

# Relationships between gross primary production, green LAI, and canopy chlorophyll content in maize: Implications for remote sensing of primary production



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## ABSTRACT

Life on Earth depends on photosynthesis. Photosynthetic systems evolved early in Earth history, providing evidence for the significance of pigments in plant functions. Photosynthetic pigments fill multiple roles from increasing the range of energy captured for photosynthesis to protective functions. Given the importance of pigments to plant functioning, greater effort is needed to determine and quantify the relationship between gross primary production (GPP) and canopy chlorophyll (Chl) content, the main photosynthetic pigment, as well as its proxy, green leaf area index (GLAI), both used as quantitative measures of plant greenness. The objective of this study is to establish relationships for GPP vs. canopy Chl content and GPP vs. GLAI in maize. The main focus of the paper is to reveal fine details of the relationships and understand their features in different stages of maize development. Data on GPP, leaf Chl content and GLAI were collected across ten years (2001–2010) at three AmeriFlux sites in Nebraska over irrigated and rainfed maize. Relationships of GPP vs. total canopy Chl content and GPP vs. GLAI were established for vegetative, tasseling and reproductive stages. In each stage, relationships were close with determination coefficients above 0.9; however, the shapes and slopes of the relationships in vegetative stages were different from reproductive stages. This difference was more pronounced for the GPP vs. GLAI relationship. In part, this difference is due to different leaf Chl contents in vegetative and reproductive stages. Smaller but detectable differences in shape and slope were also found for the GPP vs. canopy Chl relationship. Despite the differences in relationships for vegetative and reproductive stages, for the entire growing season, green LAI (GLAI) explained 90% of GPP variation with a coefficient of variation (CV) = 17%, while total canopy Chl content explained more than 92% of GPP variation with CV = 15%. Quantitative characterization of relationships between GPP and such biophysical characteristics as GLAI and canopy Chl content underlines the role of chlorophyll in photosynthesis and has significant implications on remote sensing of primary production.

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## 1. Introduction

Assessments of the exchanges of carbon between soil, vegetation, and the atmosphere remain critically important for improving our understanding of ecosystem functioning, for establishment of carbon budgets, for agricultural management and for yield forecasting among others. Terrestrial biosphere models improve the process understanding and descriptions; however, the downside of the enhanced complexity is that additional land-surface parameters are challenging to define with acceptable accuracy over spatial and temporal domains, hampering the ability to describe spatial and inter-annual variability of terrestrial carbon fluxes (Schaefer et al., 2012).

Chlorophylls are vital pigments for photosynthesis; strong correlations have been reported between leaf chlorophyll (Chl)

content and N content (Clevers & Kooistra, 2012; Houlès et al., 2006; Sage, Percy, & Seemann, 1987; Schlemmer et al., 2013). Baret, Houles, and Guerif (2007) found that canopy Chl content is a close proxy of canopy level N content and claimed that N status could be assessed through Chl content. The use of Chl as a proxy of N is more convenient as it directly relates to the plant absorption of photosynthetically active radiation (PAR) and photosynthesis. Canopy Chl content is a physically sound quantity since it represents the optical path in the canopy where absorption by Chl dominates the radiometric signal. Thus, absorption by Chl provides the necessary link between remote sensing observations and canopy state variables that are used as indicators of photosynthetic activity. Leaf and canopy Chl content can be retrieved from satellite observed radiances by inversion of leaf optics and canopy reflectance models, as well as with semi-analytical and empirical models.

The carbon exchange between the crop canopy and the atmosphere is mainly controlled by the amount of solar radiation absorbed, the

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product of the incident photosynthetically active radiation (PAR) and the fraction of PAR absorbed by photosynthetically active vegetation ( $fAPAR_{green}$ , Hall, Huemmrich, Goetz, Sellers, & Nickeson, 1992), as well as the efficiency of the plants in using this energy for photosynthesis, the light use efficiency (LUE). According to Monteith (1972), GPP can be expressed as:

$$GPP = fAPAR_{green} \times PAR \times LUE \quad (1)$$

Canopy Chl content is closely related to  $fAPAR_{green}$  (Peng, Gitelson, Keydan, Rundquist, & Moses, 2011). But, as canopy Chl exceeds  $2 \text{ g m}^{-2}$ , the sensitivity of  $fAPAR_{green}$  to estimate Chl content drops drastically and the  $fAPAR_{green}$  vs. Chl relationship becomes almost flat (Peng et al., 2011). Despite the saturation of  $fAPAR_{green}$  vs. Chl relationship, GPP does remain sensitive to total canopy Chl content even when it exceeds  $2 \text{ g m}^{-2}$ . A significant sensitivity of GPP to moderate to high canopy Chl content was explained by the increase of LUE that follows an increase in total Chl canopy content (Gitelson et al., 2006; Peng et al., 2011). This observation is supported by numerous studies. Dawson, North, Plummer, and Curran (2003) showed that the variation in foliar Chl content may account for some of the seasonal variability in LUE. Houborg, Anderson, Daughtry, Kustas, and Rodell (2010) demonstrated that variations in leaf Chl content were well-correlated with temporal changes in LUE. Kergoat, Lafont, Arneith, Le Dantec, and Saugier (2008) found that the foliar N content of the dominant plant species, closely related to Chl content, explaining 71% of the variation in LUE.

Therefore, two key physiological properties included in Eq. 1, i.e., light capture and the efficiency of the use of absorbed light, relate closely to total canopy Chl content, which subsumes a broad range of processes and can be applied as an integrative diagnostic tool (Peng et al., 2011). This means that canopy Chl content is relevant for estimating GPP in both Production Efficiency Models, using  $fAPAR$ , and Canopy Photosynthesis Models using leaf area index (LAI) as biophysical properties of vegetation.

Gitelson et al. (2006) found a close, consistent relationship between GPP and the product of canopy Chl content and incident PAR in maize and soybean. Moreover, despite great differences in leaf structure and canopy architecture in the C3 and C4 crops studied, the relationship  $GPP \text{ vs. } Chl * PAR_{in}$  was found to be nearly non-species-specific. As a result, a procedure was suggested to remotely assess GPP in crops via estimation of canopy Chl content assuming (Gitelson et al., 2003, 2006):

$$GPP \propto Chl \times PAR_{in} \quad (2)$$

Based on this model, several approaches have been developed to estimate GPP using remotely sensed data. Using Medium Resolution Imaging Spectrometer (MERIS) data, the MERIS terrestrial chlorophyll index (MTCI) was tested for evaluating GPP across a variety of land cover and vegetation types. The results showed great potential for estimating GPP in croplands, grasslands and deciduous forests (Almond et al., 2010; Harris & Dash, 2010; Wu et al., 2009). Xiao et al. (2004, 2011) assessed GPP of U.S. terrestrial ecosystems with a Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation index (VI) products as indicators of vegetation Chl content and auxiliary climate data. Gitelson, Viña, Masek, Verma, and Suyker (2008) estimated crop GPP by employing Chl-related VIs calculated using Landsat ETM+ images. Further, this finding was used for estimating GPP in maize and soybeans using close range (Peng & Gitelson, 2011, 2012; Peng et al., 2011), Landsat (Gitelson et al., 2012), and MODIS (Peng, Gitelson, & Sakamoto, 2013; Sakamoto, Gitelson, Wardlow, Verma, & Suyker, 2012) data.

