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Productivity, absorbed photosynthetically active radiation, and light use efficiency in crops: Implications for remote sensing of crop primary production

Anatoly A. Gitelson
University of Nebraska - Lincoln, agitelson2@unl.edu

Yi Peng
University of Nebraska-Lincoln, ypeng2@unl.edu

Timothy J. Arkebauer
University of Nebraska - Lincoln, tarkebauer1@unl.edu

Andrew E. Suyker
University of Nebraska-Lincoln, asuyker1@unl.edu

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Productivity, absorbed photosynthetically active radiation, and light use efficiency in crops: Implications for remote sensing of crop primary production

Anatoly A. Gitelson,[1,4] Yi Peng,[1,3] Timothy J. Arkebauer,[2] and Andrew E. Suyker[1]

1 School of Natural Resources, University of Nebraska–Lincoln, Lincoln, NE 68583-0973, USA
2 Department of Agronomy and Horticulture, University of Nebraska–Lincoln, Lincoln, NE 68583-0817, USA
3 School of Remote Sensing and Information Engineering, Wuhan University, Wuhan 430079, China
4 Faculty of Civil and Environmental Engineering, Israel Institute of Technology (Technion), Technion City, Haifa 32000, Israel

Corresponding author — A. A. Gitelson, Faculty of Civil and Environmental Engineering, Israel Institute of Technology (Technion), Technion City, Haifa 32000, Israel; tel 972 52 9544862; email agitelson2@unl.edu

Abstract

Vegetation productivity metrics such as gross primary production (GPP) at the canopy scale are greatly affected by the efficiency of using absorbed radiation for photosynthesis, or light use efficiency (LUE). Thus, close investigation of the relationships between canopy GPP and photosynthetically active radiation absorbed by vegetation is the basis for quantification of LUE. We used multiyear observations over irrigated and rainfed contrasting C3 (soybean) and C4 (maize) crops having different physiology, leaf structure, and canopy architecture to establish the relationships between canopy GPP and radiation absorbed by vegetation and quantify LUE. Although multiple LUE definitions are reported in the literature, we used a definition of efficiency of light use by photosynthetically active "green" vegetation (LUE_{green}) based on radiation absorbed by "green" photosynthetically active vegetation on a daily basis. We quantified, irreversible slowly changing seasonal (constitutive) and rapidly day-to-day changing (facultative) LUE_{green}, as well as sensitivity of LUE_{green} to the magnitude of incident radiation and drought events. Large (2–3-fold) variation of daily LUE_{green} over the course of a growing season that is governed by crop physiological and phenological status was observed. The day-to-day variations of LUE_{green} oscillated with magnitude 10–15% around the seasonal LUE_{green} trend and appeared to be closely related to day-to-day variations of magnitude and composition of incident radiation. Our results show the high variability of LUE_{green} between C3 and C4 crop species (1.43 gC/MJ vs. 2.24 gC/MJ, respectively), as well as within single crop species (i.e., maize or soybean). This implies that assuming LUE_{green} as a constant value in GPP models is not warranted for the crops studied, and brings unpredictable uncertainties of remote GPP estimation, which should be accounted for in LUE models. The uncertainty of GPP estimation due to facultative and constitutive changes in LUE_{green} can be considered as a critical component of the total error budget in the context of remotely sensed based estimations of GPP. The quantitative framework of LUE_{green} estimation presented here offers a way of characterizing LUE_{green} in plants that can be used to assess their phenological and physiological status and vulnerability to drought under current and future climatic conditions and is essential for calibration and validation of globally applied LUE algorithms.

Keywords: Gross primary production, Absorbed radiation, Light use efficiency, Remote sensing, Photosynthesis

Abbreviations: GPP, gross primary production; fAPAR, fraction of absorbed photosynthetically active radiation; $fAPAR_{green}$, fraction of radiation absorbed by photosynthetically active "green" vegetation; aPAR, absorbed photosynthetically active radiation; $aPAR_{green}$, radiation absorbed by photosynthetically active "green" vegetation; LUE, light use efficiency; LUE_{green}, efficiency of light use by photosynthetically active "green" vegetation; PAR_{in}, incident photosynthetically active irradiance; PAR_{pot}, incident potential photosynthetically active irradiance; LAI_{green}, green leaf area index; DOY, day of year

Introduction

Vegetation productivity can be defined as the production of organic matter by plants through photosynthesis. The total amount of carbon fixed by vegetation through photosynthesis is gross primary productivity (GPP; Gough, 2012). The net carbon dioxide flux between the atmosphere and land surface (the net ecosystem carbon dioxide exchange, NEE), is measured in micrometeorological studies (Baldocchi, 2003) and GPP is estimated from NEE observations and daytime ecosystem respiration (Re) as GPP = NEE – Re (Suyker and Verma, 2010).

The carbon exchange between the crop canopy and the atmosphere is mainly controlled by the amount of photosynthetically active radiation absorbed by green vegetation (aPAR) as well as the efficiency of using this energy for photosynthesis, i.e., the light use efficiency (LUE). aPAR is expressed as the product of the incident photosynthetically active radiation (PAR_{in}) and the fraction of absorbed photosynthetically active radiation (fAPAR).

In reality, both, aPAR and LUE can be modulated to varying degrees by underlying biological processes and may differ as different operational definitions of aPAR and LUE are used. Not all light absorbed by the canopy is used for photosynthesis. Only the so-called "photosynthetic" part of radiation, absorbed by photosynthetically active (green) vegetation is used for photosynthesis. This component has been termed fraction of radiation absorbed by photosynthetically active "green" vegetation ($fAPAR_{green}$) and defined (Hall et al., 1992) as:

$$fAPAR_{green} = fAPAR \times (LAI_{green} \div \text{total LAI}) \quad (1)$$

where LAI_{green} is the green leaf area index, which is the photosynthetically functional component of the total LAI. Therefore, LUE of photosynthetically active vegetation is defined as:

$$LUE_{green} = GPP \div aPAR_{green} \quad (2)$$

Efficiency of light use by photosynthetically active "green" vegetation (LUE_{green}) is a quantitative measure of the efficiency of conversion of radiation absorbed by photosynthetically active "green" vegetation ($aPAR_{green}$) into fixed carbon.

The $aPAR_{green}$ is affected by a number of factors that include magnitude and composition of incident PAR, canopy structure, photosynthetic pigment content, LAI, leaf angle distribution, and PAR absorptance. It tends to vary over long seasonal time spans; these slow or irreversible changes often termed constitutive properties (Gamon and Berry, 2012). There are also rapid and reversible changes over the short term, diurnally, termed facultative, due to changing leaf display in the case of plants exhibiting leaf movement, leaf wilting, or chloroplast movement or reaction to magnitude and composition of incident radiation (Björkman and Demmig-Adams, 1994).

