Remote estimation of gross primary production in maize and support for a new paradigm based on total crop chlorophyll content

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Abstract

The accurate quantification of gross primary production (GPP) in crops is important for regional and global studies of carbon budgets. Because of the observed close relationship between GPP and total canopy chlorophyll content in crops, vegetation indices related to chlorophyll can be used as a proxy of GPP. In this study, we justified the approach, tested the performance of several widely used chlorophyll-related vegetation indices in estimating total chlorophyll content and GPP in maize based on spectral data collected at a close range, 6 meters above the top of the canopy, over a period of eight years (2001 to 2008). The results show that GPP can be accurately estimated with chlorophyll-related indices that use near infra-red and either green or the red edge range of the spectrum. These indices provide the best approximation of the widely variable GPP in maize under both irrigated and rainfed conditions.

1. Introduction

Vegetation productivity is the basis of all the biosphere activities on the land surface that relate to global biogeochemical cycles of carbon and nitrogen (Dixon et al., 1994; Lieth and Whittaker, 1975; Myneni et al., 2001; Schimel, 1998). Gross primary production (GPP) is the rate at which an ecosystem captures and stores chemical energy. An accurate and synoptic quantification of spatially distributed carbon dioxide (CO₂) fluxes is essential for regional and global studies of carbon budgets. Agricultural crops, which are the most pervasive anthropogenic biome worldwide, play a significant role in the carbon exchange between the land and the atmosphere. In particular, the maize cropping systems, which dominate agricultural land use in the north-central USA, play an important role in the annual carbon exchange for this region.

Tower eddy covariance systems (e.g., Baldocchi, 2003) are often used to provide information on the seasonal and inter-annual dynamics of CO₂ fluxes in crops (e.g., Baker and Griffith, 2005; Hollinger et al., 2005; Verma et al., 2005). Using this technique, CO₂ fluxes can be measured with high temporal resolution, but over limited spatial footprints. Therefore, scaling up beyond these localized footprints is needed for assessments of regional and global carbon budgets. Such a process involves building an extensive infrastructure that can be costly and, in many cases, impractical. However, changes in CO₂ fluxes produce changes in vegetation biophysical characteristics, and they can be monitored by means of remote sensing. Thus, remote sensing is a viable and expedient tool to indirectly measure CO₂ fluxes through the estimation of gross primary production.

The objectives of this paper are to: 1) justify a new paradigm based on the assumption that the total chlorophyll content in a crop canopy is a main driver of GPP; and 2) test the performance of chlorophyll-related spectral vegetation indices for estimating total chlorophyll content in maize; and 3) assess the accuracy of GPP estimation using chlorophyll-related indices with specific attention given to rainfed crops associated with a significant deficiency of water availability. In Section 2 of the paper, we briefly present background information relating to the estimation of GPP in crops. In Section 3 we present and discuss the relationships involving total chlorophyll content in crops and both fraction of absorbed photosynthetically active radiation (fAPAR) and light use efficiency (LUE). This should serve to justify the paradigm. In Section 4, we presented methods and data used. In Section 5, we document the performance of chlorophyll related indices in estimating chlorophyll content and GPP.

2. Background

The carbon exchange between the crop canopy and the atmosphere is mainly controlled by the amount of solar radiation absorbed as well as the efficiency of the plants in using this energy for photosynthesis. The former is expressed as the product of the incident photosynthetically active radiation (PAR) and the fAPAR. The latter is LUE, which is the efficiency with which the absorbed PAR is converted into biomass. However, not all light absorbed by the canopy is used for photosynthesis.
Only the so-called ‘photosynthetic’ or ‘green’ part is absorbed by photosynthetically active vegetation. This component has been termed fAPAR\textsubscript{green} and defined as (Hall et al., 1992):

\[ f\text{APAR}_{\text{green}} = f\text{APAR} \times \left( \frac{\text{LAI}_{\text{green}}}{\text{total LAI}} \right) \]  

(1)

where LAI\textsubscript{green} is the green leaf area index, which is the photosynthetically functional component of the total LAI.