Given the importance of photosynthetic pigments to plant functioning and photosynthetic activity, greater effort is needed to determine and quantify the relationship between GPP and two

biophysical characteristics of vegetation that are quantitative measures of plant greenness, canopy Chl content and green LAI (GLAI). The objective of this study is to establish relationships for GPP vs. canopy Chl content and GPP vs. GLAI in maize. The main focus of the paper is to reveal the fine details of the relationships and understand their features in different stages of maize development. The results have significant implications on understanding crop photosynthetic processes and remote sensing of primary production.

## 2. Methods

### 2.1. Study area

Three AmeriFlux sites are located at the University of Nebraska-Lincoln Agricultural Research and Development Center near Mead, Nebraska, USA. They are all approximately 60-ha fields within 1.6 km of each other. Sites 1 and 2 are equipped with a center-pivot irrigation system, while site 3 relies entirely on rainfall for moisture. During 2001 through 2009, site 1 was planted in continuous maize, and sites 2 and 3 were both planted in a maize-soybean rotation with maize in odd years and soybean in even years. In 2010, sites 1 and 2 were both planted in maize, and site 3 was planted in soybean. More information about the major crop management strategies at the study sites is given in Suyker and Verma (2010).

Since 2001, each site has been equipped with an eddy covariance tower and meteorological sensors to obtain continuous measurements of  $CO_2$  fluxes, water vapor and energy fluxes, and field campaigns are carried out once or twice per week to sample plants for measuring crop parameters. In this study, ten-year-observations of maize sites were analyzed (site 1 from 2001 to 2010, site 2 and site 3 in 2001, 2003, 2005, 2007 and 2009).

### 2.2. $PAR_{in}$ observations and $PAR_{potential}$ calculations

Point quantum sensors (LI-190, LI-COR Inc., Lincoln, Nebraska) were placed in each study site, 6-m above the surface pointing toward the sky, to measure hourly incoming PAR ( $PAR_{in}$ ). Daytime  $PAR_{in}$  values were calculated by integrating the hourly measurements during a day from sunrise to sunset (the period when instantaneous measurement of  $PAR_{in}$  exceeded  $1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). Daytime  $PAR_{in}$  values were presented in  $\text{MJ m}^{-2} \text{ d}^{-1}$  (Turner et al., 2003).

Incoming radiation is an important factor affecting crop production. Under overcast conditions associated with low values of  $PAR_{in}$ , less incoming radiation is available to be absorbed by the crop thus resulting in low production. However, when incoming light is high and the crop is not under light-limited conditions, small variations of  $PAR_{in}$  do not further affect crop production. Gitelson et al. (2012) suggested using incident PAR under conditions when concentrations of atmospheric gases are minimal (they called it  $PAR_{potential}$ ) in models for GPP estimation. They showed that the model using  $PAR_{potential}$  and Landsat data was more accurate than the model using in situ measured  $PAR_{in}$ . The models with  $PAR_{in}$  and  $PAR_{potential}$  were also compared using daily MODIS data including all-weather conditions, and it has been shown that when the difference between  $PAR_{potential}$  and  $PAR_{in}$  was below 50%, the model with  $PAR_{potential}$  was more accurate than the model with  $PAR_{in}$  (Peng et al., 2013).

Unlike  $PAR_{in}$  measurements including high frequency variations relating to fluctuations of daily weather conditions,  $PAR_{potential}$  only represents the seasonal changes in hours of sunshine (i.e., day length) and it changes gradually throughout the growing season. In this study,  $PAR_{potential}$  was calculated as a function of the day of year (DOY) calibrated based on  $PAR_{in}$  observations. Observations under good weather conditions with  $(PAR_{potential} - PAR_{in}) / PAR_{potential} < 20\%$  were selected in order to exclude crop light-limited conditions.

### 2.3. Eddy covariance GPP flux measurements

At each site, hourly CO<sub>2</sub> fluxes were obtained from wind speed and CO<sub>2</sub> concentrations measured at 10 Hz. Daytime net ecosystem exchange (NEE) values were computed by integrating the hourly CO<sub>2</sub> fluxes collected during the day when instantaneous measurement of PAR<sub>in</sub> exceeded 1 μmol m<sup>-2</sup> s<sup>-1</sup>. Daytime estimates of ecosystem respiration (Re) were obtained from the night CO<sub>2</sub> exchange–temperature relationship (Xu & Baldocchi, 2003). Daytime GPP was then obtained by subtracting daytime Re from daytime NEE as:  $GPP = NEE - Re$ . GPP is presented with units of g C m<sup>-2</sup> d<sup>-1</sup>, and the sign convention used here is such that CO<sub>2</sub> flux to the surface is positive (see Verma et al., 2005 for further details of the eddy covariance measurements).

### 2.4. Determination of leaf area index (LAI) and total canopy Chl content

Within each of three study sites, six small plot areas (20 m × 20 m) were established, which represented all major occurrences of soil and crop production zones within each field (Verma et al., 2005). LAI was estimated from destructive samples at 10–14 day intervals during the growing season from 2001 to 2010. On each sampling date, plants from a 1-m length of either 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, and litter components. All leaves were run through an area meter (LI-3100, Li-Cor, Inc., Lincoln, Nebraska) and the leaf area per plant was determined. For each plot, the leaf area per plant was multiplied by the measured plant population to obtain the total LAI. Total LAI for the six plots were then averaged as a site-level value (details in Viña, Gitelson, Nguy-Robertson, & Peng, 2011). Green leaves were measured in the same way to obtain the green LAI.

The total canopy Chl content was estimated as  $Chl = Chl_{leaf} \times green\ LAI$ , where  $Chl_{leaf}$  is the Chl content of the upper-most collared or ear leaf in maize. Leaf Chl was calculated from leaf reflectance measured by an Ocean Optics radiometer using a red-edge chlorophyll index (details in Gitelson et al., 2003, 2006; Ciganda, Gitelson, & Schepers, 2009). Since green LAI and total Chl values change gradually during the growing season, daily GLAI and total Chl values were obtained by linear interpolation of sampling date measurements for each site in each year.

