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Efficiency of chlorophyll in gross primary productivity: A proof of concept and application in crops

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Abstract

One of the main factors affecting vegetation productivity is absorbed light, which is largely governed by chlorophyll. In this paper, we introduce the concept of chlorophyll efficiency, representing the amount of gross primary production per unit of canopy chlorophyll content (Chl) and incident PAR. We analyzed chlorophyll efficiency in two contrasting crops (soybean and maize). Given that they have different photosynthetic pathways (C3 vs. C4), leaf structures (dicot vs. monocot) and canopy architectures (a heliotrophic leaf angle distribution vs. a spherical leaf angle distribution), they cover a large spectrum of biophysical conditions. Our results show that chlorophyll efficiency in primary productivity is highly variable and responds to various physiological and phenological conditions, and water availability. Since Chl is accessible through non-destructive, remotely sensed techniques, the use of chlorophyll efficiency for modeling and monitoring plant optimization patterns is practical at different scales (e.g., leaf, canopy) and under widely-varying environmental conditions. Through this analysis, we directly related a functional characteristic, gross primary production with a structural characteristic, canopy chlorophyll content. Understanding the efficiency of the structural characteristic is of great interest as it allows explaining functional components of the plant system.

Keywords: Crops, Maize, Primary production, PAR, Phenology, Soybean, Water status

1. Introduction

To optimize productivity under variable environmental conditions and changing resource availability, plants modify the efficiency of use of key resources involved in photosynthesis, including solar radiation, water, and nutrients (e.g., Field, 1991; Field et al., 1995; Goetz and Prince, 1999). A vast literature exists on optimization patterns of plant productivity through maximizing the efficiency of use of photosynthetically active radiation (PAR) (Zhu et al., 2010; Gitelson et al., 2015; Retkute et al., 2015), as well as water, phosphorus, and nitrogen (N) (Anten et al., 1995; Anten et al., 1996; Buckley et al., 2002; Vico et al., 2013; Hikosaka, 2014; Osada et al., 2014) at multiple scales, from individual leaves to entire canopies (Field et al., 1995; Goetz and Prince, 1999). Many of these studies analyze the patterns of individual

components in isolation, while fewer evaluate the combination of a limited number of components for assessing synergistic relations and trade-offs (Karlsson, 1994; Herppich et al., 2002; Ali et al., 2012; Xu et al., 2013). However, a thorough understanding of the processes behind these optimization patterns is still elusive, mainly due to limitations in the scaling of photosynthesis models from individual leaves to entire canopies (Kull, 2002; Niinemets and Anten, 2009), as well as trade-offs in the use of different resources that may prevent plants from optimizing their efficiencies of use simultaneously (Hirose and Bazzaz, 1998).

Plant productivity (e.g., gross primary productivity, GPP) is quite sensitive to the variability of numerous interacting resources (Field et al., 1995; Goetz and Prince, 1999), among which the amount of absorbed PAR and water availability are two of the most important. Other important factors are those directly

involved in building and maintaining the photosynthetic machinery. For instance, N is not only a component of chlorophyll but also of photosynthetic enzymes (Evans, 1989). Thus, the acquisition, retention and utilization efficiency of these resources are also associated with the quantity and efficiency of the photosynthetic machinery. Based on this premise, we argue that to understand the processes behind photosynthetic optimization patterns from leaves to entire canopies, rather than analyzing the individual and/or simultaneous efficiency of each of these different resources, it is perhaps better to evaluate *the efficiency of chlorophyll*, as chlorophyll is one of the main components of the photosynthetic machinery. Moreover, on a mechanistic basis, chlorophyll is a unique mediator in the conversion of arguably the most important external resource for plants, the energy in light, to its internal manifestation, the chemical energy inherent in plant biomass. Chlorophyll content (hereafter Chl) is a very specific biophysical variable, given that Chl is not only the result of, but also a driver of photosynthesis (Field, 1991; Field et al., 1995). Thus, the analysis of chlorophyll efficiency may help to understand the patterns of photosynthetic optimization, namely the amount of Chl that has been produced and how this Chl affects photosynthesis under varying environmental conditions, including differences in absorbed PAR and water availability, among other factors.

The analysis of chlorophyll efficiency is particularly suitable because non-destructive and remote techniques are readily available to effectively and accurately assess the amount of Chl present at multiple scales, from leaves (Gitelson and Merzlyak, 1997; Gitelson et al., 2006a; Fassnacht et al., 2015; Kira et al., 2015) to entire canopies (Dash and Curran, 2004; Gitelson et al., 2005; Clevers and Gitelson, 2013). Thus, given that limitations due to scaling are reduced, the use of models based on chlorophyll efficiency may allow more direct assessments of plant optimization patterns under different environmental conditions, and in different species/plant functional types.

In this study, we analyze chlorophyll efficiency in two contrasting crops under varying phenological stages, water treatments and physiological states at three sites over eight growing seasons (2001–2008). The crops evaluated (soybean and maize) cover a large spectrum of biophysical conditions, given that they have different photosynthetic pathways (C3 vs. C4), leaf structures (dicot vs. monocot) and canopy architectures (a heliophilic leaf angle distribution vs. a spherical leaf angle distribution).

2. Concept of chlorophyll efficiency

Monteith (1977) linearly related two functional characteristics, GPP and fAPAR:

$$\text{GPP} = (\text{fAPAR}_{\text{green}} \times \text{PAR}_{\text{in}}) \times \text{LUE} \quad (1)$$

where $\text{fAPAR}_{\text{green}}$ is the fraction of incident PAR (PAR_{in}) absorbed by photosynthetically active vegetation and LUE is the efficiency of utilizing absorbed radiation during the photosynthesis. As fAPAR is a functional characteristic, to analyze its variability one needs to measure an action (i.e., light absorption). However, fAPAR is also a surrogate of structure as it relates to structural characteristics such as leaf chlorophyll content, leaf area index and canopy architecture.

Our goal is to directly relate a functional characteristic, gross primary production (GPP), with a structural characteristic, canopy chlorophyll content (Chl). To detect Chl, one needs to measure its amount. While a structural characteristic, chlorophyll is a driver of light absorption as well as a determinant of fAPAR. Moreover, Chl relates to leaf chemistry. Chlorophyll is directly tied to GPP via the light reactions (i.e., electron transport reactions)

of photosynthesis. Forms of chlorophyll are the molecules that transfer electrons to acceptors in both photosystems, PSI and PSII. Chlorophyll plays a unique role in converting light into biomass, which is absolutely required, mechanistically. Our emphasis on chlorophyll is analogous to the focus of mechanistic models of photosynthesis on the kinetic properties of rubisco.

