alpha = 0.05 \)). Mean LUE\(_{\text{green}}\) values in irrigated and rainfed sites were very close: 2.23 vs.
2.24 g C MJ\(^{-1}\) in maize and 1.47 vs. 1.43 g C MJ\(^{-1}\) in soybean (Table 1, Fig. 5). Standard deviation of LUE\(_{\text{green}}\) was 12.5% and 10.8% in irrigated and rainfed maize, respectively, and 12.8% and 15.2% in irrigated and rainfed soybean, respectively.

### 3.3. Short term facultative changes in LUE\(_{\text{green}}\)

Short term day-to-day facultative LUE\(_{\text{green}}\) oscillated around the almost horizontal lines representing the constitutive LUE\(_{\text{green}}\) vs. DOY relationships with a STD = 12.5% in 16 site-years of data in maize and 11.5% in 8 site-years of data in soybean (Fig. 6 for rainfed maize and soybean). Oscillations of LUE\(_{\text{green}}\) at both irrigated and rainfed sites frequently coincided with \(\Delta\text{PAR} = \text{PAR}_{\text{pot}} - \text{PAR}_{\text{in}}\). Importantly, almost every increase of \(\Delta\text{PAR}\) (i.e., decrease of \(\Delta\text{PAR}\)) corresponded to a decrease in LUE\(_{\text{green}}\), i.e., a decrease in photosynthetic efficiency. There was a consistent response of the magnitude of LUE\(_{\text{green}}\) to changes in
PARin resulting in linear LUEgreen vs. ΔPARin relationships with $R^2 = 0.44$ for maize and 0.42 for soybean ($p < 0.01$) and quite small standard error of LUE estimation by PARin: 7.11% in maize and 8.15% in soybean. The relationships for irrigated and rainfed sites were not statistically significant at the $\alpha = 0.05$ level. This strongly suggests that, in many cases, excessive PARin that cannot be efficiently utilized by the plants was the reason for the decrease of photosynthetic activity.

An additional factor contributing to the close LUEgreen vs. ΔPAR relationship was a likely increase in the fraction of diffuse radiation at high ΔPAR enhancing absorption of radiation (Norman and Arkebauer, 1991; Gu et al., 2002; Turner et al., 2003). However, our analyses were limited to PARin within 20% of PARpot with cloudiness coefficient (Turner et al., 2003) below 0.2. Thus, likely the effects of diffuse light weren’t as dramatic as shown in Turner et al. (2003) and Norman and Arkebauer (1991).

### Table 1

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<th>Irrigated</th>
<th>Rainfed</th>
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<tr>
<td>(A) Min LUEgreen, g CM J^{-1}</td>
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<td>0.49</td>
<td>1.20</td>
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<tr>
<td>Max LUEgreen, g CM J^{-1}</td>
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<td>Mean LUEgreen, g CM J^{-1}</td>
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<td>2.16</td>
<td>2.23</td>
<td>2.24</td>
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<tr>
<td>STD, g CM J^{-1}</td>
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<td>0.39</td>
<td>0.24</td>
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<tr>
<td>CV, %</td>
<td>14.7</td>
<td>18.4</td>
<td>10.8</td>
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<tr>
<td>(B) Min LUEgreen, g CM J^{-1}</td>
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<td>0.11</td>
<td>0.34</td>
<td>0.53</td>
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<tr>
<td>Max LUEgreen, g CM J^{-1}</td>
<td>2.11</td>
<td>2.6</td>
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<td>2.12</td>
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<td>Mean LUEgreen, g CM J^{-1}</td>
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<td>1.43</td>
<td>1.43</td>
<td>1.47</td>
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<td>STD, g CM J^{-1}</td>
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<td>0.37</td>
<td>0.23</td>
<td>0.19</td>
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<tr>
<td>CV, %</td>
<td>24.9</td>
<td>28.6</td>
<td>15.2</td>
<td>12.8</td>
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Availability of irrigated and rainfed sites of maize in odd years and soybean sites in even years allowed for the study of the effect of drought on LUEgreen. Several drought events with significant decreases in soil moisture occurred; the most severe droughts during the 2001–2008 period occurred in 2002 and 2003 (Suyker and Verma, 2010). We compared the temporal behavior of LUEgreen at irrigated and rainfed soybean sites in 2002 and maize sites in 2003. As indicators of the LUEgreen change we used the differences between actual LUEgreen and the mean LUEgreen for each crop (16 site-years for maize and 8 site-years

![Fig. 4](image-url) Frequency distributions of LUEgreen normalized to sample number in (A) maize irrigated (625 samples) and rainfed (189 samples) and (B) soybean irrigated (186 samples) and rainfed (184 samples). A t-test showed (95% probability) that the LUE distributions for irrigated and rainfed sites were not statistically different.