## 3. Results and discussion

### 3.1. Relationship between green LAI and Chl content

The GLAI is widely used for estimating the radiation absorbed by plants. However, as the photosynthetic component of LAI, GLAI has been traditionally determined using a visual (i.e., subjective) attribute of leaf “greenness” (Boegh et al., 2002; Ciganda, Gitelson, & Schepers, 2008; Curran & Milton, 1983; Viña et al., 2011). Leaf senescence, and concomitant changes in pigment composition, is a gradual process that varies among and within leaves. Thus, deciding whether a leaf is green or largely non-green is often subjective particularly when crops are in reproductive stages (Ciganda et al., 2008; Peng et al., 2011). Mature dark-green leaves with high Chl contents during vegetative growth stages and leaves with lower Chl contents during reproductive stages both may be designated as “green” leaves and thus contribute to the same value of GLAI (e.g., Law et al., 2008).

Therefore, GLAI represents a subjective metric, as it depends on a visual inspection, and interpretation, of leaf color. While a strong linear relationship exists between canopy Chl content and GLAI obtained using this subjective greenness attribute (Ciganda et al., 2008), this relationship exhibits hysteresis due to the leaf Chl content varying over a growing season (Fig. 1). For the same total canopy Chl content, GLAI in a vegetative stage may be much lower than the GLAI in the reproductive stage. In the maize studied, for the same total Chl content of 1 g m<sup>-2</sup>, GLAI = 1.7 in the vegetative stage and GLAI = 2.75 in the

reproductive stage (difference was 38%). The difference was even greater for lower Chl content: for Chl = 0.5 g m<sup>-2</sup>, GLAI = 0.8 in the vegetative stage and GLAI = 2.0 in the reproductive stage (the difference was 60%).

During the vegetative stage, leaf Chl is almost constant and canopy Chl content is linearly related to GLAI. During the reproductive stage, leaf Chl is declining and contributes to the non-linear relationship.

### 3.2. Hysteresis of GPP vs. GLAI \* PAR<sub>in</sub> relationship

Temporal behavior of GPP and the product of GLAI and daytime PAR<sub>in</sub> were quite similar: both increasing from the beginning of the season until day of year (DOY) 190, just before tasseling, almost synchronously and then, while GLAI \* PAR<sub>in</sub> continued to rise, GPP increased at a much slower rate (around DOY 190 to 210) than in the beginning of the growing season (Fig. 2). Both GPP and GLAI \* PAR<sub>in</sub> reached maximal values almost at the same date and then synchronously decreased during the reproductive stages toward the end of the season.

Relationships between GPP and GLAI \* PAR<sub>in</sub> were found to be close with coefficient of determination (R<sup>2</sup>) above 0.95; however, the slopes of the relationships were very different in vegetative and reproductive stages (Fig. 3), so for the same GLAI \* PAR<sub>in</sub>, GPP in vegetative and reproductive stages were different.

### 3.3. Relationships between GPP and GLAI and GPP and Chl content

#### 3.3.1. Vegetative stages

Vegetative stage was the period when GLAI increased to the maximal value and leaf Chl content was distributed almost homogeneously along the canopy. Over eight years of observation in three sites, maize GLAI varied from 0 to 6.6. Relationships for GPP vs. green LAI \* PAR<sub>in</sub> and GPP vs. canopy Chl \* PAR<sub>in</sub> for 10 years of observation (2001–2010) in irrigated and rainfed maize are presented in Fig. 4 for days when the decrease of PAR<sub>in</sub> from PAR<sub>potential</sub> was no more than 20%. Relationships for GPP vs. green LAI \* PAR<sub>potential</sub> and GPP vs. canopy Chl \* PAR<sub>potential</sub> were also established (Fig. 5). The use of PAR<sub>potential</sub> instead of PAR<sub>in</sub> reduced the uncertainties of GPP estimates due to fluctuations of PAR<sub>in</sub> that do not affect plant photosynthetic activity appreciably (Gitelson et al., 2012; Peng et al., 2013).

Despite large seasonal and inter-seasonal variations of GLAI in the sites studied, the products of GLAI \* PAR<sub>in</sub> and canopy Chl \* PAR<sub>in</sub> in the vegetative stages were related to GPP closely with R<sup>2</sup> above 0.95 (Fig. 4). Note that the patterns of the two relationships were very similar since GLAI was closely linearly related to canopy Chl in the vegetative stage (Fig. 1). The same was the case when PAR<sub>in</sub> was replaced by

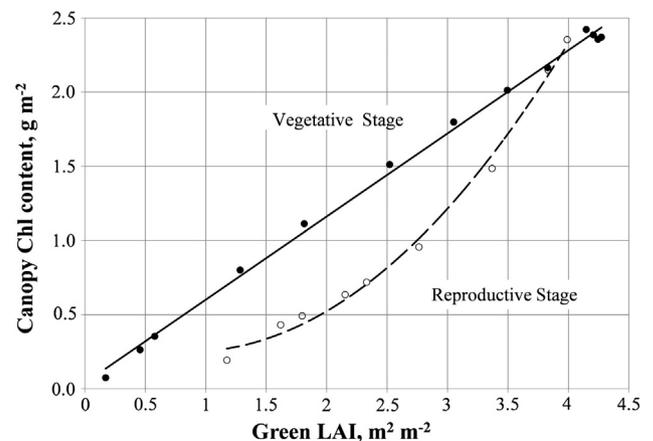
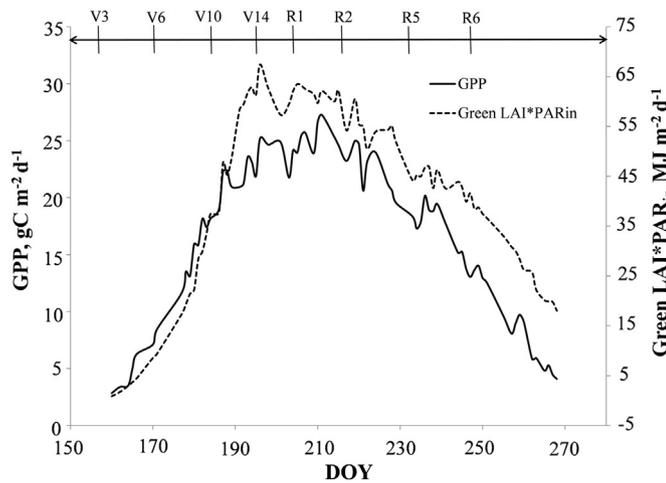


Fig. 1. Relationship of maize canopy Chl content and green LAI at the rainfed site in 2003.

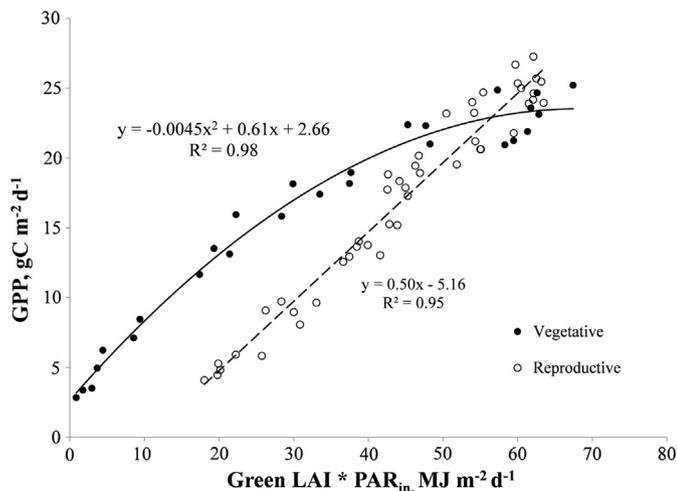


**Fig. 2.** Temporal behavior of gross primary production and the product of green LAI (GLAI) and incident photosynthetically active radiation ( $GLAI * PAR_{in}$ ) at the irrigated site 1 in 2003. Stages indicated: VN, where N is the number of fully expanded leaves; R1 – silking; 216; R2 – blister; R5 – dent; R6 – physiological maturity.