In our previous work (e.g., Gitelson et al., 2003, 2006b), we have related a functional characteristic, GPP, with a structural characteristic, Chl. But because GPP is more temporally dynamic than Chl, we incorporated a third (and external) variable that accounts for much of that variability. Thus we included PAR_{in} (Gitelson et al., 2003, 2006b) or, for a more accurate GPP estimation, potential PAR (PAR_{pot}), which is the maximal value of incident irradiation on a given day (Gitelson et al., 2012). Such inclusion leaves us with the relationship between a functional characteristic, a structural characteristic and an external characteristic (that is, external to the system of study):

$$\text{GPP} = F(\text{Chl} \times \text{PAR}_{\text{in}}) \quad (2)$$

This function was found to be essentially non-linear and with low dispersion of empirical values from the regression line in two crop species with contrasting structures and canopy architectures (Gitelson et al., 2006b, 2014). The efficiency of Chl in primary production was then defined as the slope of the relationship between GPP and $\text{Chl} \times \text{PAR}_{\text{in}}$ in the form:

$$\text{ChlE} = \text{GPP}/(\text{PAR}_{\text{in}} \times \text{Chl}) \quad (3)$$

Combining Eqs. (1) and (3) we have:

$$\text{ChlE} = (\text{fAPAR}_{\text{green}}/\text{Chl}) \times \text{LUE} \quad (4)$$

This equation shows that chlorophyll efficiency represents both the efficiency of chlorophyll in absorbing PAR (i.e., $\text{fAPAR}_{\text{green}}/\text{Chl}$) and the efficiency of the absorbed PAR to be used in photosynthesis (via LUE). In other words, the efficiency of a structural characteristic can be used to assess the efficiency of two functional characteristics. As such, understanding the efficiency of the structure of a plant system allows explanation of its function.

3. Methods

3.1. Study area

Data from three AmeriFlux sites (US – Ne1, US – Ne2, and US – Ne3) obtained during eight growing seasons (2001–2008) were used in this study. These sites are all approximately 60-ha fields within 4 km of each other, located at the University of Nebraska–Lincoln Agricultural Research and Development Center near Mead, Nebraska, USA. Site 1 was planted in continuous maize equipped with a center pivot irrigation system. Sites 2 and 3 were both planted in maize-soybean rotation, but the former was irrigated in the same way as site 1, while site 3 relies entirely on rainfall for moisture (Verma et al., 2005).

3.2. GPP measurements

For each study site, an eddy covariance tower with meteorological sensors was equipped to collect hourly measurements of CO_2 , water vapor, and energy fluxes. Daytime net ecosystem exchange (NEE) values were computed by integrating the hourly CO_2 flux collected during a day when incoming photosynthetically active radiation (PAR_{in}) exceeded $1 \mu\text{mol m}^{-2} \text{s}^{-1}$. Daytime estimates of ecosystem respiration (R_e) were obtained from the nighttime CO_2 exchange-temperature relationship (e.g., Xu and Baldocchi, 2003). The GPP was then obtained by subtracting R_e from NEE. The GPP values are presented in units of $\text{gC m}^{-2} \text{d}^{-1}$,

and the sign convention used here is such that CO_2 flux to the surface is positive so that GPP is always positive and R_e is always negative (Verma et al., 2005). This approach to estimate GPP has been widely used in the context of tower flux measurements and is considered to provide reasonable estimates at field and regional scales (Verma et al., 2005).

3.3. Incoming PAR

The PAR_{in} measurements were collected every hour by point quantum sensors (LI-190, LI-COR Inc., Lincoln, Nebraska) placed in each study site 6-m above the surface pointing toward the sky. Daytime PAR_{in} values were computed by integrating the hourly measurements during a day when PAR_{in} exceeded $1 \mu\text{mol m}^{-2} \text{s}^{-1}$, and are presented in $\text{MJ m}^{-2} \text{d}^{-1}$ (Turner et al., 2003). In this study, observations under low cloud cover conditions were used to exclude crop light-limited conditions related to daily weather fluctuations.

3.4. Fraction of absorbed photosynthetically active radiation

At each site, quantum sensors (LI-COR Inc., Lincoln, Nebraska) were used to measure hourly PAR_{in} , PAR reflected by the canopy and soil (PAR_{out}), PAR transmitted through the canopy ($\text{PAR}_{\text{transm}}$), and PAR reflected by the soil (PAR_{soil}). The PAR_{out} was measured with point quantum sensors (model LI-190) aimed downward 6-m above the ground; $\text{PAR}_{\text{transm}}$ was measured with line quantum sensors (model LI-191) placed at about 2-cm above the ground, pointing upward; PAR_{soil} was measured with line quantum sensors pointing downward about 12-cm above the ground. All the daytime radiation values were computed by integrating the hourly measurements during a day when PAR_{in} exceeded $1 \mu\text{mol m}^{-2} \text{s}^{-1}$, and fraction of absorbed PAR (fAPAR) was then calculated as:

$$\text{fAPAR} = (\text{PAR}_{\text{in}} - \text{PAR}_{\text{out}} - \text{PAR}_{\text{transm}} + \text{PAR}_{\text{soil}}) / \text{PAR}_{\text{in}} \quad (5)$$

During the vegetative stage, from the beginning of the season until maximal canopy density, fAPAR increases coincidentally with the increase in canopy Chl. However, during the reproductive stage fAPAR remains insensitive to changes in Chl (e.g., Hatfield et al., 1984). This occurs because both photosynthetic and nonphotosynthetic components are intercepting PAR, whereas the absorbed PAR is progressively less used for photosynthesis (Hall et al., 1992; Viña and Gitelson, 2005). Therefore, to obtain a measure of the fAPAR absorbed only by the photosynthetic component of the vegetation, a green fAPAR ($\text{fAPAR}_{\text{green}}$) was calculated as (Hall et al., 1992): $\text{fAPAR}_{\text{green}} = \text{fAPAR} \times (\text{LAI}_{\text{green}} / \text{LAI}_{\text{total}})$, in which, $\text{LAI}_{\text{green}}$ and $\text{LAI}_{\text{total}}$ represent green and total leaf area index, respectively. Both $\text{LAI}_{\text{green}}$ and $\text{LAI}_{\text{total}}$ were determined through destructive sampling taken at 10–14 day intervals during the growing seasons studied (Viña et al., 2011).

3.5. Canopy reflectance measurements

Canopy reflectance was measured using hyperspectral radiometers mounted on an all-terrain sensor platform (Rundquist et al., 2004, 2014). A dual-fiber optic system, with two inter-calibrated Ocean Optics USB2000 radiometers, was used to collect radiometric data in the range 400–1100 nm with a spectral resolution of about 1.5 nm. One radiometer was equipped with a 25° field-of-view optical fiber pointed downward, to measure the upwelling radiance of the crop, at 6-m above the top of canopy throughout the growing season. The optical fiber from the other radiometer was pointed upward to obtain simultaneous incident irradiance. Percent reflectance was then computed as the ratio of upwelling radiance to incident irradiance.