Based on the assumption that maximum LUE is relatively conservative within broad categories of plant functional type (Monteith, 1977; Field, 1991; Goetz and Prince, 1999), LUE is commonly regarded as a constant, though biome-specific (e.g., Ruimyet al., 1999; Gower et al., 1999). However, similar to $aPAR_{green}$, LUE is affected by a number of processes that affect the energy distribution within the photosynthetic system ranging from pigment composition (chlorophyll and carotenoid content, and the relative levels of xanthophyll cycle pigments), to enzyme kinetics (Björkman and Demmig-Adams, 1994; Gamon and Qiu, 1999; Turner et al., 2003). This physiological response may vary over diurnal and seasonal time scales, depending on changing environmental conditions and plant ontogeny. Recent studies have shown that LUE varies considerably within vegetation types, at different phenological stages, and under varying environmental conditions (Prince, 1991; Medlyn, 1998; Gower et al., 1999; Ruimy et al., 1999; Turner et al., 2003; Xu and Baldocchi, 2003; Houborg et al., 2011, 2013). Analysis by Kergoat et al. (2008) strongly supports the view that LUE varies significantly not only across and within biomes, but also among plant functional types. Thus, there is little doubt that the assumption of a constant LUE does not provide an accurate description of terrestrial ecosystems (Binkley et al., 2004; Bradford et al., 2005; Kergoat et al., 2008). These studies highlight the need to account for variations in LUE related to changing irradiation, temperature, water and nutrient resources among others.

The objective of this paper was to establish GPP vs. $aPAR_{green}$ relationships and quantify LUE in different hybrids of two contrasting species (maize, a C4 species, and soybean, a C3 species; both irrigated and rainfed) having different physiology, phenology, leaf structure and canopy architecture. A primary focus was to (a) quantify facultative, short term (day-to-day), and constitutive, long term (seasonal), behaviors of LUE_{green}, (b) quantify LUE_{green} sensitivity to dry weather conditions, and (c) understand the effect of LUE_{green} variation on the results and interpretation of the LUE model. The ultimate goal of this analysis was to draw attention to significant diurnal and seasonal variation of LUE_{green} in crops and the consequences of this variation on remote estimation of productivity using LUE models.

Methods

Study sites

Three AmeriFlux sites (Mead Irrigated/US – Ne1, Mead Irrigated Rotation/US – Ne2, and Mead Rainfed Rotation/US – Ne3), located at the University of Nebraska-Lincoln Agricultural Research and Development Center near Mead, Nebraska, USA, were studied during growing seasons from 2001 to 2008. They are all approximately 60 ha fields within 4 km of each other. Site 1 and site 2 were irrigated sites equipped with a center pivot irrigation system, while site 3 was a rainfed site relying entirely on rainfall for moisture. Site 1 was planted in continuous maize, site 2 and site 3 were both planted with maize–soybean rotation with maize in odd years (2001, 2003, 2005, and 2007) and soybean in even years (2002, 2004, 2006, and 2008). More information about these study sites is given in Suyker and Verma (2010).

Incoming and potential photosynthetically active radiation

At each study site, hourly incoming PAR (PAR_{in}) was measured by point quantum sensors (LI-190, Li-Cor Inc., Lincoln, Nebraska) placed 6 m above the surface pointing toward the sky. Daytime PAR_{in} values were calculated by integrating the hourly measurements during a day from sunrise to sunset (period when PAR_{in} exceeding 1 μmol $m^{-2}s^{-1}$). Daytime PAR_{in} values are reported in MJ $m^{-2}d^{-1}$ (Turner et al., 2003).

Daytime potential PAR (incident potential photosynthetically active irradiance (PAR_{pot})) is the maximal value of daytime PAR_{in} that may occur when the concentrations of atmospheric gases and aerosols are minimal (Gitelson et al., 2012). PAR_{pot} represents the seasonal changes in hours of sunshine (i.e., day length) and it varies gradually throughout the growing season (Gitelson et al., 2012). In this study, daytime PAR_{pot} was calculated as a maximal value of daytime PAR_{in} for each day of year (DOY) recorded for eight years of observation.

The PAR_{in} variations are not only affected by fluctuations of daily weather conditions but also by gradual seasonal change of day length. The difference between PAR_{pot} and PAR_{in} ($PAR_{pot} - PAR_{in}$) was introduced in this study to indicate daily weather fluctuations. Low values of PAR_{in} (cloudy and/or hazy days) correspond

to high difference (PAR_{pot} − PAR_{in}), while high PAR_{in} values (sunny days) correspond to low (PAR_{pot} − PAR_{in}). Such (PAR_{pot} − PAR_{in}) differences reflect the day-to-day weather variation, which is not affected by seasonal change of day length.

For the facultative component of LUE, irradiance is particularly critical due to the asymptotic shape of the photosynthetic light response relationship which results in a progressive lowering of LUE as a plant is exposed to higher irradiance (Gamon and Berry,2012). An understanding of the effect of incident irradiance on the GPP vs. absorbed photosynthetically active radiation (aPAR) relationship and LUE is essential for remote estimation of GPP using LUE models. So, we used a PAR_{in} constraint criterion in order to select days when sites were under "cloud-free" conditions with clear satellite images available. For the same sites in Nebraska that were used in this study, as well for sites in Minnesota, Iowa and Illinois, it was found that about 90% of "cloud free" TM/ETM+ Land-sat images were obtained when PAR_{in} was greater than 80% of PAR_{pot} (Gitelson et al., 2012). Therefore, in this study, we focused our attention on days when PAR_{in} was above 80% of PAR_{pot}.

Destructive determination of leaf area index

Within each of three study sites, six small plot areas (20 m × 20 m), representing all major occurrences of soil and crop production zones, were established (Verma et al., 2005). The leaf area index (LAI) was estimated from destructive samples at 10–14 day intervals during the growing season from 2001 to 2008. On each sampling date, plants from a 1 m 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, dead leaves, stems, and reproductive components. Green and dead leaves were run through an area meter (Model LI-3100, Li-Cor, Inc., Lincoln, Nebraska) 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 (details in Viña et al., 2011). Green leaves were handled in the same way to obtain the green leaf area index (LAI_{green}). Since LAI values change gradually during the growing season, daily total LAI and LAI_{green} values were interpolated based on measurements on sampling dates for each site in each year.

Fraction of radiation absorbed by photosynthetically active vegetation

Quantum sensors were placed in each study site 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 using point quantum sensors (Model LI-190, Li-Cor Inc., Lincoln, Nebraska) 6 m above the surface pointing toward the sky; PAR_{out} was measured with point quantum sensors aimed downward placed at 6 m above the ground; PAR_{transm} was measured with line quantum sensors (Model LI-191, Li-Cor Inc., Lincoln, Nebraska) placed at about 2 cm above the ground, pointing upward; and PAR_{soil} was measured with line quantum sensors placed about 12 cm above the ground, pointing downward (details in Hanan et al., 2002; Burba, 2005). All daily values of radiation were computed by integrating the hourly measurements during a day when hourly PAR_{in} exceeded 1 μmol $m^{-2}s^{-1}$. Daily values of the fraction of PAR absorbed by the whole canopy ($fAPAR_{total}$) were then calculated as (Goward and Huemmrich, 1992; Viña and Gitelson, 2005):

$$fAPAR_{total} = (PAR_{in} - PAR_{out} - PAR_{transm} + PAR_{soil}) \div PAR_{in}$$

During the vegetative stage, when LAI_{green} is equal to total LAI, $fAPAR_{total}$ represents fraction of absorbed photosynthetically active radiation (fAPAR) used for photosynthesis. However, during the reproductive and senescence stages $fAPAR_{total}$ became insensitive 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 PAR_{in} but progressively less was used for photosynthesis (Hall et al., 1992; Viña and Gitelson, 2005). Therefore, to obtain a measure of the fAPAR absorbed solely by the photosynthetic component of the vegetation, fraction of radiation absorbed by photosynthetically active "green" vegetation ($fAPAR_{green}$) was calculated using equation (1) (Hall et al.,1992).