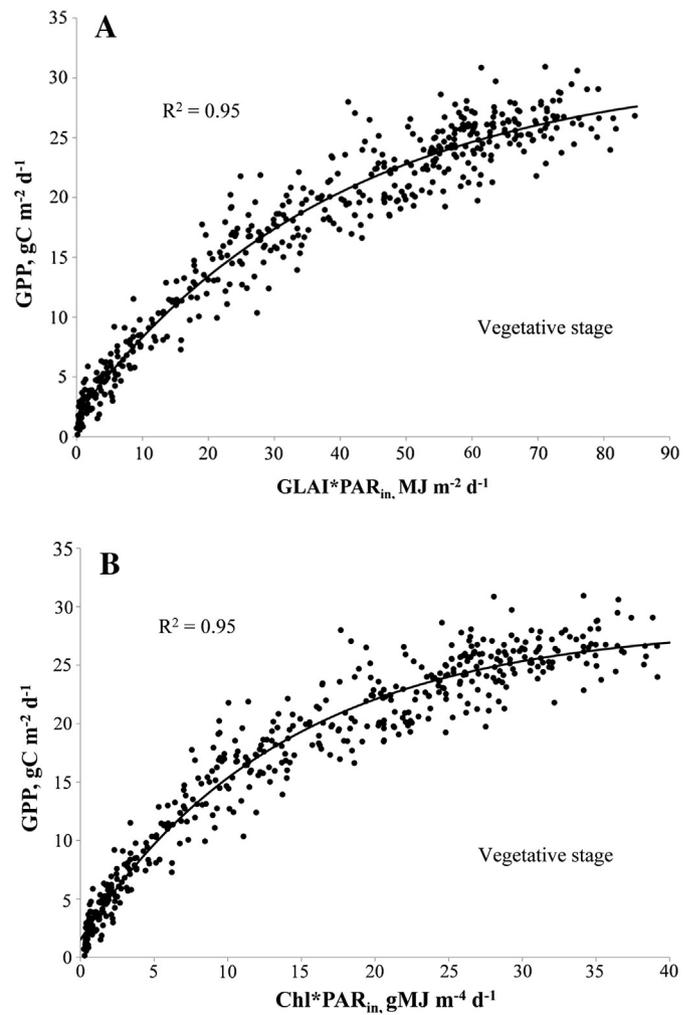
$PAR_{potential}$  (Fig. 5). GLAI and canopy Chl content times either  $PAR_{in}$  or  $PAR_{potential}$  explained more than 94% of GPP variation in 21 maize site-years with different treatments, climatic conditions, maize hybrid varieties, etc. The slopes of the relationships were much higher when GLAI, canopy Chl content, and vegetation fractions were low and Chl worked more efficiently for absorbing light for photosynthesis (Fig. 4). Overall, the light climate in the beginning of the season was very different from that later in the season. For GLAI below 3, the slope was  $10 \text{ g C m}^{-2} \text{ d}^{-1}$  and declined to around  $6 \text{ g C m}^{-2} \text{ d}^{-1}$  when GLAI ranged from 3 to more than 6. Importantly, while  $fAPAR_{green}$  was insensitive to GLAI above 4 (Fig. 2 in Peng et al., 2011), GPP remained quite sensitive to changes in GLAI and canopy Chl content over the whole range of absorbed PAR.

### 3.3.2. Tasseling

During this period, GPP decreased while GLAI and canopy Chl slightly increased - DOY 206 - 210 (Fig. 6). Later, when GLAI and canopy Chl content were still quite high (GLAI around 5–6) and stable, GPP was relatively virtually invariant DOY 210 - 216. Note that the slight decrease in  $GLAI * PAR_{potential}$  during tasseling (Fig. 7) was primarily due to the decrease in  $PAR_{potential}$  as day length decreased (Gitelson et al., 2012; Peng et al., 2013). The relationships between GPP vs.  $GLAI * PAR_{potential}$  and



**Fig. 3.** Relationships between maize GPP and  $GLAI * PAR_{in}$  in vegetative and reproductive stages at the irrigated site 1 in 2003.



**Fig. 4.** Relationships between GPP and  $GLAI * PAR_{in}$  (A) and GPP and canopy  $Chl * PAR_{in}$  (B) in rainfed and irrigated maize during vegetative stages from 2001 to 2010.

GPP vs. canopy  $Chl * PAR_{potential}$  for vegetative and tasseling stages remained close with coefficients of determination above 0.95 (Fig. 7).

### 3.3.3. Reproductive stages and whole growing season

In reproductive stages, GPP vs.  $GLAI * PAR_{potential}$  and GPP vs. canopy  $Chl * PAR_{potential}$  relationships were close with  $R^2$  above 0.93 (Fig. 8). However, these relationships were very different from those during the vegetative stages with significant hysteresis of the relationship for the whole growing season. For the same  $GLAI * PAR_{potential}$  value, GPP was higher in the vegetative stages. The difference between GPP in the vegetative and reproductive stages was minimal for GLAI above 4 (below 2% of GPP in vegetative stages) and increased significantly as GLAI declined. It was 12% for  $GLAI = 3$ , 30% for  $GLAI = 2$ , and 73% for  $GLAI = 1$ .

In vegetative and reproductive stages, GPP vs. canopy  $Chl * PAR_{potential}$  relationships were closer (Fig. 8B) than GPP vs.  $GLAI * PAR_{potential}$  (Fig. 8A). However, for the same  $Chl * PAR_{potential}$  value, GPP was still higher in the vegetative stages. At the same  $GLAI * PAR_{potential}$ , the maximal difference in GPP was 31%; however, for the same canopy  $Chl * PAR_{potential}$ , the difference in GPP decreased to 16%. There was no difference for canopy Chl content above  $2 \text{ g m}^{-2}$ , the difference was 14% for  $Chl = 2 \text{ g m}^{-2}$  and peaked at 25% for  $Chl$  below  $0.2 \text{ g m}^{-2}$ . It is worth mentioning that, in this study, the hysteresis of the GPP vs.  $Chl * PAR_{potential}$  relationship was much more pronounced in irrigated sites than in the rainfed site.