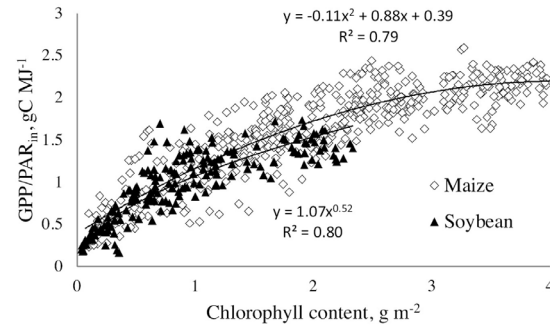


Fig. 1. Relationship between gross primary production (GPP) normalized to incident PAR (PAR_{in}) and chlorophyll content in irrigated and rain-fed maize and soybean.

Thirty-six reflectance measurements were obtained per site during each sampling date, and their median was used as the site reflectance. All spectral measurements were conducted between 11:00 and 13:00 local time, close to solar noon, when changes in solar zenith angle were minimal. Such measurements were conducted from May to October during the growing seasons of 2001 through 2008, which resulted in a total of 314 reflectance spectra for maize and 145 for soybean.

3.6. Total canopy chlorophyll content

Total canopy Chl was determined from reflectance spectra taken at close range (6 m above the canopy) using a spectroradiometer (Gitelson et al., 2005). The red edge chlorophyll index $\text{CI}_{\text{red-edge}} = (\rho_{760-780} / \rho_{720-740} - 1)$ where $\rho_{760-780}$ and $\rho_{720-740}$ are reflectances in the NIR range of the spectrum from 760 to 780 nm and red edge range from 720 to 740 nm, respectively, was used. $\text{CI}_{\text{red-edge}}$ has been shown to be an accurate measure of canopy Chl in contrasting vegetation canopies with different architectures and leaf structures without the need for re-parameterization (Gitelson et al., 2005; Ciganda et al., 2009). Total canopy Chl (in g m^{-2}) was calculated using the $\text{CI}_{\text{red-edge}}$ following the equation:

$$\text{Chl} = 3 \times (\text{CI}_{\text{red-edge}}) - 0.8645 \quad (6)$$

For both crops combined, the coefficient of determination of this relationship was above 0.9, the root mean square error of Chl estimation was below 0.35 g m^{-2} and the normalized root mean square error was less than 13% (Ciganda et al., 2009).

4. Results

4.1. Gross primary production and chlorophyll content

The $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl relationships for the maize and soybean presented in Fig. 1 are close. Chl was responsible for 80% of $\text{GPP}/\text{PAR}_{\text{in}}$ variation in soybean and 79% in maize. The relationship of $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl for both C3 and C4 crops combined exhibited an $R^2 = 0.84$. The non-linearity of these relationships is noteworthy. When $\text{Chl} < 1.5 \text{ g m}^{-2}$, GPP was very sensitive to Chl. However, for moderate to high Chl, when canopy light extinction is complete or close to complete, crop photosynthesis was less sensitive to Chl, increasing only 30% for a doubling of Chl in

For $\text{Chl} < 1 \text{ g m}^{-2}$, the relationships for both crops were very close and there was no statistically significant difference between them ($p = 0.62$). However, for $\text{Chl} > 1.5 \text{ g m}^{-2}$ they diverged, with maize exhibiting higher $\text{GPP}/\text{PAR}_{\text{in}}$ values than soybean for the same Chl ($p < 0.005$). Using a more limited data set, the relationships for maize and soybean were found to be quite close to each other, leading to the conclusion that the GPP vs. $\text{Chl} \times \text{PAR}_{\text{in}}$ relationship was almost non-species specific (Gitelson et al., 2006b). However using a larger dataset, this study shows that the $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl relationships are species specific at moderate-to-high Chl.

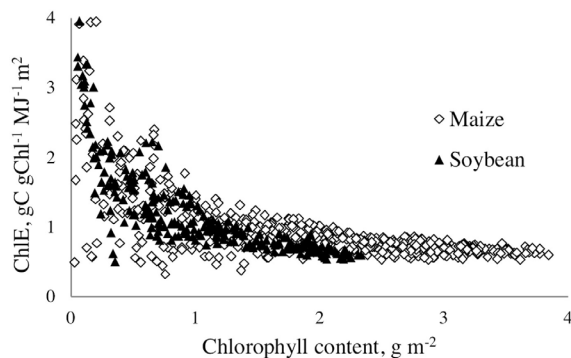


Fig. 2. Relationships between chlorophyll efficiency (ChlE) and chlorophyll content in irrigated and rainfed maize and soybean sites.

4.2. Chlorophyll efficiency

Chlorophyll efficiency decreased with increase in Chl and for the same Chl it was widely variable, especially in the range of low to moderate Chl ($<1.5 \text{ g m}^{-2}$, Fig. 2). The chlorophyll efficiency of low Chl was high ($>4 \text{ gC gChl}^{-1} \text{ m}^2 \text{ MJ}^{-1}$) and declined more than 5 fold as Chl reached moderate values around 1.5 g m^{-2} . Chlorophyll efficiency decreased with further increase in Chl above 1.5 g m^{-2} but in a smaller degree. For both crops, Chl efficiencies almost coincided in the range of Chl $< 1.5 \text{ g m}^{-2}$ but were significantly different (with higher values for maize) for higher Chl, reaching differences of about 30% for Chl around 2 g m^{-2} .

4.3. Chlorophyll efficiency in maize

To understand the reason for the high variability of chlorophyll efficiency for the same Chl, especially when Chl was low to moderate, we examined the relationships between $\text{GPP}/\text{PAR}_{\text{in}}$ and Chl in different phenological stages and under different water availabilities (Fig. 3). During the vegetative stages, from the beginning of the season to the time of maximal Chl, the relationships for irrigated and rainfed maize were very similar (Fig. 3A). At the sites studied, irrigation was conducted based on measurements of soil water content. Since there was sufficient rainfall between early May and early June, irrigation usually was not required. Thus, it is not surprising that the effect of irrigation was not pronounced during the vegetative stage, which for maize in Nebraska is usually completed in early July (day of year, DOY, 180–190). During the vegetative stages, Chl at irrigated and rainfed sites were quite close and diverged only at the end of this stage after DOY 180 (Figs. 4A and B). In the vegetative stages, Chl efficiencies at irrigated and rainfed sites decreased with increasing Chl, with minimal values corresponding to maximal crop density.

During the reproductive stages, $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl relationships for irrigated and rainfed sites were different (Fig. 3B). At rainfed sites, the $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl relationship was close exhibiting an $R^2 = 0.87$ while it was much more scattered at irrigated sites ($R^2 = 0.79$). Importantly, for the same Chl, $\text{GPP}/\text{PAR}_{\text{in}}$ was higher at rainfed than at irrigated sites. During this stage, Chl contents at irrigated and rainfed sites were substantially different with irrigated sites exhibiting considerably higher values than rainfed sites (Fig. 4A and B). The difference in Chl efficiencies became notable when the difference in Chl reached maximal values (around DOY 200, Fig. 4C and D) with chlorophyll efficiency at rainfed sites higher than at irrigated sites. Thus, the water treatment played a significant role in the primary production of maize.