Gross primary production (GPP), absorbed PAR and light use efficiency (LUE)

In this study, 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 PAR_{in} 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). GPP was then obtained by subtracting Re from NEE as: GPP = NEE − Re. GPP values are presented in units of g C $m^{-2}d^{-1}$; the sign convention used here was such that CO_2 flux to the surface was positive so that GPP was always positive and Re was always negative (Verma et al., 2005). This approach has been widely used in the context of tower flux measurements and is considered to provide reasonable GPP estimates at the landscape level (details in Verma et al., 2005; Suyker et al., 2005).

Daytime PAR absorbed by the whole canopy ($aPAR_{total}$) was calculated as the product of $fAPAR_{total}$ and daytime incoming PAR: $aPAR_{total} = fAPAR_{total} \times PAR_{in}$. PAR absorbed only by the photosynthetic component of the vegetation was calculated as: radiation absorbed by photosynthetically active "green" vegetation ($aPAR_{green}$) = $fAPAR_{green} \times PAR_{in}$. Based on Monteith's model (Monteith, 1972), LUE of photosynthetically active vegetation was calculated as:

$$LUE_{green} = GPP \div aPAR_{green}$$

which is a quantitative measure of the efficiency of conversion of $aPAR_{green}$ into fixed carbon (Gitelson and Gamon, 2015) at the canopy scale.

In order to better understand interactions between GPP and $aPAR_{green}$, both GPP and $aPAR_{green}$ values were scaled to range between 0 and 1 as $GPPsc = (GPP - GPP_{min}) \div (GPP_{max} - GPP_{min})$ and $(aPAR_{green})sc = [aPAR_{green} - (aPAR_{green})min] \div [(aPAR_{green})_{max} - (aPAR_{green})_{min}]$, where GPP and $aPAR_{green}$ are current values of GPP and $aPAR_{green}$, respectively, and subscripts "min" and "max" define minimal and maximal values of GPP and $aPAR_{green}$ for each site and each year. For further analysis, the difference between scaled GPP and $aPAR_{green}$ $\delta = GPPsc - (aPAR_{green})sc$ was used.

Results and discussion

Temporal behavior of GPP, radiation absorbed by green vegetation and green LUE

The temporal behavior of the scaled GPPsc and $(aPAR_{green})sc$ presented in Figure 1 for maize irrigated and rainfed sites illustrated clearly physiological status of crops. When the difference between scaled GPP and $aPAR_{green}$ values $\delta = GPPsc - (aPAR_{green})sc \approx 0$, the

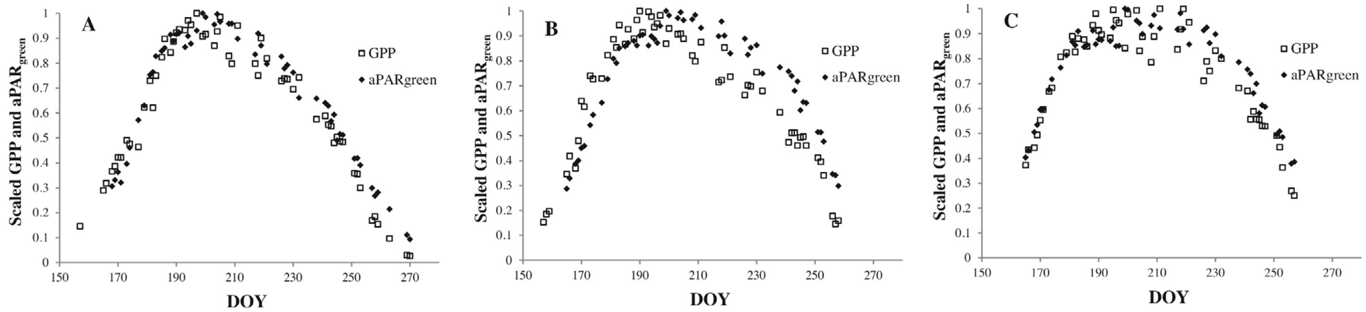

Figure 1. Temporal behavior of scaled GPP (GPPsc) and scaled radiation absorbed by photosynthetically active green vegetation, $(aPAR_{green})sc$, in three maize sites, irrigated sites 1 and 2 (A and B, respectively) and rainfed site 3 (C) in 2005.

plants were in "normal" conditions, which are photosynthetically active and $aPAR_{green}$ was used effectively for photosynthesis. When $\delta < 0$, the efficiency of light use is smaller than in "normal" conditions, which is indicative of plant stress. Positive values of δ show that photosynthetic activity was higher than in "normal" conditions or due to errors arising from uncertainties in fAPAR measurements when the density of vegetation was low or from small but inevitable errors related to the scaling procedure.

Generally, during the vegetative growth stages (day of year (DOY) 150–190) at all irrigated and rainfed maize sites GPPsc was almost equal to $(aPAR_{green})sc$ (Figure 1) indicating effective photosynthetic activities of the crops. In the beginning of the reproductive stages (DOY 190–210), GPPsc was slightly lower than $(aPAR_{green})sc$, signaling a decrease of photosynthetic activity compared to the values at vegetative stages. Tassel appearance is a main feature of this stage. Tassels greatly affect the magnitude and composition of absorbed light (Viña et al., 2004). They are located at the top of each plant, modifying the spectral characteristics of the canopy as a whole, reducing the absorption of radiation in the visible region, particularly in the red region (around 670 nm). Thus, even if the magnitude of absorbed light does not change, the spectral composition of it does change decreasing light absorbed in the red absorption band of chlorophyll and thus affecting crop production.

Later (DOY 210–250), GPPsc was lower than $(aPAR_{green})sc$. During the late reproductive stages and senescence (DOY > 250), at all three sites, $\delta < 0$, indicating decreased photosynthetic activity. However, it is noted that the behaviors of GPPsc and $(aPAR_{green})sc$ were quite different during the reproductive stage at irrigated site 2 (Figure 1B). At site 2, GPPsc was much lower than $(aPAR_{green})sc$ until the end of the season showing that the crop at this site utilized aPAR not as effectively as at the other sites even though the water treatment (i.e., amount of irrigation) was similar to the irrigated site 1. Thus, the difference of scaled GPP and aPAR, δ, was a sensitive indicator of crop physiological status as well as the efficiency of transferring the absorbed light into carbon fixation and may be used to detect photosynthetic efficiency along with LUE.

There were two types of variations in efficiency of light used by photosynthetically active "green" vegetation (LUE_{green}) and δ (Figure 2). One type was a high frequency facultative variation, referring to their short term (day-to-day) variation (symbols and solid lines in Figure 2), and the other type was a low frequency constitutive variation, referring to seasonal change during the growing season (dashed lines in Figure 2). Daily LUE_{green} and δ oscillated around long term seasonal change.

Short term LUE_{green} variation

$fAPAR_{green}$ is closely related to leaf structure, leaf chlorophyll content, LAI_{green} and plant architecture and thus depends on crop phenological and physiological state; however, $fAPAR_{green}$ may not change significantly from day-to-day. In contrast, the magnitude and composition of PAR_{in} may change diurnally as well as from day-to-day. LUE_{green} was calculated based on values of $fAPAR_{green}$ and PAR_{in}. Thus our hypothesis was that day-to-day changes in LUE_{green} relate to changes in PAR_{in}.