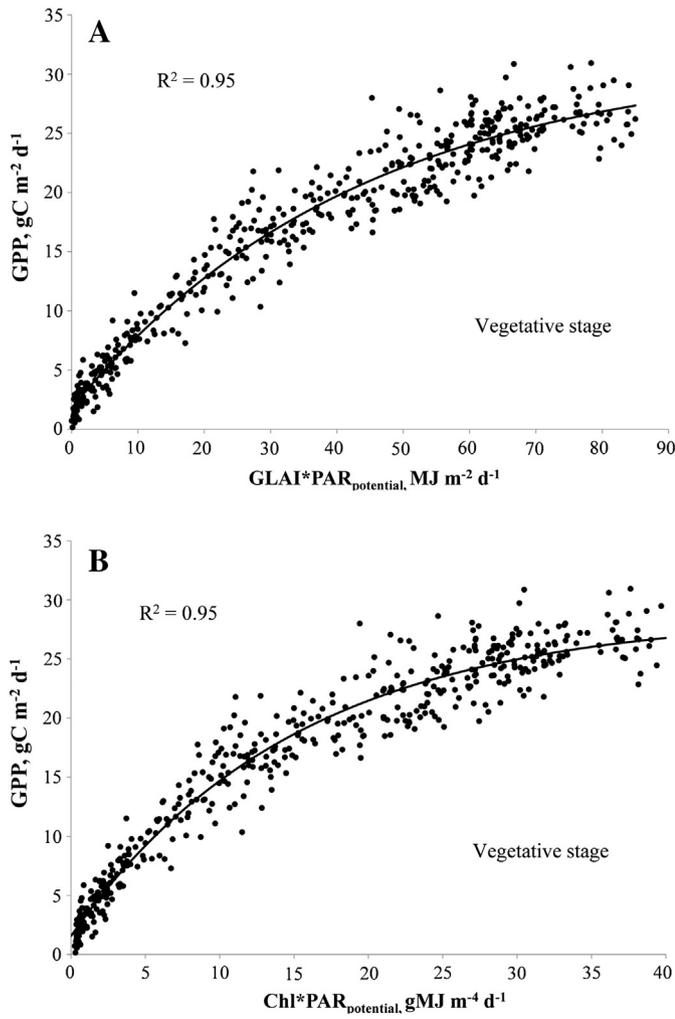


Fig. 5. Relationships between GPP and  $GLAI * PAR_{potential}$  (A) and GPP and canopy  $Chl * PAR_{potential}$  (B) in rainfed and irrigated maize during vegetative stages from 2001 to 2010.

Hysteresis of the GPP vs.  $GLAI * PAR_{potential}$  relationship (Figs. 3 and 8A) was discussed above (see Section 3.2). It became clear that there are two reasons for that. The primary one is due to the difference in leaf Chl content in vegetative and reproductive stages that occurred for the same green LAI. The second reason is due to

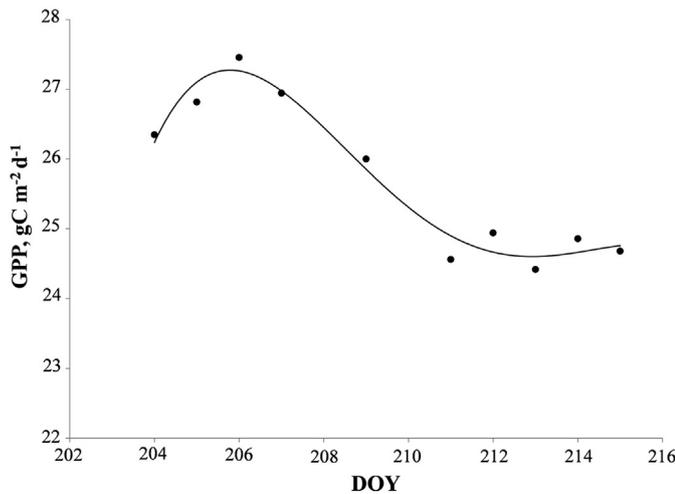


Fig. 6. Temporal behavior of maize GPP during tasseling and early reproductive stages at the irrigated site 1 in 2009.

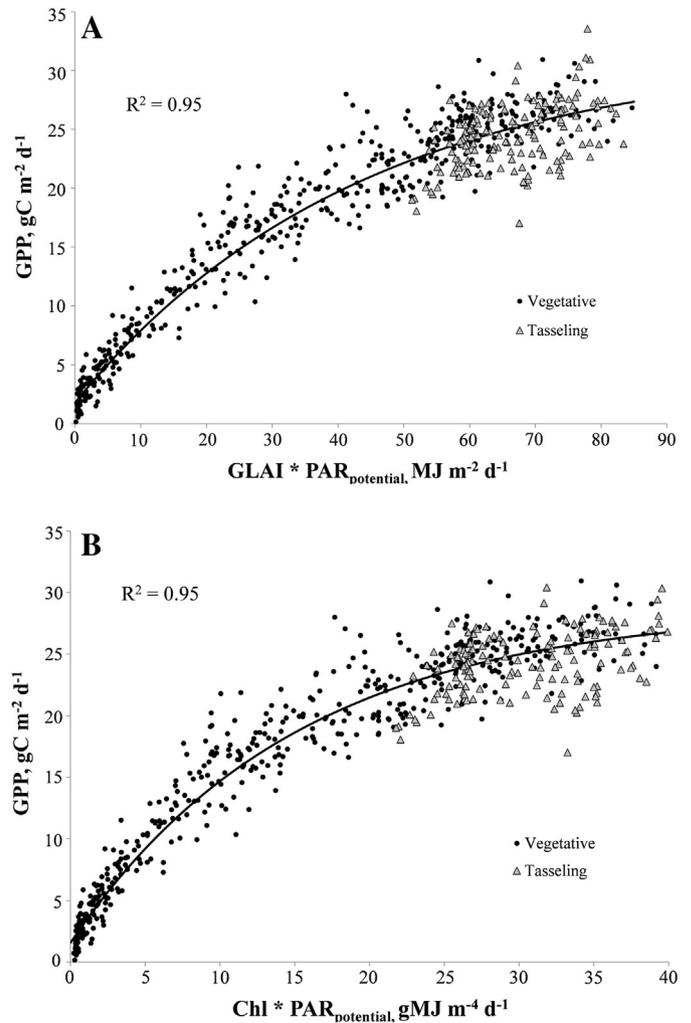
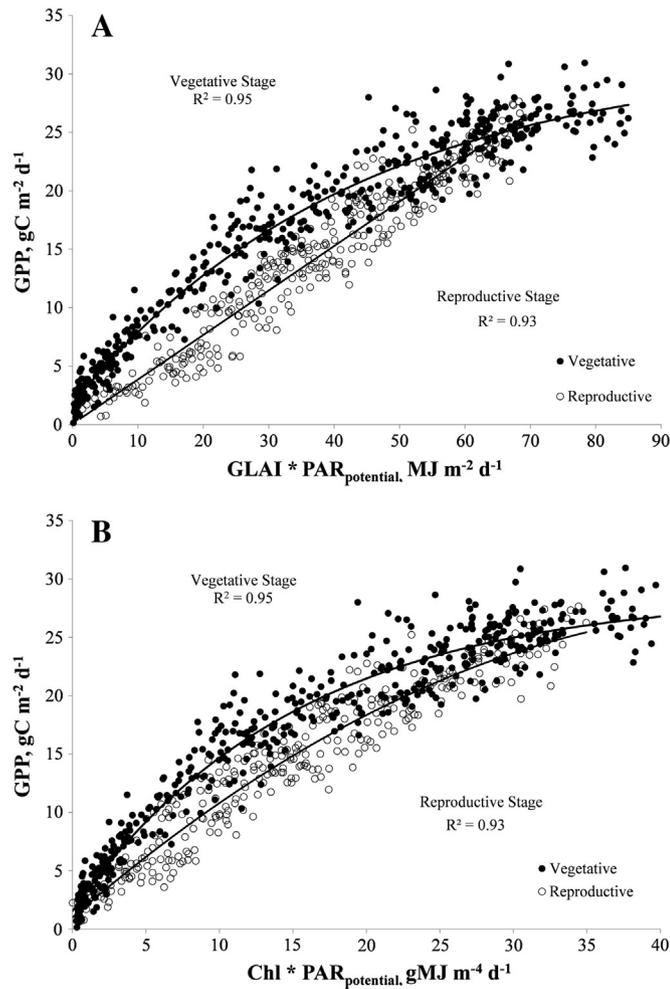