It is important to underline that during the vegetative stages (DOY before 180), “the same Chl” in irrigated and rainfed sites occurred on almost the same dates (Fig. 4A and B), but

this was not the case during the reproductive stages. For example, in 2003 (a dry year; Fig. 4A) a Chl of about 2 g m^{-2} occurred in the rainfed site during the early reproductive stage (around DOY 215) while in the irrigated site it occurred at the end of the season, i.e., more than one month later (DOY around 250, early grain fill stage). In wetter years (e.g., 2005) the difference in the timing of reaching “the same Chl” in irrigated and rainfed sites during the reproductive stage was smaller but never less than 15–20 days (Fig. 4B). Thus, the same Chl at irrigated and rainfed sites occurred at different stages of maize development, at different PAR_{in} and at different photosynthetic activities. These differences in plant development are a source of variability in the chlorophyll efficiency in crops with different water treatments.

Chlorophyll efficiency was affected by maize phenology (Fig. 3C and D); it was slightly higher in irrigated sites during the vegetative stage than in the reproductive/senescence stage. The opposite occurred in rainfed sites where Chl efficiency was higher in the reproductive stages than in the vegetative stages. For both irrigated and rainfed maize, chlorophyll efficiency was the highest at the beginning and at the end of the season, with minimal values in the middle of the season as canopy Chl peaked (Fig. 3C and D).

Despite the differences mentioned above, the $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl relationship in maize during eight years of observations was strong, with Chl explaining about 80% of the $\text{GPP}/\text{PAR}_{\text{in}}$ variation (Fig. 1). During the vegetative stages this relationship was even stronger, explaining more than 90% of $\text{GPP}/\text{PAR}_{\text{in}}$ variation (not shown).

4.4. Chlorophyll efficiency in soybean

The relationship between $\text{GPP}/\text{PAR}_{\text{in}}$ and Chl for soybean is shown in Fig. 5. During the vegetative stages, from the beginning of the season to the time of maximal Chl, the relationships for irrigated and rainfed soybean were similar, with somewhat higher Chl efficiencies in the irrigated sites (Fig. 5A and C). In Nebraska, soybean is planted later than maize, thus irrigation was applied at soybean sites during the vegetative stages.

During the reproductive stages, the $\text{GPP}/\text{PAR}_{\text{in}}$ vs. Chl relationships were almost flat over the range of Chl from 2.7 g m^{-2} to around 1 g m^{-2} , showing low sensitivity of GPP to a decrease in Chl. In senescence, as Chl declined below 1 g m^{-2} , a sharp decrease of GPP occurred (Fig. 5B). Chlorophyll efficiency increased with a decrease in Chl, exhibiting a small variability during the reproductive stages and a larger variability during senescence.

Fig. 6 shows the temporal behavior of Chl (A and B) and chlorophyll efficiency (C and D) in soybean for two years with different temperature and precipitation regimes. By comparison, 2002 was a dry year while 2006 was wetter although a short stage of high temperatures occurred in July and August. In 2002, Chl at the rainfed and irrigated sites were almost equal at the beginning of the season before DOY 190 (Fig. 6A). Chlorophyll efficiency was highest at the beginning of the season and decreased as Chl increased (Figs. 6A and C) in both irrigated and rainfed sites, although the irrigated site exhibited higher values overall. The difference in Chl between the irrigated and rainfed sites became noticeable around DOY 200 and continued to increase thereafter, reaching maximal values around DOY 220 (Fig. 6A). Chlorophyll efficiency in the rainfed site became higher than in the irrigated site and remained higher until the end of the season (Fig. 6C). Thus, as was observed in maize (Fig. 4), while Chl in the rainfed site beyond DOY 210 was smaller than in irrigated site (Fig. 6A), chlorophyll efficiency in the rainfed site was considerably higher than in the irrigated site (Fig. 6C). A smaller difference in Chl between the irrigated and the rainfed sites occurred in 2006 (Fig. 6B). However, while beyond DOY 210 Chl in the rainfed site was smaller than in irrigated site, its efficiency was higher (Fig. 6D).