We had a unique possibility to study the physical and biological mechanisms of short term day-to-day variation of LUE_{green}. Among three maize sites in odd years, two were irrigated and one was rainfed. In even years, among two soybean sites one of them was irrigated and the other was rainfed. These sites were located close to each other (within 4 km) and the magnitude and composition of incident irradiance were the same. Thus, comparing short-term oscillations of LUE_{green} at two sites with the same PAR_{in} but different water treatment (irrigated vs. rainfed), phenological and physiological states allowed us to understand the effect of PAR_{in} variation on crop photosynthetic activity. It was found that LUE_{green} in irrigated and rainfed sites oscillated almost synchronously. Such behavior of high frequency variation of the LUE_{green} was observed at all irrigated and rainfed maize and soybean sites for all the years of observation. The main common factor for the irrigated and rain-fed sites affecting crop LUE_{green} was PAR_{in}, which was variable due to daily weather changes. These results suggested that the main reason for the day-to-day LUE_{green} and δ oscillation may be the day-to-day variability of PAR_{in}.

To prove it, we compared the high frequency variation of LUE_{green} with the variation of PAR_{in}. The PAR_{in} varies both seasonally and from day-to-day. To separate these two types of variation, we calculated the difference between seasonal trend of PAR_{in} (that is PAR potential, incident potential photosynthetically active irradiance (PAR_{pot})) and actual measured PAR_{in}. PAR_{pot} was the maximal value of PAR_{in} for the site on a certain DOY (Gitelson et al., 2012). Increase of ($PAR_{pot} - PAR_{in}$) corresponds to a decrease of PAR_{in} and vice versa. Thus, the difference ($PAR_{pot} - PAR_{in}$) depends only on day-to-day weather variation and was not affected by seasonal change of day length. The use of ($PAR_{pot} - PAR_{in}$) allowed comprehensive comparison between LUE_{green} and oscillation of PAR_{in}.

Oscillations of LUE_{green} and ($PAR_{pot} - PAR_{in}$) at both irrigated and rainfed sites frequently coincided (Figure 3). Importantly, almost every increase of PAR_{in} (i.e., decrease of $PAR_{pot} - PAR_{in}$) corresponded to a decrease in LUE_{green}, i.e., a decrease in photosynthetic efficiency. There was a consistent response of the magnitude of LUE to changes in the magnitude of PAR_{in}: in more than 45% cases for maize and 51% for soybean, increases in magnitude of PAR_{in} corresponded to decreases in magnitude of LUE_{green} and vice versa (Figure 4). Note that only days when sites were under "cloud-free" conditions were selected; PAR_{in} was greater than 80% of PAR_{pot}.

These results strongly suggest that, in many cases, the decrease of photosynthetic activity was due to excessive PAR_{in} that cannot be efficiently utilized (i.e., used for photosynthesis) by the plants.

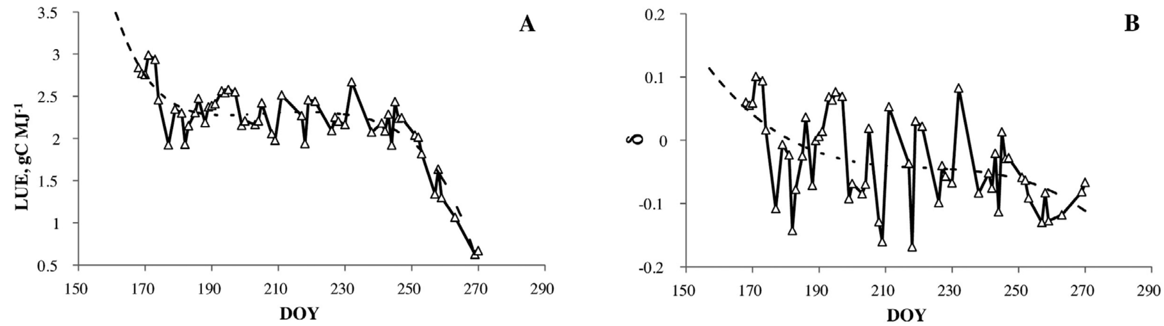

Figure 2. Light use efficiency (A) and δ = (GPPsc − $(aPAR_{green})$sc (B) at irrigated maize site in 2005. Dashed lines are best fit of seasonal LUE_{green} and δ change.

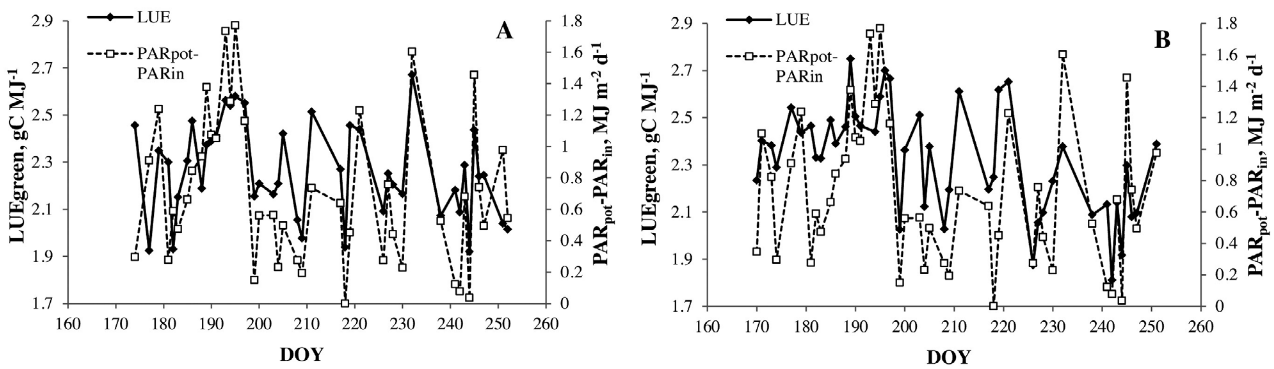

Figure 3. Temporal behaviors of the LUE_{green} and difference between potential PAR (PAR_{pot}) and incident PAR (PAR_{in}) for rainfed (A) and irrigated (B) maize sites in 2005.

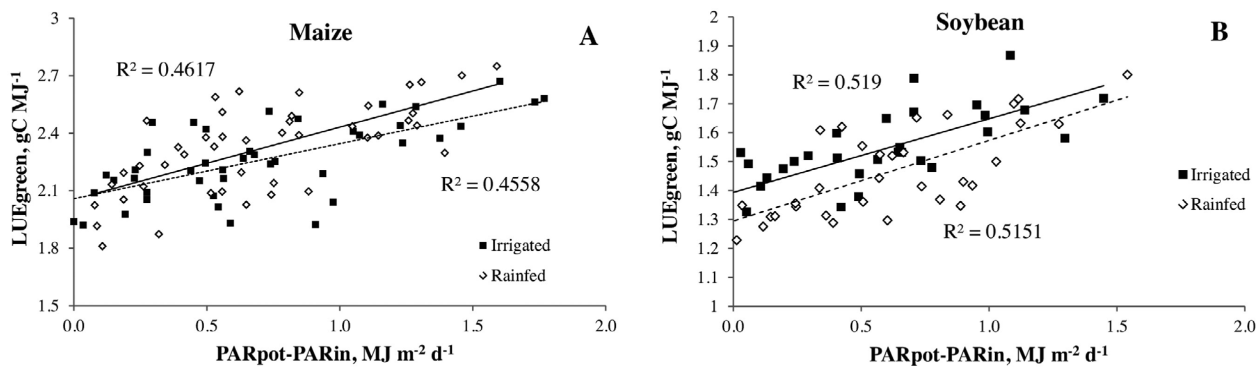

Figure 4. LUE_{green} vs. the difference PAR_{pot} − PAR_{in} for maize in 2005 (A) and soybean in 2006 (B). LUE_{green} increased with decrease of PAR_{in}, i.e., when difference (PAR_{pot} − PAR_{in}) became larger.