According to Monteith (1972, 1977), GPP can be expressed as:

\[ \text{GPP} = f\text{APAR}_{\text{green}} \times \text{PAR} \times \text{LUE} \]  

(2)

This equation provides the linkage between GPP and vegetation greenness and, thus, forms the basis for remote estimation of GPP via transforms of spectral reflectance, called vegetation indices (VIs). Biophysical characteristics of vegetation that relate to the amount of absorbed radiation, such as fAPAR\textsubscript{green} and/or green LAI, can be measured remotely, allowing one to quantitatively relate remotely sensed data to plant productivity. The procedures developed so far can be classified into two broad categories according to the way they model the absorption of solar radiation and its conversion into dry matter (e.g., Ruimy et al., 1999): 1) Production Efficiency Models (PEMs); and 2) Canopy Photosynthesis Models (CPMs).

In the case of PEMs, the fAPAR\textsubscript{green} is usually approximated by the Normalized Difference Vegetation Index, or NDVI (Rouse et al, 1974). LUE is commonly regarded as a constant, though biome-specific (e.g., Ruimy et al., 1999). The problems in using PEM's are, (a) a significant decrease in the sensitivity of NDVI to moderate-to-high vegetation density when fAPAR\textsubscript{green} exceeds 0.7 (e.g., Asrar et al., 1984; Gitelson et al., 2006b; Kanemasu, 1974; Viña and Gitelson, 2005), and (b) the species-specific rather than the merely biome-specific variation of LUE (e.g., Ahl et al., 2004). A certain variation of LUE is expected because GPP varies not only with absorbed PAR but also with other factors; e.g., soil water and nutrient availability, the ratio of direct to diffuse radiation, canopy age, and/or site history (Alton et al., 2007; DeLucia et al., 2007). LUE also varies considerably among vegetation types, in different phenological stages and under different environmental conditions such as stresses (Cower et al., 1999; Medlyn, 1998; Prince, 1991; Ruimy et al., 1994). Thus, there is little doubt overall 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). Recent analysis by Kergoat et al. (2008) strongly supports the view that LUE varies significantly not only both across and within biomes, but also among plant functional types.

The variations of LUE do need to be carefully considered, but a model that effectively accounts for the variations of LUE, resulting in a significant increase in the accuracy of GPP estimation, is yet to be developed. Many remote sensing models use look-up tables of maximum LUE for specific vegetation types. These values are then adjusted downward by considering environmental stress factors (Anderson et al., 2000; Ruimy et al., 1994; Running et al., 2004; Xiao et al., 2004; Yuan et al., 2007). Gamon et al. (1992) introduced the Photochemical Reflectance Index (PRI) and it was found that PRI can be used as a proxy of LUE at different scales from leaves to entire canopies (e.g., Garbulska et al., 2010). However, no significant improvement was observed by the use of PRI as an approximation of LUE for GPP estimation in crops compared with the use of a constant LUE (Gitelson et al., 2006b; Wu et al., 2010).

In the case of CPMs, GPP is first estimated at leaf level, and then integrated over the entire canopy. In these models, fAPAR\textsubscript{green} is expressed as a function of green LAI (e.g., Ruimy et al., 1999) in the form:

\[ f\text{APAR}_{\text{green}} = 0.95 \left( 1 - \exp \left( -k \times \text{LAI}_{\text{green}} \right) \right) \]  

(3)

where k is the coefficient of light extinction. The probability of interception of solar radiation is related to foliage orientation and density as well as the path length of light inside the canopy. So, the extinction coefficient is affected by many factors such as leaf structure and canopy architecture, both of which affect the rate and extent of the absorption of incoming radiation. Thus, the relationship fAPAR\textsubscript{green} vs. LAI\textsubscript{green} might be species specific and may vary even within a species, and the assumption that fAPAR is the radiometric equivalent of LAI is not valid in many cases.

A physically-based algorithm for estimating LAI from NDVI observations has been developed (e.g., Myneni et al., 1997). However, the relationship between NDVI and LAI\textsubscript{green} is essentially non-linear and suffers a rapid decrease of sensitivity at moderate-to-high densities of photosynthetic green biomass when LAI exceeds 3 (e.g., Asrar et al., 1984; Gitelson et al., 2003b; Kanemasu, 1974; Myneni et al., 1997).