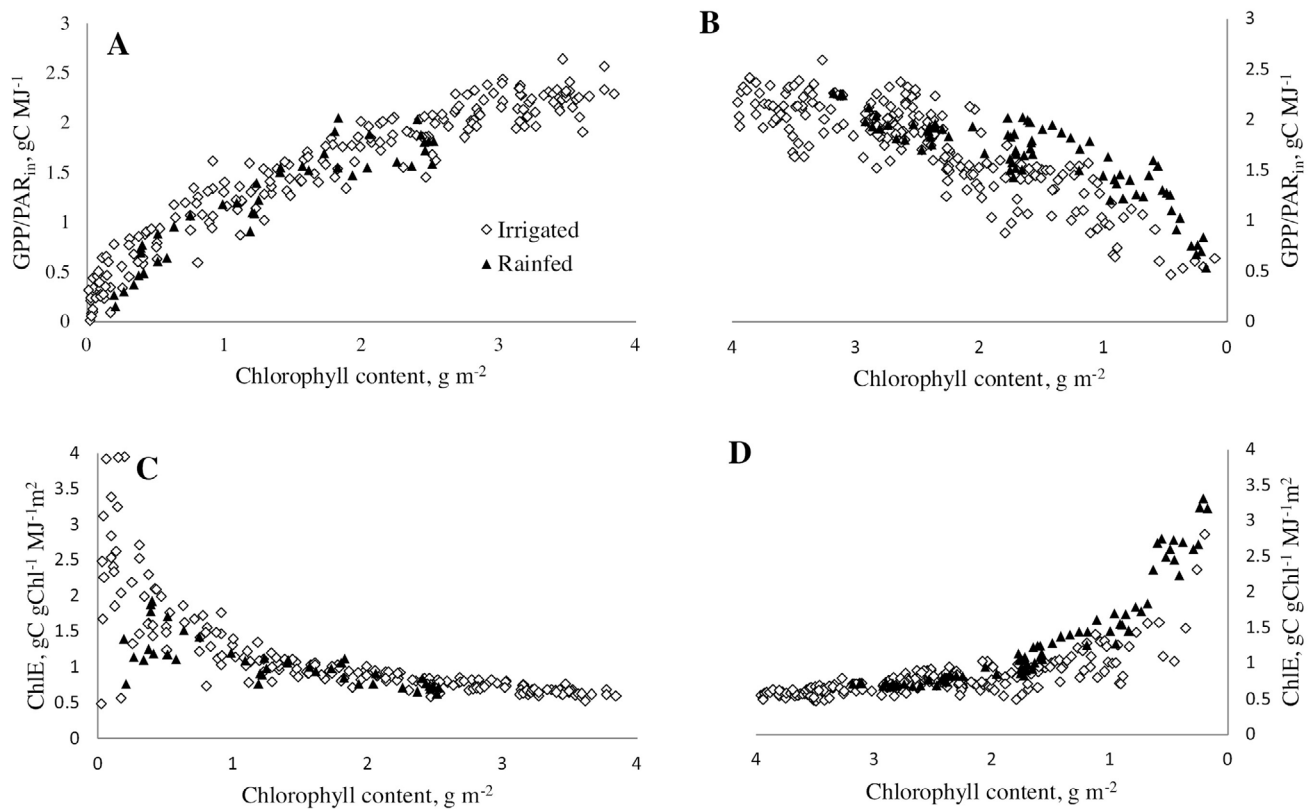


Fig. 3. Relationships GPP/PAR_{in} vs. chlorophyll content (A and B) and chlorophyll efficiency vs. chlorophyll content (C and D) at irrigated and rainfed maize sites in vegetative stages (A and C) and reproductive stages (B and D) in 2001 through 2008.

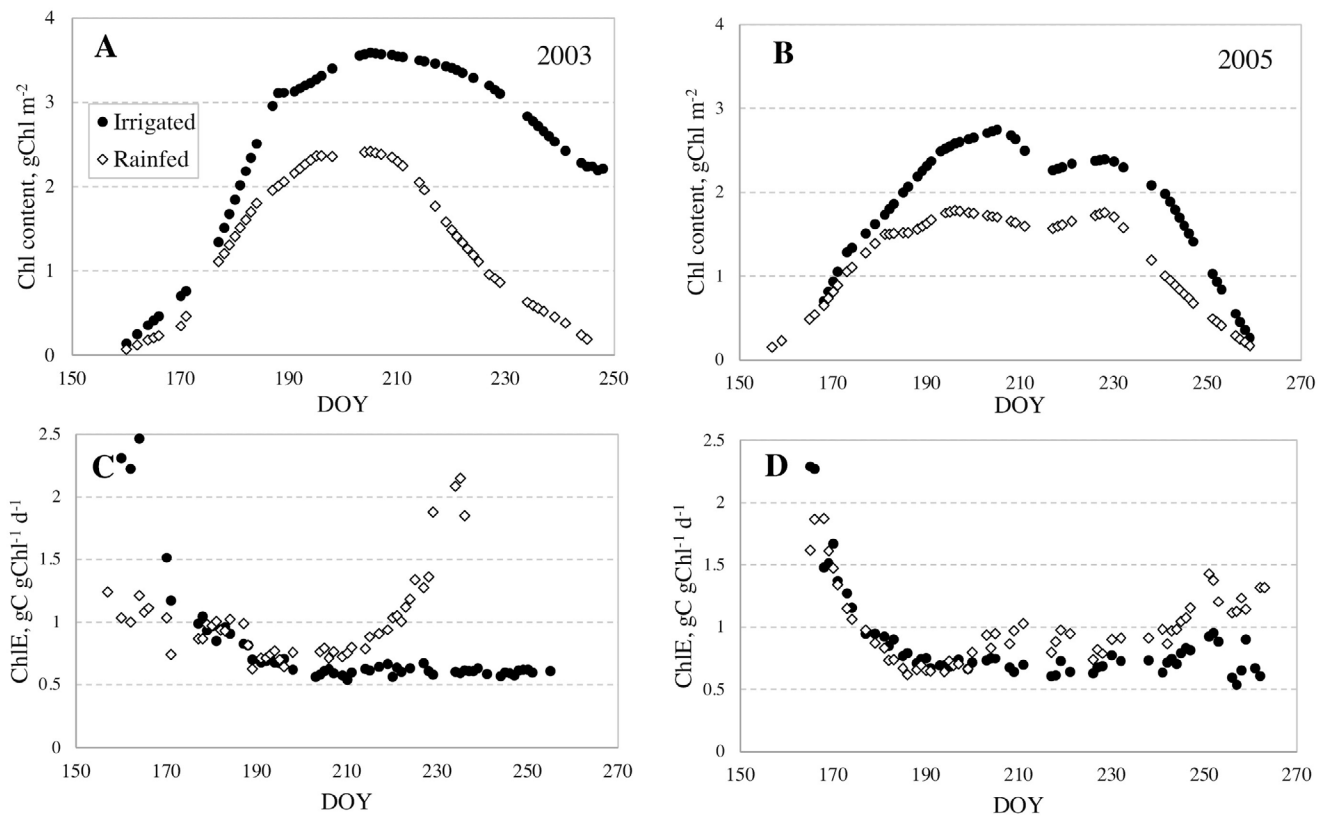


Fig. 4. Temporal behavior of canopy chlorophyll (Chl) content (A, B) and chlorophyll efficiency (C, D) at rainfed and irrigated maize in 2003 (dry year) and 2005 (moderate weather conditions). Difference in Chl and in chlorophyll efficiencies between irrigated and rainfed sites was higher in the dry year (2003). Maximal difference in chlorophyll efficiency occurred when difference in Chl was the highest.