An additional factor contributing to the increase of LUE_{green} with decreasing PAR_{in} was likely a rise of fraction of diffuse radiation that enhances absorption of radiation (Norman and Arkebauer, 1991). Increases in LUE in response to increasing proportions of diffuse radiation have also been reported by Gu et al. (2002) and Turner et al. (2003). In addition, LUE-based estimates of GPP have been shown to be improved by the incorporation of the effect of diffuse radiation on LUE (Knohl and Baldocchi, 2008; Nguy-Robertson et al.,2014). However, we limited our analyses to conditions when PAR_{in} was at least 80% of PAR_{pot} ; i.e., the cloudiness coefficient (Turner et al., 2003) was below 0.2; thus we believe that the effects of diffuse light are not as dramatic as shown in Turner et al. (2003) and Norman and Arkebauer (1991).

Long term LUE_{green} variation

The low-frequency variation of LUE_{green} during the growing season indicated a change of crop photosynthetic activity affected by plant phenological and physiological states. LUE_{green} and δ change at irrigated maize site 1 is shown in Figure 2. Between DOY 170 and 250 seasonal trends of both LUE_{green} and δ were almost invariant (LUE_{green} ≈ 2.3 gC MJ^{-1} and δ ≈ −0.03) with a noted decrease occurring in the senescence stage (DOY beyond 250). Daily LUE_{green} and δ oscillated around the long term trend. A similar seasonal trend of LUE_{green} and δ was observed in the rainfed site during the same year (not shown). However, seasonal trends of LUE_{green} in two irrigated sites were substantially different (Figure 5). Irrigated sites 1 and2, located adjacent to each other, were both planted with maize irrigated in the same way. However, the difference in LUE_{green} of these two irrigated sites is detectable; in the vegetative stage (DOY 179–200), LUE_{green} was higher in site 2 than in site 1 but smaller in the reproductive stage (DOY 200–260). Physical features of the crops and different hybrids used in the two irrigated sites may have contributed to these differences. While both sites were planted at about 82,500 seeds ha^{-1}, the final plant populations were 69,200 (site 1) and 76,300 (site 2) plants ha^{-1}. So the higher LUE_{green} early in the

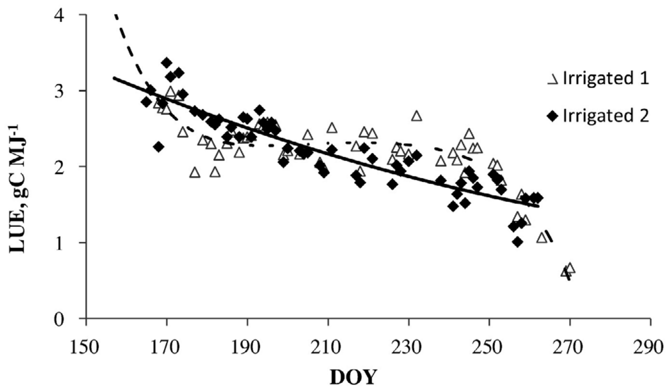

Figure 5. The seasonal behavior of LUE_{green} at two irrigated maize sites in 2005. Dashed and solid lines are seasonal trends of LUE_{green} in site 1 and site 2, respectively.

season at site 2 was likely due to a 10% higher plant population. In the middle of the season at DOY 200–230, GPPsc at the irrigated site 2 was substantially, at least 20%, lower than aPARsc (Figure 1B). LUE_{green} reflected this change decreasing about 10% compared to that at the irrigated site 1 (Figure 5). One of the reasons for that is likely decrease of absorption efficiency in crops with higher density due to more self-shadowing. It illustrates that the difference of LUE_{green} between the two sites managed in the same way may be larger than the difference between irrigated and rainfed sites.

An interesting difference of LUE_{green} between irrigated and rainfed maize sites in the reproductive stage was observed in 2003 (Figure 6). The difference of GPP between the irrigated and rain-fed sites after DOY 210 became large (~5 gC $m^{-2}d^{-1}$) and almost invariant until the end of the season (Figure 6A). In contrast, the difference between $aPAR_{green}$ at these sites substantially increased toward end of the season (Figure 6B): for DOY 210 the difference was 0.2 MJ $m^{-2}d^{-1}$, while for DOY 250 it was above 5.5 MJ $m^{-2}d^{-1}$. The sharp decrease of $aPAR_{green}$ at the rainfed site after DOY 220 was due to a significant decrease of LAI_{green} (at DOY 220 it was 3.4 and dropped to 1.7 at DOY 240 and near zero at DOY 260), while at the irrigated site LAI_{green} remained quite high (at DOY 220 it was 5.3 and decreased to 4.6 at DOY 240 and 3.2 at DOY 260).

Very different behaviors of scaled values of GPP and $aPAR_{green}$ in irrigated and rainfed sites in reproductive stages can be clearly seen in Figure 7. At the rainfed site, there was an almost synchronous decrease of both GPPsc and $(aPAR_{green})$sc: at DOY 250 they both dropped to 25–30% of their maximal values (Figure 7A). Notably, the difference (GPP)sc − $(aPAR_{green})$sc remained slightly positive or close to zero during the reproductive stage, *indicating effective use of absorbed radiation for photosynthesis at the rainfed site.* In contrast, at the irrigated site there was a distinguishable discrepancy between (GPP)sc and $(aPAR_{green})$sc: at DOY 250 (GPP)sc dropped to 40% of its maximal value while $(aPAR_{green})$sc declined gradually to around 70% of its maximal value (Figure 7B). The difference (GPP)sc − $(aPAR_{green})$sc was increasingly negative toward the end of growing season demonstrating that the efficiency of light use for photosynthesis at the irrigated site was lower than that at the rainfed site.

Thus, in reproductive stage after DOY 220 the LUE_{green} was higher in the rainfed site than in the irrigated one (Figure 8A). The ratios of GPP, $aPAR_{green}$, and LUE_{green} at the irrigated site to those at the rainfed site are shown in Figure 8B. The ratio of $aPAR_{irrigated}/aPAR_{rainfed}$ was higher than the ratio of $GPP_{irrigated}/GPP_{rainfed}$: at DOY 230, the difference in $aPAR_{green}$ between irrigated and rainfed sites was 46% while the difference in GPP was only 32%; at DOY 240, a 140% difference in $aPAR_{green}$ only corresponded to a 62% difference in GPP. This figure highlights the difference in the efficiency of the use of radiation absorbed by irrigated and rainfed crops in the reproductive stage. To our knowledge such behavior of LUE_{green} has not yet been conclusively demonstrated except for a brief discussion in Gitelson et al. (2014). Further experimental work is needed to explore the possible reason for this result.