3. Basic concept

3.1. The basis for using total crop chlorophyll content as a proxy of GPP

Since the early 1960's, scientists have looked for natural short-cuts to estimating productivity based on the biophysical characteristics of vegetation related to photosynthesis. Among them was the total chlorophyll content per unit area (e.g., Whittaker and Marks, 1975). It was shown that canopy chlorophyll is a very direct expression of the photosynthetic apparatus of a plant community, and it was found that for a given species or type of community, chlorophyll content may be strongly related to productivity. Medina and Lieth (1964) found a very close linear relationship between chlorophyll content and productivity (as indicated by the seasonal maximum biomass) with determination coefficient of $R^2>0.99$. Chlorophyll content per unit area has been correlated with crop productivity, net photosynthesis and absorbance (Osborne and Raven, 1986 and references within). Since long- or medium-term changes in canopy chlorophyll content are related to both crop phenology and photosynthetic capacity, and may also be affected by water and thermal stresses, (e.g., Ustin et al., 1998, Zarco-Tejada et al., 2002), the canopy chlorophyll content is related to GPP. Houborg et al. (submitted for publication) indicated significant potential for using remotely sensed leaf chlorophyll content for quantifying variability of photosynthetic efficiency across a heterogeneous corn field that was exposed to severe environmental stresses. Wu et al. (2009) found a close relationship between GPP and total chlorophyll content, with $R^2=0.87$, for wheat encompassing three classes of canopy leaf orientation (erectophile, spherical, and planophile).

At the leaf level, numerous studies have demonstrated a strong link between nitrogen content and photosynthesis (Field and Mooney, 1986; Wullschleger, 1993). Kergoat et al. (2008) analyzed the relationship between foliar nitrogen content and eddy covariance CO$_2$ flux measurements obtained at a range of diverse sites located in the mid to high latitudes, which encompass managed and unmanaged stands, mono- or pluri-specific canopies. They concluded that leaf nitrogen content is a strong factor influencing both optimum canopy LUE and canopy photosynthesis rate. On the other hand, Baret et al. (2007) found that canopy chlorophyll content is well suited for quantifying canopy level nitrogen content. They concluded that canopy chlorophyll content is a physically sound quantity since it represents the optical path in the canopy where absorption by chlorophyll dominates the radiometric signal. Thus, absorption by chlorophyll provides the necessary link between remote sensing observations and canopy state variables that are used as indicators of nitrogen status. A close relationship between contents of nitrogen and chlorophyll at canopy level rather than at leaf level was also clearly demonstrated in an experiment conducted over wheat crops subjected to a range of nitrogen stresses (Houle’s et al., 2006).
Recently, Gitelson et al. (2003b, 2006b) found a close, consistent relationship between GPP and total chlorophyll content in maize and soybean. Total chlorophyll content was defined as the product of leaf chlorophyll content and total leaf area index (Ciganda et al., 2009; Gitelson et al., 2005). Moreover, it was shown that despite great differences in leaf structure and canopy architecture in the C3 and C4 crops studied, the relationship GPP vs. chlorophyll content was not species specific.

Thus, total canopy chlorophyll content relates to both GPP and leaf nitrogen content, which, in turn, relate directly to photosynthesis. Therefore, this biophysical characteristic seems to be an accurate proxy of GPP in crops and can be employed for estimating GPP using vegetation indices related to canopy chlorophyll content.

3.2. Advantages of using chlorophyll-related indices for GPP estimation

The approach for estimating GPP via total chlorophyll content has advantages when used in both CPM and PEM models. In CPM models, the green LAI is used as a measure of the amount of radiation absorbed by the plants. However, a potential bias will be introduced when measuring the green LAI, because it is somewhat subjective to decide whether a leaf is green or non-green when crops are at either the reproductive or senescence stage (Ciganda et al., 2008). In practice, mature dark green leaves with high chlorophyll content during the green-up stage and leaves with much lower chlorophyll content during the reproductive and senescing stages are both designated as ‘green’ leaves (e.g., Law et al., 2008). For the same green LAI, the chlorophyll content in a leaf taken in the green-up stage might be more than two times higher than the chlorophyll content in a leaf taken in the reproductive and senescing stages (Fig. 1). Thus, the total chlorophyll content is a much more objective parameter than the green LAI in quantifying the amount of absorbed radiation. Therefore, the use of total canopy chlorophyll content instead of green LAI can decrease uncertainties in CPM models due to the bias involved in determining green LAI.