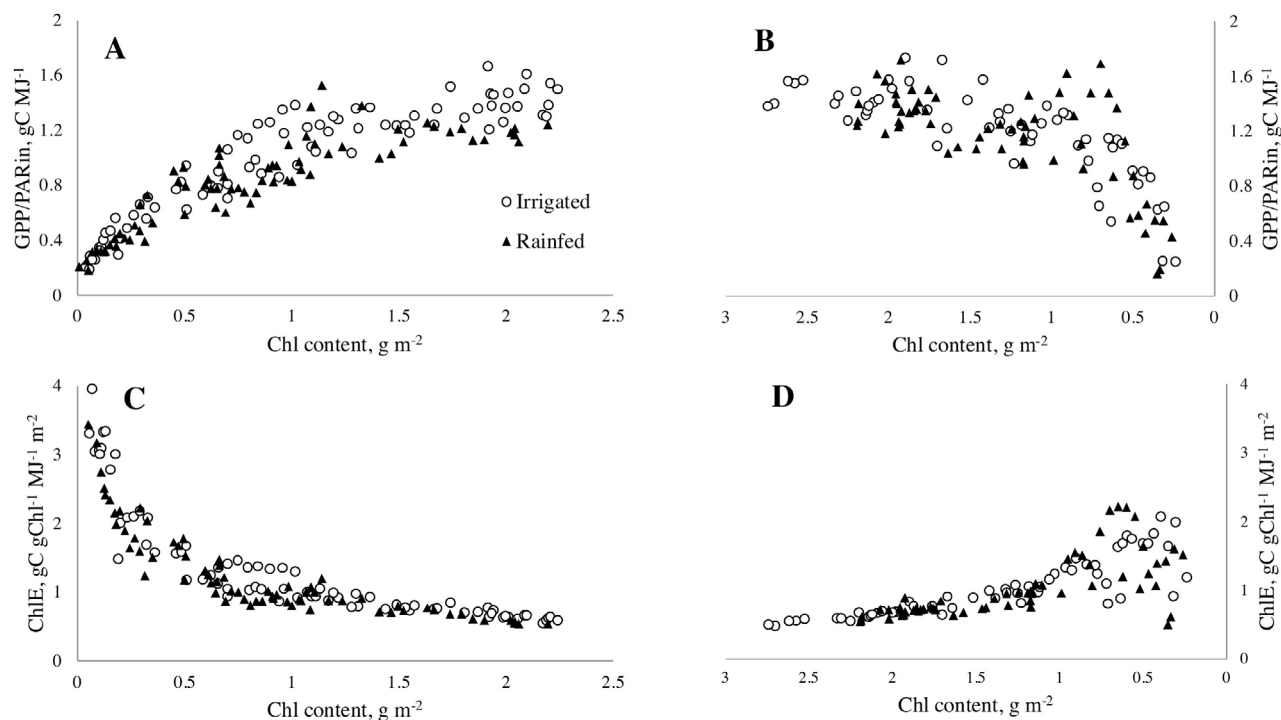


Fig. 5. Relationships GPP/PARin vs. chlorophyll (Chl) content (A and B) and chlorophyll efficiency vs. chlorophyll content (C and D) at irrigated and rainfed soybean sites in vegetative stages (A and C) and reproductive stages (B and D) in 2002, 2004 and 2006.

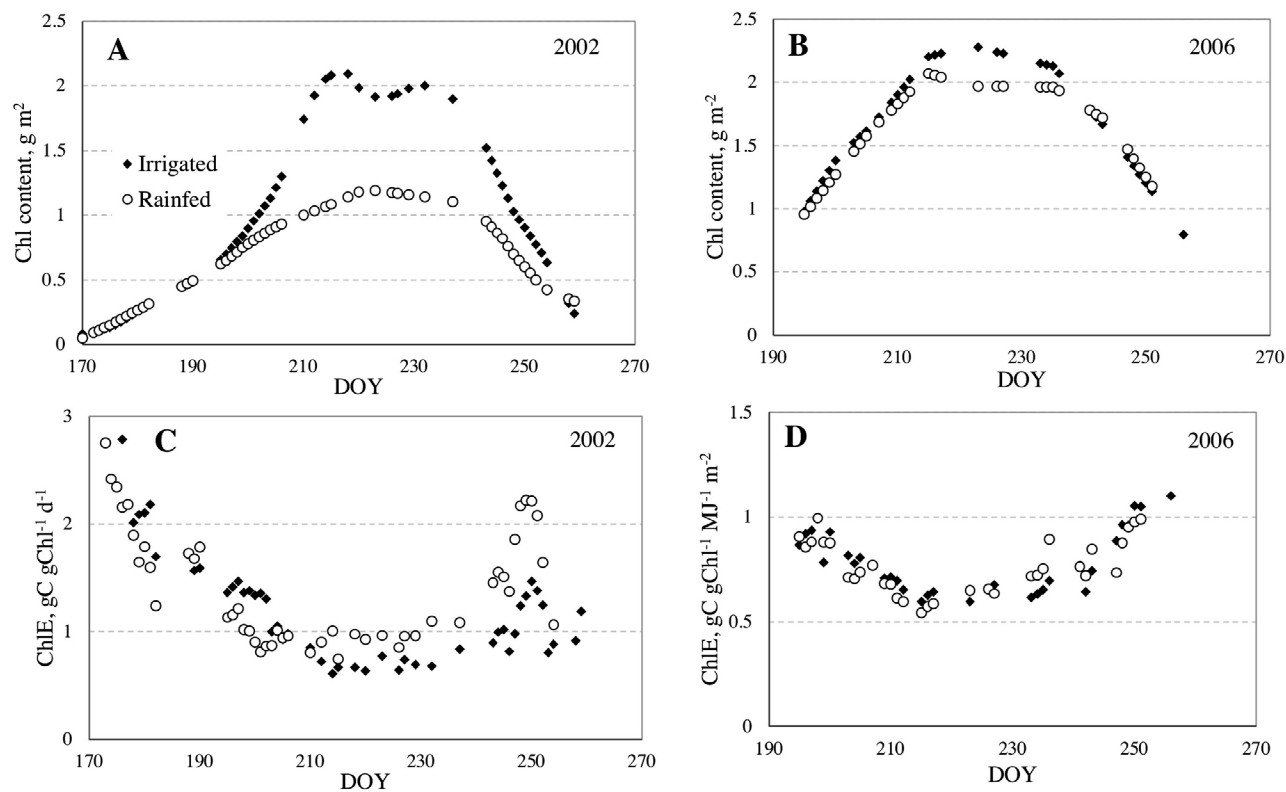


Fig. 6. Temporal behavior of canopy chlorophyll (Chl) content (A, B) and chlorophyll efficiency, ChlE (C, D) in rainfed and irrigated soybean in 2002 (dry year) and 2006 (moderate weather conditions). Difference in Chl and in chlorophyll efficiencies between irrigated and rainfed sites was much higher in dry year 2002 than in 2006. Maximal difference in chlorophyll efficiency occurred when difference in Chl was the highest.

The main features of the relationship between chlorophyll efficiency and Chl seen in maize were also evident for soybean. However, while 12 irrigated and four rainfed maize sites were

studied, only three rainfed and three irrigated soybean sites were studied. The richer data set for maize allowed a more definitive view of the decrease in chlorophyll efficiency at irrigated

compared to rainfed sites. A similar difference was observed in soybean (Fig. 6), however, this difference was not as pronounced as it was in maize.

Despite the differences mentioned above, the GPP/PAR_{in} vs. Chl relationship in soybean during the three years of observations was close; Chl explained 80% of the GPP/PAR_{in} variation (Fig. 1). During the vegetative stages this relationship was stronger, with Chl explaining 88% of the GPP/PAR_{in} variation (not shown).

4.5. Effect of water status on chlorophyll efficiency

For maize, Chl was smaller at the rainfed sites and the difference in Chl was larger for years with higher temperature and lower precipitation. However, *the chlorophyll efficiency at the rainfed sites was higher than at the irrigated sites*. The ratios of GPP, fAPAR and Chl at irrigated-to-rainfed sites give insight into the differences in chlorophyll efficiencies affected by water treatment (Fig. 7).

At the rainfed site in a dry year (2003), soil moisture at DOY 210 was less than half of that at the irrigated site and remained almost invariant until the end of the season. Due to water deficiency, the irrigated-to-rainfed ratio of Chl steadily increased reaching 3.5 at DOY 230 and 12 at DOY 245 (not shown in Fig. 7A). However, when the irrigated-to-rainfed ratio for Chl was equal to 2, the irrigated-to-rainfed ratio for fAPAR was close to one. Until DOY 220, the higher Chl in the irrigated site did not alter the amount of absorbed radiation. This suggests that the depth of light penetration inside the dense irrigated maize canopy was so limited that the so-called "illuminated chlorophyll" (Gamon, 2015) was the same as the one in rainfed canopies with lower Chl. With further increase in the irrigated-to-rainfed ratio of Chl above 2 the irrigated-to-rainfed ratio of fAPAR increased; however, the slope of this increase was 5-fold smaller than the slope of increase in the irrigated-to-rainfed Chl ratio.