LUE_{green} response to dry weather conditions

The response of LUE_{green} to dry weather conditions was studied in years when dry periods, 2003 for maize and 2006 for soybean, were detected by Suyker and Verma (2010).

At the rainfed maize site in 2003, a sharp decrease of soil moisture occurred at around DOY 170; however neither GPP nor $aPAR_{green}$ responded to it; they continued to increase (Figure 6). A second drop of soil moisture occurred following DOY 187 and at about four days later (at DOY 191) GPP at this rainfed site became notably smaller than at the irrigated site (arrow in Figure 6A). Importantly, $aPAR_{green}$ values at both irrigated and rainfed sites were quite close, and a substantial difference between them did not occur until DOY 206 (arrow in Figure 6B), i.e., about 15 days after the difference between GPP at these sites became detectable. The difference in LUE_{green} between the irrigated and rainfed sites became substantial at around DOY 195 (Figure 8A). During the dry period, LUE_{green} in rainfed maize changed more than 15%, dropping from 2.5 to about 2.1 gC $MJ^{-1}d^{-1}$.

A decrease in soil moisture at the rainfed soybean site occurred around DOY 190 and reached a minimum by DOY 220 (Figure 9). The level of stress was apparently so substantial that almost immediately (at DOY 193) GPP in the rainfed site dropped about 20% and remained lower than GPP at the irrigated site until DOY 230. Even though in rainfed site green LAI decreased much sharper than in irrigated site (from 4.5 at DOY 210 to 3.2 at DOY 240 in the rainfed site, while from 4.5 to 4 in the irrigated site), $aPAR_{green}$ was almost the same at the two sites. These observations imply that at the beginning of the reproductive stage as leaf chlorophyll content of the top canopy began decreasing, increase in depth of light penetration inside the canopy allowed maintenance of $aPAR_{green}$ at rainfed site close to that at irrigated site (Gitelson et al., 2014b). During this period LUE_{green} decrease in rainfed site was in average about 20%.

GPP and LUE_{green} vs. $aPAR_{green}$ relationships

The long periods of observation in both maize and soybean allowed assessment of the variability of LUE_{green}. The LUE_{green} in both crops studied varied widely (Figure 10): the coefficient of variation of LUE_{green} was 20.3% in maize and 39.8% in soybean. In maize, LUE_{green} slightly increased with increasing $aPAR_{green}$ (Figure 10A). The slope of this relationship is governed by lower LUE_{green} values that are a distinguishing characteristic of early vegetative stages as well as late reproductive and senescence stages. The large LUE_{green} variability in the early season may be related to uncertainties (mainly overestimation) of fAPAR measurements as vegetation density is low and clumped into rows. In senescence stages, the LUE_{green} decrease was more pronounced in soybean than in maize due to sharp decrease of soybean leaf chlorophyll content/greenness. In both crops decrease of LUE_{green} in reproductive and senescence stages was likely due to overestimation of $aPAR_{green}$ as it was calculated using LAI_{green} (Gitelson et al., 2014a). For the same destructively determined LAI_{green}, 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). This is due to the subjective procedure for LAI_{green} determination that recognizes both slightly green and dark green leaves as “green” leaves. The uncertainties of such LAI_{green} determination increase in the reproductive stage when leaf chlorophyll content/greenness decreases (Gitelson et al., 2014a).

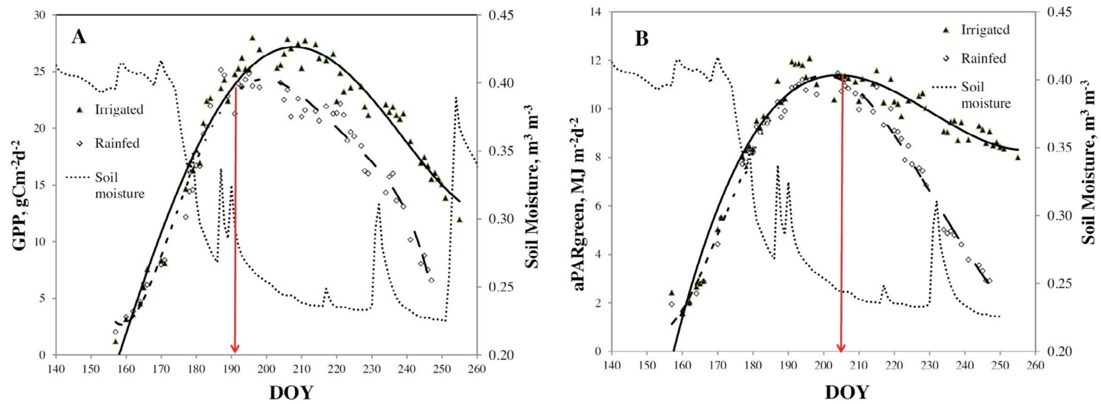

Figure 6. Temporal behavior of GPP (A) and $aPAR_{green}$ (B) in irrigated and rainfed maize sites in 2003. Soil moisture at 1 m depth at the rainfed site is presented by dash line.

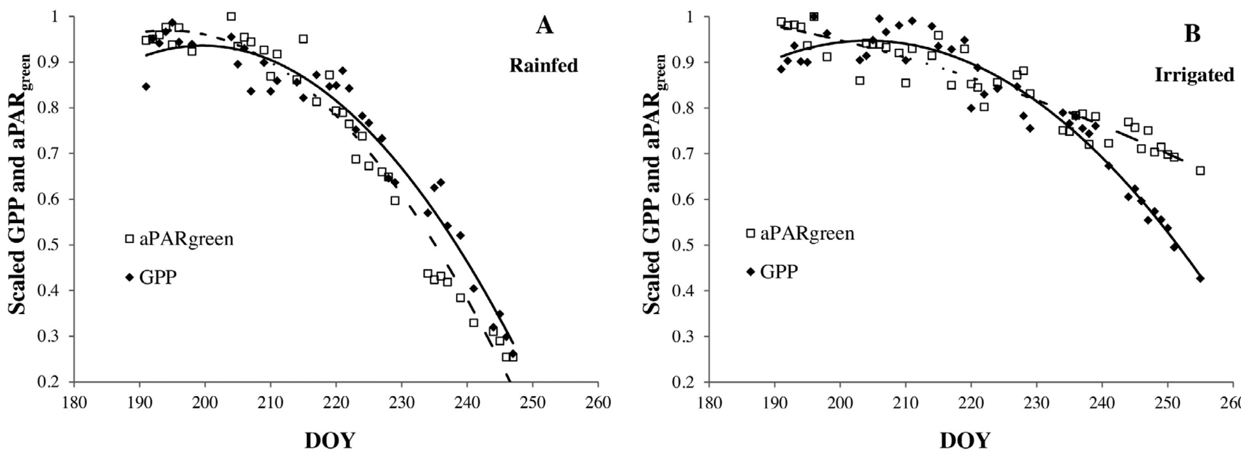

Figure 7. Scaled GPP and $aPAR_{green}$ in (A) irrigated and (B) rainfed maize sites in 2003. At the rainfed site there was an almost synchronous decrease of both GPP and $aPAR_{green}$. In contrast, in the irrigated site GPP dropped to 40% of its maximal value while $aPAR_{green}$ declined to around 70% of its maximal value.