Fig. 7. Relationships between GPP and  $GLAI * PAR_{potential}$  (A) and canopy  $Chl * PAR_{potential}$  (B) in rainfed and irrigated maize during vegetative and tasseling stages from 2001 to 2010.

hysteresis of the GPP vs. canopy  $Chl * PAR_{potential}$  relationship (Fig. 8B). The causes for differences in the GPP vs. canopy  $Chl * PAR_{potential}$  relationship in different stages of development (Fig. 8B) are very important to understand and, to the best of our knowledge, have previously been neither reported nor explained.

The hysteresis indicates that the efficiencies of Chl in absorbing light and contributing to GPP in the vegetative stages and in the reproductive stages are different. In both stages, the maize canopy has vertically variable GLAI and leaf Chl contents (Ciganda, Gitelson, & Schepers, 2012; Ciganda et al., 2009). However, during the vegetative stages almost all leaves are “green” with quite high Chl content (above  $300 \text{ mg m}^{-2}$ ). During the reproductive stages, the greenest leaves are located around the ear leaf (approximately 8th from the top of canopy for the hybrids used in these studies) while leaves at the bottom of the canopy are senescing and almost chlorophyll-free. Thus, during these two stages of maize development the light climate inside the canopy is different.

The light climate inside the canopy could play a role in the efficiency of Chl to absorb light. Huemmrich (2013) used the SAIL model for simulating reflectance in a canopy containing a few layers with different leaf angle distributions (LAD) and found that variation of LAD in each layer affected the fraction of absorbed photosynthetically active radiation (fAPAR). Using this model, Gitelson, Peng, and Huemmrich (2013) found that the vertical distribution of Chl content greatly affected the PAR absorbed by plants. Thus, radiative transfer modeling could probably provide a quantitative estimate of how the canopy light



**Fig. 8.** Relationships between GPP and  $GLAI * PAR_{potential}$  (A) and canopy  $Chl * PAR_{potential}$  (B) in rainfed and irrigated maize during vegetative stage (before tasseling) and reproductive stage (after tasseling) from 2001 to 2010.

climate affects  $fAPAR$  and whether differences in canopy structure, vertical LAI and Chl content distributions during vegetative and reproductive stages may be a reason for differences in GPP vs. canopy  $Chl * PAR_{potential}$  relationships in these stages.

The hysteresis presented in the GPP vs. canopy  $Chl * PAR_{potential}$  relationship in the later reproductive stages (Fig. 8B) may be due to factors other than the canopy light climate. For example, the maximum rate of carboxylation is directly related to the amount and activity of photosynthetic enzymes (e.g., rubisco, PEP carboxylase) that act as catalysts for carbon fixation within the leaf chloroplasts. Photosynthetic enzyme properties are, in turn, closely related to the N content of leaves. At the same time, since chlorophylls are vital pigments for photosynthesis, strong correlations have been reported between leaf Chl and N

contents. Thus, the availability of N to the plant affects both Chl and photosynthetic enzyme kinetics. Moreover, it is well known that there are differences in the ratio of Chl to photosynthetic enzymes in sun-grown versus shade-grown leaves (e.g., Anderson, Chow, & Goodchild, 1988). It is also understood that fully developed leaves are able to alter the ratio of Chl to photosynthetic enzymes within a few days in response to changes in the canopy light environment (Björkman & Demmig-Adams, 1994). Such changes in the ratio would be expected to alter the GPP vs. canopy  $Chl * PAR_{potential}$  relationship.

Schlemmer et al. (2013) showed that the relationship between leaf level N and Chl contents is strongly linear; however, the slope of this relationship is two-fold higher early in the season than in the reproductive stages. Thus, for the same leaf Chl content, N content may be different in vegetative than in reproductive stages. Plants may also take up more N than they need if it is available early in the season. Plant N concentrations can also decrease if N uptake is reduced later in the season as plant biomass increases; this likely happens when, as at the rainfed sites in this study, all fertilizer N is applied at the time of planting. Thus, the possibility exists that leaf N content could be one of the factors influencing the hysteresis of the GPP vs. canopy  $Chl * PAR_{potential}$  relationship. Moreover, leaf N content also influences the rates of respiration – a direct contributor to GPP. Clearly, further research in this area is warranted.

Relationships GPP vs.  $GLAI * PAR_{potential}$  and GPP vs. canopy  $Chl * PAR_{potential}$  for vegetative, reproductive stages and the entire season were shown in Table 1. Despite the hysteresis effect, the GPP vs.  $GLAI * PAR_{potential}$  relationship for the whole growing season was close with  $R^2 = 0.90$  and coefficient of variation,  $CV = 17\%$ . The GPP vs. canopy  $Chl * PAR_{potential}$  relationship for the entire growing season was also close with  $R^2 = 0.92$  and  $CV = 15.3\%$ . Thus, the product of canopy Chl content and  $PAR_{potential}$ , which represents the seasonal change of incident radiation, explained about 92% of GPP variation in rainfed and irrigated maize grown across very different weather conditions. Note that the scatter within this relationship included uncertainties in measuring GPP, leaf area index, and leaf Chl content in very vertically heterogeneous maize canopies.