![Fig. 5](image-url) LUEgreen plotted versus PAR absorbed by photosynthetically active green vegetation (APARgreen) for irrigated and rainfed (A) maize and (B) soybean for the period June 1 to August 30 when APARgreen was below 5 MJ m^{-2} d^{-1} for maize and 4 MJ m^{-2} d^{-1} for soybean and green leaf area index in both crops exceeded 2 m^2 m^{-2}. Descriptive statistics of LUEgreen for this period are given in the right-hand sections of Table 1. Solid lines are best-fit functions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
for soybean) during the season (Fig. 7).

With a decrease of the 0.5 m soil volumetric water content (VWC) at the rainfed maize site in 2003 (Fig. 7A), LUEgreen remained very close or higher than the mean value for at least 20 days (DOY 180 to 200). During this period fAPARgreen decreased almost synchronously with the decrease in GPP (Fig. 7A in Gitelson et al., 2015), thus, LUEgreen remained quite stable. At that time, leaf chlorophyll content kept invariant and the decrease in fAPARgreen was likely caused by photoprotective mechanisms such as changes in leaf inclination/leaf rolling, chloroplast avoidance movement, etc. Later, when VWC dropped below 0.25 m$^3$ m$^{-3}$, LUEgreen in the rainfed site decreased and was smaller than in the irrigated site, although it did not drop below the standard deviation of the multiyear mean LUEgreen values for maize and soybean.

In soybean (Fig. 7B) when the 0.5 m VWC at the rainfed site was below 0.25 m$^3$ m$^{-3}$, LUEgreen, oscillated around its multiyear mean value not dropping below the STD of LUEgreen. Thus, during drought events in both crops the day-to-day LUEgreen oscillated with a magnitude about half of the standard deviation of the multiyear mean LUEgreen.

4. Discussion and conclusions

For the data used in this paper it was shown that LUEgreen is affected by many factors, specifically cloudiness coefficient (Suyker and Verma, 2012) as well as daytime temperature, vapor pressure deficit, and phenology (in Nguy-Robertson et al., 2015). Our results showed that the effect of all these factors on LUEgreen resulted in normalized standard deviations of LUEgreen for irrigated and rainfed maize of 11.9% and for irrigated and rainfed soybean of 13.3% thus demonstrating convergence of LUEgreen to quite a narrow range.

In both maize and soybean, C3 and C4 crops, LUEgreen in irrigated and rainfed sites are statistically indistinguishable showing low sensitivity to water availability. This conclusion is also supported by findings that (i) about 90% of GPP variation in crops and grasslands is explained by total canopy chlorophyll content (Gitelson et al., 2003; Peng et al., 2011; Gitelson et al., 2015; Sakowska et al., 2016; Wu et al., 2009), (ii) assuming an invariant LUEgreen, GPP in crops and grasslands may be accurately retrieved from close range and satellite data (e.g., Gitelson et al., 2006, 2012; Harris and Dash, 2010, 2011; Peng et al., 2013; Rossini et al., 2012, 2014; Sakowska et al., 2014, 2016; Wu et al., 2009), and (iii) the maximum daily LUE based on PAR absorption by canopy chlorophyll, unlike other expressions of LUE, tends to converge across biome types (Zhang et al., 2018).

Seasonal constitutive changes of LUEgreen remained remarkably small over a wide range of water supply in rainfed and irrigated maize and soybean, crops with different photosynthetic pathways, leaf
structures and canopy architectures. The magnitude and composition of incident radiation affect the magnitude of the day-to-day facultative LUE\textsubscript{green} change. Increases in incident PAR caused decreases of LUE\textsubscript{green}.

Is limited resource availability and high resource acquisition costs at rainfed sites a reason for efficient resource use and convergence of LUE\textsubscript{green}? Such a scenario results in an optimization of resource allocation, which then results in a maximization of carbon gains and a convergence on a narrow range of LUE\textsubscript{green} (Field, 1991; Goetz and Prince, 1999). In this case, the plant response to stress is a decrease in APAR\textsubscript{green} such that LUE\textsubscript{green} remains relatively invariant.

To make conclusions about facultative and constitute LUE\textsubscript{green} changes in other crops and vegetation types and to identify the causes underlying the LUE\textsubscript{green} values, it is necessary to assess fAPAR\textsubscript{green} and LUE\textsubscript{green} using consistent procedures (Gitelson and Gaman, 2015).

Our results bring important implications for remote estimating of primary production in crops. Convergence of LUE\textsubscript{green} allows the use of simple robust gross primary production models and also allows a better understanding of the role and constraints of LUE\textsubscript{green} in process-based models. Assuming invariant LUE\textsubscript{green} the models based on either the canopy/stand/community chlorophyll content or green LAI may facilitate accurate assessments of primary production and plant optimization patterns at multiple scales, from leaves to canopies and entire regions.

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