Total chlorophyll content is a main factor that influences the amount of PAR absorbed by photosynthetically active vegetation. It relates closely to fAPARgreen, which is used in PEM models (Fig. 2). But, as chlorophyll exceeds 2.3 g/m², the sensitivity of the relationship fAPARgreen vs. chlorophyll content drops drastically. Osborne and Raven (1986) noted that although proportional changes in light absorption will not occur at high chlorophyll content, they may be important in situations where low incident radiation severely limits photosynthesis, as may occur within crop canopies or in deep shade, or for shaded leaves of single plants. Importantly, contrary to the saturation evident in the fAPARgreen vs. chlorophyll content relationship, the GPP does remain sensitive to total chlorophyll content even when it exceeds 2.3 g/m² (in Fig. 3 it corresponds to Chl × PAR above 3.5E+04 g/m² × mmol/m²/d).

This behavior of the relationship between GPP and chlorophyll content may be explained by the increase in LUE that follows an increase in total chlorophyll content. Our data show that LUE does indeed relate to the chlorophyll content of a crop. The relationship LUE vs. chlorophyll content is based on the data collected in both irrigated and rainfed sites for different maize hybrids, phenological stages, environmental conditions, field management procedures, and growing situations (Fig. 4). The relationship is positive and statistically significant (R² = 0.46, P-value = 0.0078). One of the reasons for the close relationship LUE vs. chlorophyll content is the enhanced electron transport activity, which directly relates to chlorophyll content (Terry, 1980; Terry, 1983).

Thus, while the relationship fAPARgreen vs. chlorophyll content saturates at chlorophyll contents above 2.3 g/m² and the amount of radiation absorbed by the crop remains almost invariant at moderate-to-high levels of chlorophyll content, LUE increases; it results in an increase in GPP (Fig. 3). Our finding supports also the results obtained in several recent studies. Dawson et al. (2003) showed that the

![Fig. 1. Relationship between total chlorophyll content vs. green LAI. Mature dark green leaves with high chlorophyll content in the green-up stage (point a) and leaves with much lower chlorophyll in reproductive and senescing stages (point b) are both designated as 'green' leaves. Thus, for the same green leaf area index total chlorophyll content in maize may be significantly different.]

![Fig. 2. Fraction of PAR absorbed by photosynthetically active vegetation plotted versus total maize canopy chlorophyll content. When chlorophyll content exceeds 2.3 g/m², fAPARgreen virtually does not change with further increase in chlorophyll content.]

![Fig. 3. Gross primary production of rainfed and irrigated maize plotted versus the product of total crop chlorophyll content and incident PAR. Results of five years of observation at three test sites are presented.]

![Fig. 4. Relationship between LUE and total maize canopy chlorophyll content in maize and soybean. Total chlorophyll content is a main factor that influences the amount of PAR absorbed by photosynthetically active vegetation. It relates closely to fAPARgreen, which is used in PEM models (Fig. 2). But, as chlorophyll exceeds 2.3 g/m², the sensitivity of the relationship fAPARgreen vs. chlorophyll content drops drastically. Osborne and Raven (1986) noted that although proportional changes in light absorption will not occur at high chlorophyll content, they may be important in situations where low incident radiation severely limits photosynthesis, as may occur within crop canopies or in deep shade, or for shaded leaves of single plants. Importantly, contrary to the saturation evident in the fAPARgreen vs. chlorophyll content relationship, the GPP does remain sensitive to total chlorophyll content even when it exceeds 2.3 g/m² (in Fig. 3 it corresponds to Chl × PAR above 3.5E+04 g/m² × mmol/m²/d). This behavior of the relationship between GPP and chlorophyll content may be explained by the increase in LUE that follows an increase in total chlorophyll content. Our data show that LUE does indeed relate to the chlorophyll content of a crop. The relationship LUE vs. chlorophyll content is based on the data collected in both irrigated and rainfed sites for different maize hybrids, phenological stages, environmental conditions, field management procedures, and growing situations (Fig. 4). The relationship is positive and statistically significant (R² = 0.46, P-value = 0.0078). One of the reasons for the close relationship LUE vs. chlorophyll content is the enhanced electron transport activity, which directly relates to chlorophyll content (Terry, 1980; Terry, 1983). Thus, while the relationship fAPARgreen vs. chlorophyll content saturates at chlorophyll contents above 2.3 g/m² and the amount of radiation absorbed by the crop remains almost invariant at moderate-to-high levels of chlorophyll content, LUE increases; it results in an increase in GPP (Fig. 3). Our finding supports also the results obtained in several recent studies. Dawson et al. (2003) showed that the
variation in foliar chlorophyll content may account for some of the seasonal variability in LUE. Houborg et al. (submitted for publication) demonstrated that variations in leaf chlorophyll content were well-correlated with temporal changes in LUE. Kergoat et al. (2008) found that foliar nitrogen of the dominant plant species explained 71% of the variation in LUE.