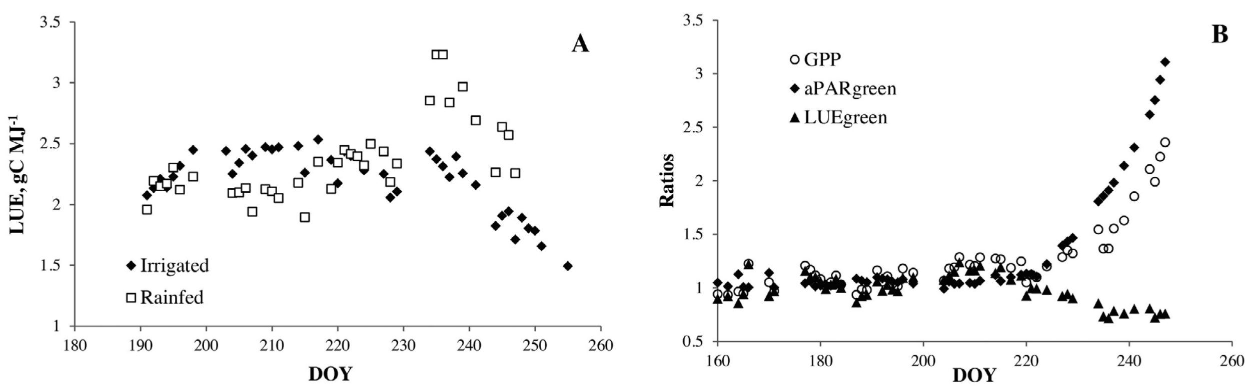

Figure 8. Light use efficiency at irrigated and rainfed maize sites in 2003 (A) and ratios of GPP, $aPAR_{green}$ and LUE_{green} at irrigated site to that at rainfed site (B).

To make accurate comparison across sites and years, following Turner et al. (2003) and Schull et al. (2014), in addition to whole growing season change (Figure 10), GPP and aPAR data for the period June 1 to August 30 were used. The temporal constraint criteria served to eliminate days early in the growing season (green LAI < 2) when uncertainties of aPAR and GPP were greatest. The month of September was omitted from comparisons because in senescence stages foliage was rapidly changing from green to yellow and brown and LUE_{green} may be biased due to $aPAR_{green}$ calculation using subjective LAI_{green} values. As a result, for such conditions in both crops, the LUE_{green} vs. $aPAR_{green}$ relationship was virtually horizontal (not shown). In maize, LUE_{green} was around 2.25 gC MJ^{-1} with a standard error of estimation, STE = 0.22 gC MJ^{-1} and a coefficient of variation CV = 10%. In soybean, LUE_{green} was around 1.46 gC MJ^{-1} with STE = 0.18 gC MJ^{-1} and CV = 11%.

In addition to the quite different seasonal trends of LUE_{green} from year to year, day to day oscillations contributed substantially to total LUE_{green} variation. In maize, LUE_{green} oscillated around the seasonal trend with a magnitude typically ±0.25 gC MJ^{-1} and with maximal values exceeding 0.4 gC MJ^{-1}. In soybean, the magnitude of the oscillation was ±0.2 gC MJ^{-1} with maximal values up to 0.38 gC MJ^{-1}. The coefficient of variation of day to day LUE_{green} was around 10%

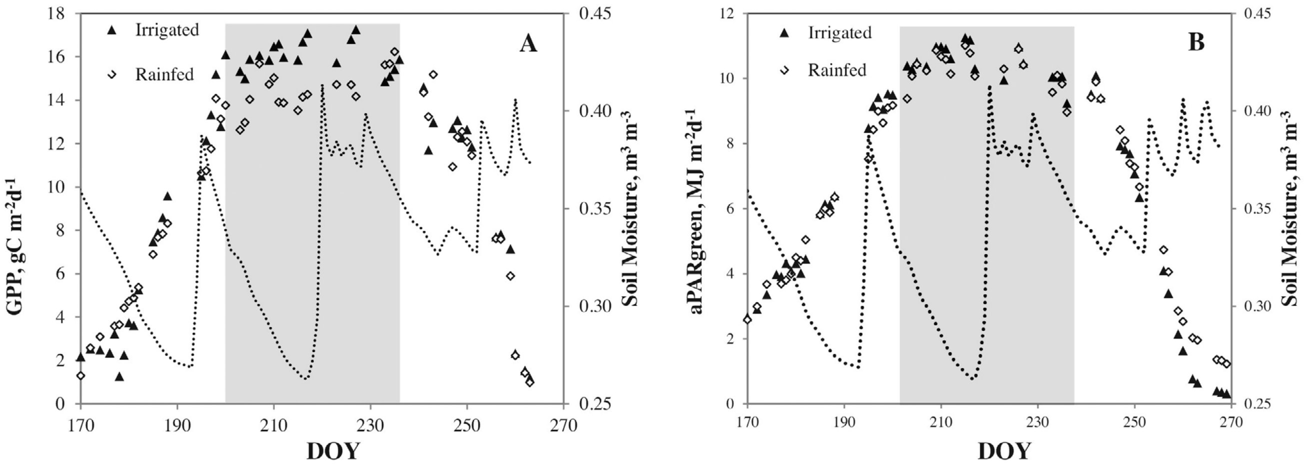

Figure 9. Temporal behavior of GPP (A) and $aPAR_{green}$ (B) at irrigated and rainfed soybean sites in 2006. Soil moisture at rainfed site is presented by dashed line.

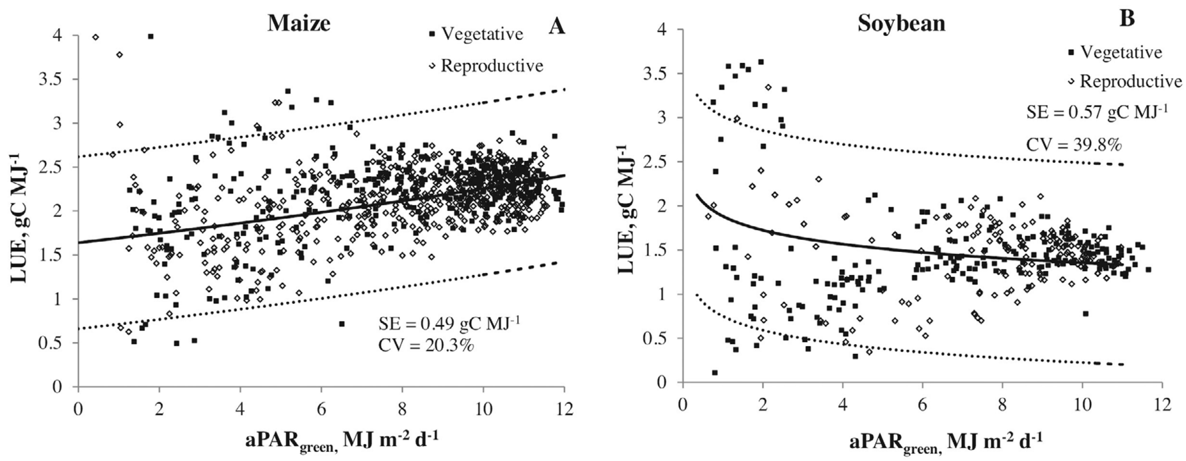

Figure 10. Relationships between light use efficiency (LUE_{green}) and PAR absorbed by photosynthetically active vegetation ($aPAR_{green}$) for maize in 2001–2008 (A), and soybean in 2002, 2004, 2006, 2008 (B) in vegetative and reproductive stages.