The low sensitivity of fAPAR to Chl in the irrigated site affected the sensitivity of GPP to Chl. From the beginning of the season until DOY 225 when the irrigated-to-rainfed ratio of Chl exceeded 3, the irrigated-to-rainfed ratio of GPP was close to one. When Chl in the irrigated site was 3-fold higher than in the rainfed site, GPP was only 30% higher. Further increases of the irrigated-to-rainfed ratio of Chl above 3.5 corresponded to some increase in GPP. However, when the irrigated-to-rainfed ratio of Chl reached a value of 12, the irrigated-to-rainfed ratio of fAPAR was 2.7, while the irrigated-to-rainfed ratio of GPP was just below 2.

For soybean in 2002, the irrigated-to-rainfed ratios of biophysical characteristics (Chl, fAPAR and GPP), as well as chlorophyll efficiency are shown in Fig. 8. At the peak of the season, canopy Chl in the irrigated site was 2.6-fold higher than in the rainfed site. However, this corresponded only to a 25% increase of fAPAR and GPP; thus, chlorophyll efficiency at the irrigated site was half that of the rainfed site.

In both crops, the higher amounts of Chl *produced* at irrigated sites were less effective as *drivers* of photosynthesis than Chl *produced* at the rainfed sites with limited water resources. Due to the limited water supply, leaf Chl decreased; this led to an increase of leaf transmittance and an increase in the optical depth of the canopy in the PAR spectral region. Thus, the amount of illuminated chlorophyll related to APAR became higher and chlorophyll efficiency increased. Thus, PAR absorption by the rainfed canopy was close or equal to the PAR absorption by the irrigated canopy with higher Chl. In maize, a 50% higher Chl in the irrigated vs. rainfed sites did not bring any difference in fAPAR. In soybean, 2.6-fold higher Chl in the irrigated site produced a 30% difference in fAPAR.

5. Discussion

The GPP/PAR_{in} vs. Chl relationship was found to be essentially non-linear with a higher slope at the beginning of the season and in the end of the reproductive stage than through the middle of the season. Thus, chlorophyll efficiency was the highest at the beginning of the season when the canopy density/vegetation fraction was small, leaf Chl was moderate to high and the entire canopy was illuminated. Chlorophyll efficiency was also high at the end of the season when leaf Chl decreased while total LAI remained quite high.

Thus, chlorophyll worked very effectively for primary production at the beginning and at the end of the season when the canopy density and leaf area index were small to moderate. In addition, since leaf N content typically decreases during the reproductive stage (e.g., Muchow, 1988; Uhart and Andrade, 1995), chlorophyll efficiency may also decrease. Muchow and Davis (1988) showed that, in maize, radiation use efficiency was more sensitive to N supply than was radiation interception. Therefore, late in the reproductive stage, when leaf N contents may in fact be lower, particularly at the irrigated compared to the rainfed site, photosynthetic capacity, which is strongly related to N content, would also be smaller.

In the vegetative stage, with the increase in canopy density, self-shadowing increases. During this time, the depth of light penetration inside the canopy (which is inversely proportional to leaf absorption, Merzlyak and Gitelson, 1995) becomes limited by the upper leaf layers. As a result, with an increase in green LAI, the fAPAR stops increasing and remains almost insensitive to changes in green LAI (Figs. 3 B and 4 B in Gitelson et al., 2014). This is especially pronounced in soybean (a planophile), where fAPAR remains almost invariant as green LAI increased from 3 to more than 5.

Chlorophyll efficiencies of maize and soybean differed significantly at moderate to high Chl. The likely reason for this is the different canopy structures of these crops. Canopy structure/leaf angle distribution strongly affects fAPAR (e.g., Huemmrich, 2013). Unlike the maize canopy that is "open" to incident light (spherical), allowing a significant fraction of incident light to penetrate directly inside the canopy, the soybean canopy is more "closed" to light penetration (planophilic). In addition, in a maize canopy, leaf Chl and green LAI gradually increase from the top of canopy, reaching maximal values in the middle of the canopy (Ciganda et al., 2008). Thus, leaf transmittance of the upper leaf layers of maize is higher than that of the top-of-canopy soybean leaves, which supports a high light level in the middle of the maize canopy. In the soybean canopy, leaf Chl is distributed more evenly than in maize canopy. The light transmitted by the uppermost soybean leaf layer inside the canopy is only 1–2% in the blue and red ranges of the spectrum and does not exceed 3–5% in the green (Gitelson et al., 2006a). The "closed" soybean canopy structure and lower light inside the canopy (as compared to that of maize at moderate to high canopy density) may be one of the reasons for the lower chlorophyll efficiency in soybean, due to documented diminishing returns from N investment at low light conditions (Gulman and Chu, 1981).

Plant canopies are constructed so that the distribution of the photosynthetic capacity parallels the gradient of incident radiation inside the canopy (Field, 1991). The distribution of photosynthetic capacity depends on LAI. While at low LAI an optimal canopy yields less than a 5% increase in daily production than a canopy with a uniform distribution of capacity (Field, 1983), the advantage of an optimal canopy may be more than 100% when LAI is high. This effect may be another reason for the difference in chlorophyll efficiencies in maize, with closer to optimal photosynthetic capacity distribution, compared to soybean.

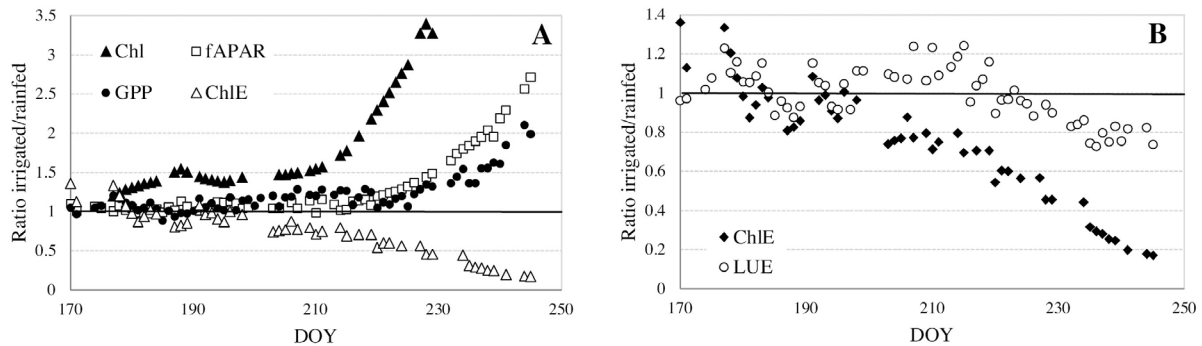


Fig. 7. Temporal behaviors of irrigated-to-rainfed ratios of (A) chlorophyll content (Chl), fraction of absorbed photosynthetically active radiation (fAPAR), gross primary production (GPP) and chlorophyll efficiency (ChIE). (B) Chlorophyll efficiency (ChIE) and light use efficiency (LUE) at maize sites in a dry year. DOY is day of year.