Therefore, two key physiological properties included in Eq. (2), light capture and the efficiency of the use of absorbed light, relate closely to total canopy chlorophyll content, which subsumes a broad range of processes and can be applied as an integrative diagnostic tool. It means that chlorophyll content is relevant for estimating GPP in PEMs and CPMs. As a result, a procedure was suggested to remotely assess GPP in crops via estimation of total crop chlorophyll content, Chl, (Gitelson et al., 2006b). It takes the form:

$$GPP \propto \text{Chl} \times \frac{\text{PAR}_{\text{in}}}{\text{PAR}_{\text{out}}}$$  \hspace{1cm} (4)

4. Data and methods

In this study, we investigated the potential of the model (Eq. (4)) to estimate GPP in maize. We tested the performance of several widely used vegetation indices; namely, Simple Ratio (SR), Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index 2 (EV2), Wide Dynamic Range Vegetation Index (WDRVI), and green and red edge Chlorophyll Indices (CIgreen and CIred edge) for estimating GPP in maize. The work is based upon remotely sensed data taken in three rainfed and irrigated sites over a period of 8 years.

Data were collected from three AmeriFlux study sites located at the University of Nebraska–Lincoln Agricultural Research and Development Center near Mead, NE, USA. Sites 1 and 2 are 65-hectare fields equipped with center pivot irrigation systems. Site 3 is of approximately the same size, but relies entirely on rainfall. Site 1 has continuous cultivation of maize, while sites 2 and 3 have maize-soybean rotations (Table 1, http://publicornl.gov/ameriflux/site-select.cfm). Site 1 has been under no-till management until the harvest of 2005. Following the harvest in 2005, the conservation–plow tillage operation was initiated and followed from 2006 through 2008. Sites 2 and 3 have been under no-till management from 2001 until 2008.

4.1. CO2 fluxes, incoming PAR and fAPAR

The micrometeorological eddy covariance data used in this study were collected each year from 2001 through 2008. To have sufficient upwind fetch (in all directions), eddy covariance sensors were mounted at 3 m above the ground while the canopy was shorter than 1 m, and later moved to a height of 6.2 m until harvest (details are given in Verma et al., 2005). The study sites represented approximately 90%–95% of the flux footprint during daytime and 70–90% during nighttime (e.g., Schuepp et al., 1990). Daytime net ecosystem exchange (NEE) values were computed by integrating the hourly CO2 fluxes collected by the eddy covariance tower during a day when PARin exceeding 1 mmol/m2/d. Daytime estimates of ecosystem respiration (Re) were obtained from the night CO2 exchange and temperature relationship (e.g., Falge et al., 2002). The daytime GPP was then obtained by subtracting daytime respiration from NEE. This approach has been widely used in the context of tower flux measurements and is considered to provide reasonable estimates at the landscape level. Daily GPP was expressed as the integral of the organic matter in grams of carbon produced by all the individual plants through photosynthesis per meter square during a day (gC/m2/d).