Canopy Chl content is a more objective biophysical characteristic than GLAI in quantifying the amount of absorbed radiation, LUE and primary production. Therefore, the use of canopy Chl content instead of GLAI can decrease uncertainties in Canopy Photosynthesis Models due to the subjectivity involved in determining GLAI. Canopy Chl content, which has been related with the GPP of vegetation canopies (Gitelson et al., 2003, 2006, 2008; Harris & Dash, 2010; Hilker, Gitelson, Coops, Hall, & Black, 2011), may actually provide a more accurate representation of the photosynthetically active component of the GLAI.

#### 4. Summary

Close relationships were found between GPP of maize and GLAI as well as between GPP and canopy Chl content. The shape of the GPP vs. GLAI relationship demonstrated hysteresis: for the same GLAI, GPP was higher in vegetative stages than in reproductive stages. In part, this hysteresis is due to hysteresis of the GLAI vs. canopy Chl content

**Table 1**  
Best-fit functions, determination coefficients ( $R^2$ ), root mean square errors (RMSE) in  $gC\ m^{-2}\ d^{-1}$ , coefficients of variation (CV) and sample number for the relationships GPP vs. green LAI  $* PAR_{potential}$  and GPP vs. canopy  $Chl * PAR_{potential}$  during vegetative and reproductive stages and for the entire season.

	Development stage	Sample No.	GPP vs. $GLAI * PAR_{potential}$ GPP vs. $Chl * PAR_{potential}$	$R^2$	RMSE	CV, %
GPP vs. $GLAI * PAR_{potential}$	Vegetative	518	$y = 31.5 - 13472 / (1 + e^{(x + 265) / 43.4})$	0.95	1.92	11
	Reproductive	311	$y = 0.38x + 0.06$	0.93	1.81	12
	Entire season	829	$y = -0.0016x^2 + 0.455x + 1.844$	0.90	2.41	15
GPP vs. $Chl * PAR_{potential}$	Vegetative	518	$y = 28.7 - 44016 / (1 + e^{(x + 111.7) / 15.1})$	0.95	2.02	12
	Reproductive	311	$y = 0.01x^2 + 1.09x + 1.01$	0.93	1.83	13
	Entire season	829	$y = -0.014x^2 + 1.17x + 2.126$	0.92	2.25	13

relationship, since for the same GLAI, leaf Chl content in the vegetative stage is higher than in the reproductive stage. Detectable hysteresis, while less pronounced, was also observed in the GPP vs. canopy Chl relationship. This implies that the efficiency of canopy Chl content in photosynthesis was different during vegetative and reproductive stages. Among likely factors causing the hysteresis is the very different light climate inside the canopy in vegetative stages, when almost all maize leaves are green, while in the reproductive stages, when leaf inclination changes drastically due to leaves breaking and hanging free and the vertical distribution of leaf Chl content becomes very heterogeneous with completely chlorophyll-free bottom leaves. Another possible reason may be the documented higher leaf N content in vegetative stages compared to reproductive stages. This may have an effect on the ratio of Chl to photosynthetic enzymes in the canopy. Further study is required to understand the reasons for the different Chl efficiencies in photosynthesis during vegetative and reproductive stages in crops. Despite hysteresis, during the whole growing season,  $GLAI * PAR_{potential}$  was found to be responsible for 90% of GPP variation and the coefficient of variation in GPP estimation via GLAI was below 17%. The product of canopy Chl content and  $PAR_{potential}$  explained more than 92% of GPP variation and the coefficient of variation of GPP estimation via canopy Chl was below 15.3%. The results underline the role of Chl content in photosynthesis and have great implications for remote estimation of primary production because canopy Chl content may be retrieved from satellite observed radiances by inversion of leaf optics and canopy reflectance models as well as semi analytical and empirical models.