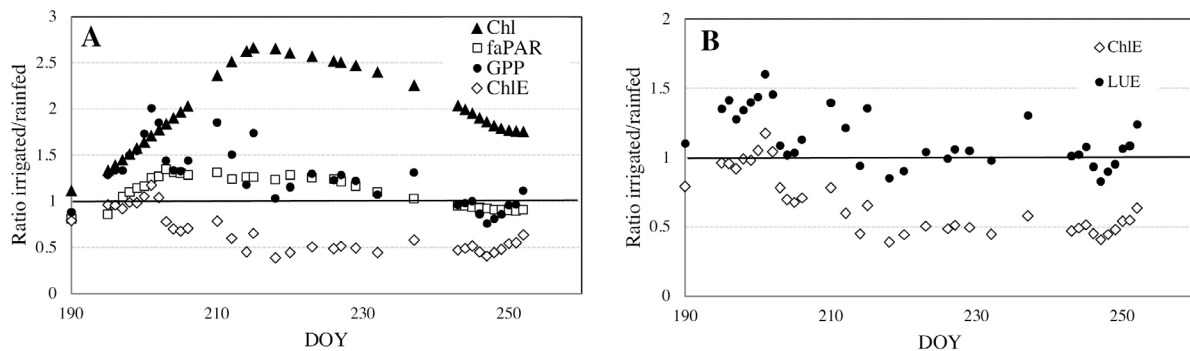


Fig. 8. Temporal behaviors of irrigated-to-rainfed ratios of (A) chlorophyll content (Chl), fraction of absorbed photosynthetically active radiation (fAPAR), gross primary production (GPP) and chlorophyll efficiency (ChIE), and (B) chlorophyll efficiency (ChIE) and light use efficiency (LUE) at soybean sites in 2002.

As a *driver* of photosynthesis, decreased canopy Chl was very effective in capturing light, facilitating deeper light penetration inside the canopy and maximizing photosynthetic rate under conditions of limited water availability. Such effective use of limited resources is remarkable. It demonstrates the elastic adaptation of plants to environmental conditions.

In spite of the wide seasonal variation of Chl efficiency in both crops, LUE remained, if not constant, remarkably invariant. LUE was less affected by severe water stress than Chl and fAPAR. During a dry year, when maize irrigated-to-rainfed ratio of Chl exceeded 2.5, the irrigated-to-rainfed ratio of LUE oscillated around one (Fig. 7B). It was only when the irrigated-to-rainfed Chl ratio increased to 5, and the irrigated-to-rainfed chlorophyll efficiency ratio dropped to 0.4, that the LUE at the irrigated site decreased 20% as compared to the rainfed site. This was also the case for soybean during a dry year, where irrigated-to-rainfed LUE ratio was remarkably invariant during the growing season, oscillating around one, while the irrigated-to-rainfed ratio of Chl exceeded 2.6 and the irrigated-to-rainfed ratio of Chl efficiency dropped below 0.4 (Fig. 8).

Factors that constrain productivity, like low resource availability, may reduce GPP by reducing APAR, LUE or both (Field, 1991). The results of this study indicate that if a limitation in resource availability occurs in a stage during which the plant has the capacity to respond by altering canopy characteristics to "balance" its available resources, the response is a change in APAR such that LUE remains relatively invariant. Thus, in both rainfed maize and soybean, water stress resulted in a decrease of GPP comparable to those of the irrigated sites, however LUE was not affected.

Extensive study of the GPP vs. APAR relationship for maize and soybean showed that GPP and APAR are highly correlated

with limited scattering of the points (in maize $R^2 = 0.9$ and in soybean $R^2 = 0.83$, Gitelson et al., 2015). Remarkably, the GPP vs. APAR relationships were not statistically different for irrigated and rainfed maize ($p = 0.94$), soybean ($p = 0.69$) and for both crops combined ($p = 0.29$).

Efficient resource use is an indication of limited resource availability and high resource acquisition costs that result in an optimization of resource allocation, which then results in a maximization of carbon gains and a convergence on a narrow range of LUE (Field, 1991; Goetz and Prince, 1999). These results thus confirm those of Goetz and Prince, (1999) who found a convergence in the amount of GPP per unit of APAR (i.e., LUE).

Net primary production (Field et al., 1995) and GPP (Goetz and Prince, 1999) are basically *integrators of resource availability* with plant processes *tending toward making all resources equally limiting* (Bloom et al., 1985). In this study, the most limiting factor was water; in reaction to water stress, plants decreased another resource, absorbed light, by decreasing Chl and making absorbed light also limiting.

Rainfed sites in dry years presented extreme cases of resource imbalance. When water is limiting and plants cannot redirect harvest potential to other resources, then plants do not invest in light harvesting over that which can be utilized for growth. By decreasing Chl, the plant decreases light harvesting, making the absorbed light more effective for photosynthesis than when Chl is higher. The decrease in Chl is the result of effective use of limited resources in accord with the resource balance perspective.

Irrigated sites may be seen as examples of "*wasteful allocation*" of resources (Goetz and Prince, 1999), with development of unnecessary light harvesting and photosynthetic machinery. However, it is also possible that the N stored in these seemingly "unnecessary" components is later remobilized into the grain.

This underlines the importance of finding the precise balance for irrigation as well as for N use. Both are sensitive to a number of controls and finding that balance requires an understanding of the effects of each control.

6. Conclusions

This study introduced the concept of chlorophyll efficiency of primary production, which gives insights into the processes behind photosynthetic optimization patterns from leaves to entire canopies. Chlorophyll is one of the main components of the photosynthetic machinery and its efficiency was found to be widely variable and very sensitive to crop physiology, phenology and water status. Chlorophyll efficiency is greatly affected by green LAI and canopy chlorophyll content, diminishing in dense crops. With a decrease of water supply, and thus Chl content, chlorophyll efficiency increases optimizing the use of resources. Despite the very wide variability of chlorophyll efficiency, light use efficiency remained if not constant, remarkably invariant, supporting the concept of an optimization of resource allocation and the functional convergence hypothesis in vegetation with very different physiological states and subjected to different environmental conditions. Since chlorophyll content is accessible through non-destructive, remotely sensed techniques, the use of chlorophyll efficiency for modeling and monitoring plant optimization patterns is practical at different scales (e.g., leaf, canopy) and under different environmental conditions.

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