Incoming Photosynthetically Active Radiation (PARin) was measured with point quantum sensors (LI-190, LI-COR Inc., Lincoln, NE) aimed upward, and placed 6 m above the surface. PAR reflected by the canopy and soil (PARout) was measured with Li-Cor point quantum sensors aimed downward, and placed at 6 m above the ground. PAR transmitted through the canopy (PARtransm) was measured with Li-Cor line quantum sensors placed at about 2 cm above the ground, pointing upward; PAR reflected by the soil (PARtransf) was measured with Li-Cor line quantum sensors placed about 12 cm above the ground, pointing downward. Absorbed PAR (APAR) was calculated as:

$$\text{APAR} = \text{PAR}_{\text{in}} - \text{PAR}_{\text{out}} - \text{PAR}_{\text{transm}} + \text{PAR}_{\text{soil}}$$  \hspace{1cm} (5)

All the daytime radiation values were computed by integrating the hourly measurements during a day, and fAPAR was then calculated as APAR/PARin.

4.2. Total and green LAI and total canopy chlorophyll content

Total canopy chlorophyll content, Chl, was estimated as Chl = Chl_{leaf} × LAI, where Chl_{leaf} is the chlorophyll content of the collar or ear leaves in maize (Ciganda et al., 2009; Gitelson et al., 2005). Leaf chlorophyll content was retrieved from leaf reflectance measured by an Ocean Optics radiometer using a red edge chlorophyll index (details are in Gitelson et al., 2003a, 2006a; Ciganda et al., 2009).

LAI was determined destructively. Within each study site, six small intensive measurement zones (IMZ) were established to represent all major occurrences of soil and crop production. On each sampling date, plants from a 1 m length of either of two rows were collected and the total number of plants recorded. Collection rows were alternated on successive dates to minimize edge effects on subsequent plant growth. Plants were kept on ice and transported to the laboratory. In the lab, plants were separated into green leaves, dead leaves, and litter components. Sample leaves were run through an area meter (Model LI-3100, Li-Cor, Inc., Lincoln NE) and the leaf area per plant was determined. For each IMZ, the leaf area per plant was multiplied by the plant population to obtain a total LAI. Total LAI for the six IMZs were then averaged to obtain a site-level value (details in Gitelson et al., 2003b). Green and dead leaves were separated and measured in
the same way to obtain the green and dead LAI. These LAI values were then linearly interpolated on a daily basis.

4.3. Canopy reflectance

Reflectance measurements were made using hyperspectral radiometers mounted on “Goliath”, an all-terrain sensor platform (Rundquist et al., 2004). 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. Radiometer 1, equipped with a 25° field-of-view optical fiber was pointed downward to measure the upwelling radiance of the crop. The position of the radiometer above the top of canopy was 5.4 m and kept constant throughout the growing season, yielding a sampling area with a diameter of around 2.4 m. Radiometer 2, equipped with an optical fiber and a cosine diffuser (yielding a hemispherical field of view), was pointed upward to simultaneously measure incident downwelling irradiance. In order to match the transfer functions of both radiometers, inter-calibration was accomplished by measuring the upwelling radiance of a white Spectralon® (Labshere, Inc., North Sutton, NH) reflectance standard simultaneously with incident downwelling irradiance.

Radiometric data were collected close to solar noon (between 11:00 and 13:00 local time), when changes in solar zenith angle were minimal. For each measurement site, six randomly selected plots were established per field, each with six randomly selected sampling points. Thus, a total of 36 points within these areas were sampled per site at each data acquisition, and their median was used as the site reflectance. Measurements took about 5 min per plot and about 30 min per field. The two radiometers were inter-calibrated immediately before and immediately after measurement in each field. Reflectance measurements were carried out during the growing season from May to October over the eight-year period. This resulted in 173 measurement campaigns (18 in 2001, 31 in 2002, 34 in 2003, 31 in 2004, 21 in 2005, 15 in 2006, 14 in 2007, and 9 in 2008).

4.4. Chlorophyll-related vegetation indices

Several remote sensing techniques have been proposed to estimate greenness/chlorophyll content of vegetation. NDVI was found to be a good indicator of low-to-moderate crop chlorophyll content. However, saturation of red reflectance and much higher NIR reflectance compared to red reflectance ($\rho_{\text{NIR}} \gg \rho_{\text{red}}$) at intermediate to high Chl content (e.g., Buschmann and Nagel, 1993; Gitelson, 2004; Kanemasu, 1974) limit the applicability of NDVI for estimating Chl content above 1 g/m² (Gitelson et al., 2005). It has been shown that reflectances in the green and the red edge regions are sensitive to a wide range of Chl content (Buschmann and Nagel, 1993; Chappelle et al., 1992; Gitelson et al., 1996; Lichtenhalter et al., 1996; Thomas and Gaussmann, 1977; Yoder and Waring, 1994). Several vegetation indices based on these spectral regions have been developed and used successfully to estimate Chl content (e.g., Broge and Mortensen, 2002; Dash and Curran, 2004; Gitelson, 2004; Gitelson et al., 2005; Huete et al., 1997; Jiang et al., 2008).