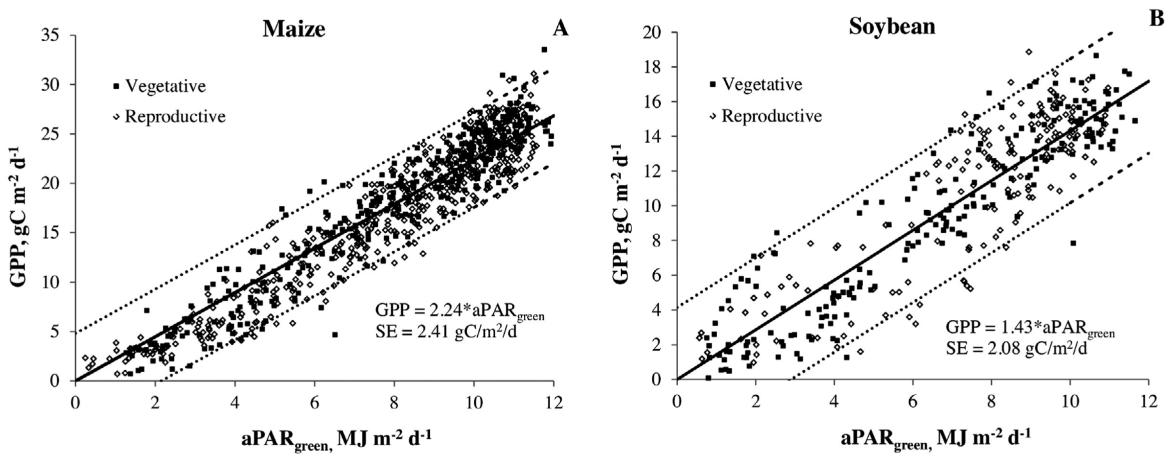

Figure 11. Relationships between gross primary production (GPP) and PAR absorbed by photosynthetically active vegetation ($aPAR_{green}$) for maize in 2001–2008 (A), and soybean in 2002, 2004, 2006, 2008 (B) in vegetative and reproductive stages.

in maize and over 14% in soybean. Importantly, these day-to-day facultative changes in LUE_{green} took place under "cloud-free" conditions when PAR_{in} was higher than 0.8 * PAR_{pot} and cloudiness coefficient (Turner et al., 2003) was below 0.2. To our knowledge such strong effect of incident irradiance on LUE_{green} has not been demonstrated and has not yet been explored.

This study quantified the variability of maize and soybean LUE_{green} during the growing season. The ability of the two crops to utilize $aPAR_{green}$ for GPP varied widely due to differences in crop physiological and phenological status, hybrids, water treatment, soil moisture, magnitude and composition of incident radiation. For maize and soybean, the GPP vs. $aPAR_{green}$ relationship was linear in

both vegetative and reproductive stages; however, the slopes were slightly different between stages: 2.28 gC MJ^{-1} vs. 2.20 gC MJ^{-1} for maize and 1.42 gC MJ^{-1} vs. 1.45 gC MJ^{-1} for soybean.

For eight years of observation (n = 880), the GPP vs. $aPAR_{green}$ relationship for maize was linear with a determination coefficient R^2= 0.9, a standard error of 2.41 gC $m^{-2}d^{-1}$, and a coefficient of variation (CV) of 13.9% (Figure 11A). There was no statistical difference between relationships in vegetative and reproductive stages (*p*-value for *t*-test was 0.73).

For soybean data collected in 2002, 2004, 2006, and 2008 over two sites in each year (n = 423), the GPP vs. $aPAR_{green}$ relationship was also linear with a determination coefficient R^2= 0.83, a standard deviation of 2.08 gC $m^{-2}d^{-1}$ and a CV of 20.8% (Figure 11B), which is considerably higher than in maize (Figure 11A). As in maize, in soybean there was no statistical difference between relationships in vegetative and reproductive stages (*p*-value for *t*-test was 0.76). Importantly, the GPP vs. aPAR relationships for maize and soybean were statistically different; the *p*-value for the *t*-test was 0.00012. The ratio of the slope of the relationship for maize to that for soybean was 1.56, showing a very significant difference in LUE_{green} between these two crop species.

Conclusions

The temporal behaviors of LUE_{green} in maize and soybean were characterized by short term facultative (day-to-day) and long term constitutive (seasonal) variations. In the two crops studied, LUE_{green} varied more than 3-fold during the growing season with no clear seasonal pattern, while showing lots of day-to-day variability, depending on the physiological status of vegetation, in response to PAR magnitude and composition.

The magnitude of the day-to-day oscillations typically was around 10% of the LUE_{green} in maize and 15% in soybean while maximal values exceeded 20% in both crops. It was found that the main reason for the day-to-day LUE_{green} oscillation is the daily variability of incident PAR; quite often a decrease of LUE_{green} corresponded to an increase of incident irradiation. Moreover, a significant relationship between the magnitudes of LUE_{green} and PAR with a determination coefficient higher than 0.45 has been found. Thus, in many cases, the decrease of LUE_{green} was due to excessive PAR_{in} that cannot be efficiently utilized by the plants.

The long term behavior of LUE_{green} is affected by crop physiological status and phenology, as well as the changes over time of the brown/yellow and green foliage. Further analyses of vegetation stands having vastly different canopy structure, phenology, or environmental constraints on canopy growth and physiology would likely add additional complexity to these effects.

The high variability of LUE_{green} within a single crop (i.e., maize or soybean) and between C3 and C4 crops revealed in this study showed that assuming a constant LUE_{green} value in GPP models is not warranted for the crops studied and brings unpredictable uncertainties of GPP estimation. The uncertainty of estimates for GPP due to LUE_{green} variation can be considered as a critical component of the total error budget in the context of remotely sensed based estimations of GPP. Thus, these findings have implications for the use of LUE models by the remote sensing and carbon flux modeling communities.

More attention should be given to the operational definitions of aPAR and LUE used, as the several definitions currently in use are not equivalent, and this can have large consequences for the estimated GPP (Gitelson and Gamon, 2015). Given the findings here, we recommend using an LUE metric, LUE_{green} that is minimally confounded by changing pigmentation and green canopy structure during plant growth and senescence. However, this LUE metric may be biased in late reproductive and senescence stages as it depends on a visual inspection and interpretation of leaf color. A standard procedure for measurement of $aPAR_{green}$ should be established and routinely used for accurate assessment of LUE_{green}. One challenge lies in the direct measurement of the proportion of green vegetation, which typically requires tedious and destructive sampling that is subject to error. A solution may lie in using results of spectral measurements and applying greenness/chlorophyll vegetation indices or inversion models to assess this term. If properly measured, standardized, and interpreted, the normalized difference vegetation index (NDVI) or other similar greenness indices, as well as radiative models could provide a rapid means to do this, as is currently done using satellite data (Running et al., 2004; Gitelson et al., 2014a,b), although further work is needed to standardize methodology and interpretation, particularly for field studies.

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