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## References

- Anderson, J. M., Chow, W. S., & Goodchild, D. J. (1988). Thylakoid membrane organization in sun/shade acclimation. *Australian Journal of Plant Physiology*, 15, 11–26.
- Almond, S., Boyd, D. S., Dash, J., Curran, P. J., Hill, R. A., & Foody, G. M. (2010). Estimating terrestrial gross primary productivity with the Envisat Medium Resolution Imaging Spectrometer (MERIS) Terrestrial Chlorophyll Index (MTCI). *Geoscience and remote sensing symposium (IGARSS) 2010 IEEE International*, 4792–4795, Honolulu, HI.
- Baret, F., Houles, V., & Guerif, M. (2007). Quantification of plant stress using remote sensing observations and crop models: The case of nitrogen management. *Journal of Experimental Botany*, 58(4), 869–880. <http://dx.doi.org/10.1093/jxb/erl231>.
- Björkman, O., & Demmig-Adams, B. (1994). Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. In E. -D. Schulze, & M. M. Caldwell (Eds.), *Ecophysiology of photosynthesis* (pp. 17–47). Berlin: Springer.
- Boegh, E., Soegaard, H., Broge, N., Hasager, C. B., Jensen, N. O., Schelde, K., et al. (2002). Airborne multispectral data for quantifying leaf area index, nitrogen concentration, and photosynthetic efficiency in agriculture. *Remote Sensing of Environment*, 81, 179–193.
- Ciganda, V., Gitelson, A. A., & Schepers, J. (2008). Vertical profile and temporal variation of chlorophyll in maize canopy: Quantitative “crop vigor” indicator by means of reflectance-based techniques. *Agronomy Journal*, 100, 1409–1417. <http://dx.doi.org/10.2134/agronj2007.0322>.
- Ciganda, V., Gitelson, A. A., & Schepers, J. (2009). Non-destructive determination of maize leaf and canopy chlorophyll content. *Journal of Plant Physiology*, 166, 157–167.
- Ciganda, V. S., Gitelson, A. A., & Schepers, J. (2012). How deep does a remote sensor sense? Expression of chlorophyll content in a maize canopy. *Remote Sensing of Environment*, 126, 240–247.
- Clevers, J. G. P. W., & Kooistra, L. (2012). Using hyperspectral remote sensing data for retrieving canopy chlorophyll and nitrogen content. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 5, 574–583.
- Curran, P. J., & Milton, E. J. (1983). The relationships between the chlorophyll concentration, LAI and reflectance of a simple vegetation canopy. *International Journal of Remote Sensing*, 4, 247–255.
- Dawson, T. P., North, P. R. J., Plummer, S. E., & Curran, P. J. (2003). Forest ecosystem chlorophyll content: Implications for remotely sensed estimates of net primary productivity. *International Journal of Remote Sensing*, 24, 611–617.
- Gitelson, A. A., Peng, Y., Masek, J. G., Rundquist, D. C., Verma, S. B., Suyker, A., et al. (2012). Remote estimation of crop gross primary production with Landsat data. *Remote Sensing of Environment*, 121, 404–414.
- Gitelson, A. A., Viña, A., Masek, J. G., Verma, S. B., & Suyker, A. E. (2008). Synoptic monitoring of gross primary productivity of maize using Landsat data. *IEEE Geoscience and Remote Sensing Letters*, 5, 2. <http://dx.doi.org/10.1109/LGRS.2008.915598>.
- Gitelson, A. A., Viña, A., Verma, S. B., Rundquist, D. C., Arkebauer, T. J., Keydan, G., et al. (2006). Relationship between gross primary production and chlorophyll content in crops: Implications for the synoptic monitoring of vegetation productivity. *Geophysical Research Letter*, 111, D08S11. <http://dx.doi.org/10.1029/2005JD006017>.
- Gitelson, A. A., Verma, S. B., Viña, A., Rundquist, D. C., Keydan, G., Leavitt, B., et al. (2003). Novel technique for remote estimation of CO<sub>2</sub> flux in maize. *Geophysical Research Letter*, 30(9), 1486. <http://dx.doi.org/10.1029/2002GL016543>.
- Gitelson, A. A., Peng, Y., & Huemmrich, K. F. (2013). Relationship between fraction of radiation absorbed by photosynthesizing maize and soybean canopies and NDVI from remotely sensed data taken at close range and from MODIS 250 m resolution data (in revision).
- Hall, F. G., Huemmrich, K. F., Goetz, S. J., Sellers, P. J., & Nickeson, J. E. (1992). Satellite remote sensing of surface energy balance: Success, failures and unresolved issues in FIFE. *Journal of Geophysical Research*, 97, 19,061–19,089.
- Harris, A., & Dash, J. (2010). The potential of the MERIS terrestrial chlorophyll index for carbon flux estimation. *Remote Sensing of Environment*, 114, 1856–1862.
- Hilker, T., Gitelson, A., Coops, N. C., Hall, F. G., & Black, T. A. (2011). Tracking plant physiological properties from multi-angular tower-based remote sensing. *Oecologia*, 165(4), 865–876.
- Houborg, R., Anderson, M. C., Daughtry, C. S. T., Kustas, W. P., & Rodell, M. (2010). Using leaf chlorophyll to parameterize light-use-efficiency within a thermal-based carbon, water and energy exchange model. *Remote Sensing of Environment*, 115, 1694–1705.
- Houlès, V., Gue'rif, M., Mary, B., Gate, P., Machet, J. M., & Moulin, S. (2006). Elaboration d'un indicateur de nutrition azotée du blé basé sur l'indice foliaire et la teneur en chlorophylle pour la préconisation de doses d'azote. In M. Gue're'f, & D. King (Eds.), *Hétérogénéité parcellaire et gestion des cultures; vers une agriculture de précision. Editions QUAE* (pp. 179–198).
- Huemmrich, K. F. (2013). Simulations of seasonal and latitudinal variations in leaf inclination angle distribution: Implications for remote sensing. *Advances in Remote Sensing*, 2, 93–101.
- Kergoat, L., Lafont, S., Arneth, A., Le Dantec, V., & Saugier, B. (2008). Nitrogen controls plant canopy light-use-efficiency in temperate and boreal ecosystems. *Journal of Geophysical Research*, 113(G04017), 1–19. <http://dx.doi.org/10.1029/2007JG000676>.
- Law, B. E., Arkebauer, T., Campbell, J. L., Chen, J., Sun, O., Schwartz, M., et al. (2008). Terrestrial carbon observations: Protocols for vegetation sampling and data submission. *Global Terrestrial Observing System, FAO, Rome, Report*, 55, 87.
- Monteith, J. L. (1972). Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*, 9, 744–766.
- Peng, Y., & Gitelson, A. A. (2011). Application of chlorophyll-related vegetation indices for remote estimation of maize productivity. *Agricultural and Forest Meteorology*, 151, 1267–1276.
- Peng, Y., Gitelson, A. A., Keydan, G., Rundquist, D. C., & Moses, W. (2011). Remote estimation of gross primary production in maize and support for a new paradigm based on total crop chlorophyll content. *Remote Sensing of Environment*, 115, 978–989.
- Peng, Y., & Gitelson, A. A. (2012). Remote estimation of gross primary productivity in soybean and maize based on total crop chlorophyll content. *Remote Sensing of Environment*, 117, 440–448.
- Peng, Y., Gitelson, A. A., & Sakamoto, T. (2013). Remote estimation of gross primary productivity in crops using MODIS 250 m data. *Remote Sensing of Environment*, 128, 186–196.
- Sakamoto, T., Gitelson, A. A., Wardlow, B.D., Verma, S. B., & Suyker, A. E. (2012). Estimating daily gross primary production of maize based only on MODIS WDRVI and shortwave radiation data. *Remote Sensing of Environment*, 115(3091), 3101.
- Sage, R. F., Pearcy, R. W., & Seemann, J. R. (1987). The nitrogen use efficiency of C3 and C4 plants. *Plant Physiology*, 85, 355–359.
- Schaefer, K., Schwalm, C. R., Williams, C., Arain, M.A., Barr, A., Chen, M., et al. (2012). A model-data comparison of gross primary productivity: Results from the North American Carbon Program site synthesis. *Journal of Geophysical Research*, 117, 1–15.
- Schlemmer, M., Gitelson, A. A., Schepers, J., Ferguson, R., Peng, Y., Shanahan, J., et al. (2013). Remote estimation of nitrogen and chlorophyll contents in maize at leaf and canopy levels. *International Journal of Applied Earth Observation and Geoinformation*, 25, 47–54.
- Suyker, A. E., & Verma, S. B. (2010). Coupling of carbon dioxide and water vapor exchanges of irrigated and rainfed maize-soybean cropping systems and water productivity. *Agricultural and Forest Meteorology*, 150, 553–563.
- Turner, D. P., Urbanski, S., Bremer, D., Wofsy, S., Meyers, T., Gower, S. T., et al. (2003). A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biology*, 9, 383–395.

- Verma, S. B., Dobermann, A., Cassman, K. G., Walters, D. T., Knops, J. M., Arkebauer, T. J., et al. (2005). Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. *Agricultural and Forest Meteorology*, *131*, 77–96.
- Viña, A., Gitelson, A. A., Nguy-Robertson, A. L., & Peng, Y. (2011). Comparison of different vegetation indices for the remote assessment of green leaf area index of crops. *Remote Sensing of Environment*, *115*, 3468–3478.
- Wu, C., Niu, Z., Tang, Q., Huang, W., Rivard, B., & Feng, J. (2009). Remote estimation of gross primary production in wheat using chlorophyll-related vegetation indices. *Agricultural and Forest Meteorology*, *149*, 1015–1021.
- Xiao, X., Zhang, Q., Braswell, B., Urbanski, S., Boles, S., Wofsy, S., et al. (2004). Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data. *Remote Sensing of Environment*, *256*–270.
- Xiao, J., Zhang, Q., Law, B., Baldocchi, D.D., Chen, J., Richardson, A.D., et al. (2011). Assessing net ecosystem carbon exchange of U.S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. *Agricultural and Forest Meteorology*, *151*, 60–69.
- Xu, L., & Baldocchi, D.D. (2003). Seasonal trend of photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree Physiology*, *23*, 865–877.