Huete et al. (1997) introduced the Enhanced Vegetation Index (EVI), which has a higher sensitivity to moderate-to-high vegetation biomass and is widely used as a product of the MODIS (MEdium Resolution Imaging Spectroradiometer) system. The EVI was shown to be much more accurate than NDVI in estimating GPP for different vegetation types, including crops (e.g., Sims et al., 2006; Xiao et al., 2004). EVI2 (Jiang et al., 2008) containing only the red and NIR bands was formulated in the form:

$$\text{EVI2} = 2.5 \times \frac{(\rho_{\text{NIR}} - \rho_{\text{red}})}{(1 + \rho_{\text{NIR}} + 2.4 \times \rho_{\text{red}})}$$

$$\text{WDRVI} = (\alpha \times \rho_{\text{NIR}} - \rho_{\text{red}}) / (\alpha \times \rho_{\text{NIR}} + \rho_{\text{red}})$$

The weighting coefficient $\alpha$ (0 < $\alpha$ < 1) is introduced to attenuate the contribution of the NIR reflectance at moderate-to-high green biomass, and to make it comparable to that of the red reflectance (Gitelson, 2004; Viña et al., 2004).

Recently, a conceptual model that relates reflectance with pigment content (chlorophyll, carotenoids, and anthocyanins) in leaves and chlorophyll content in maize and soybean canopy (Gitelson et al., 2003a) was developed in the form:

$$\text{Pigment content} = \alpha (\rho(\lambda_1)^{-1} - \rho(\lambda_2)^{-1}) \times \rho(\lambda_3)$$

Special cases of the conceptual model for estimating particular pigment contents are achieved by appropriately choosing the locations of the wavelengths in the model, based on the optical characteristics of the object containing the pigment of interest. For estimating total canopy chlorophyll content in maize and soybean, based on their optical characteristics, the optimal location for $\lambda_1$ was either in the green (540–560 nm) or red edge (700–730 nm); $\lambda_2 = \lambda_3$ was optimally located in the NIR region beyond 750 nm (Gitelson et al., 2005). Thus the Chlorophyll Indices, CI, for estimating total canopy chlorophyll content were suggested in the form:

$$\text{Cl}_{\text{green}} = \rho_{\text{NIR}} / \rho_{\text{green}} - 1$$

$$\text{Cl}_{\text{red edge}} = \rho_{\text{NIR}} / \rho_{\text{red edge}} - 1$$

In this study, we compared the performances of several chlorophyll related vegetation indices for GPP estimation. In addition to EVI2, WDRVI with $\alpha = 0.1$, CIgreen and CIred edge, the widely used Simple Ratio (SR) and NDVI were also tested.

Simple ratio (Jordan, 1969):

$$\text{SR} = \rho_{\text{NIR}} / \rho_{\text{red}}$$

Normalized Difference Vegetation Index (Rouse et al., 1974):

$$\text{NDVI} = (\rho_{\text{NIR}} - \rho_{\text{red}}) / (\rho_{\text{NIR}} + \rho_{\text{red}})$$

The collected reflectance spectra were resampled to the following spectral bands of Landsat: red (630–690 nm), green (520–600 nm), NIR (760–900 nm), and red edge band (703–713 nm) of MERIS (MEdium Resolution Imaging Spectrometer) using the spectral response functions of ETM Landsat and MERIS to calculate the above mentioned vegetation indexes.

5. Results and discussion

GPP followed seasonal change in chlorophyll content. The temporal behavior of canopy chlorophyll content and GPP were very similar (Fig. 5). Thus, the total chlorophyll content for maize seems to be a good proxy of GPP. The next step was to compare the performances of several widely used vegetation indices for estimating total chlorophyll content (Fig. 6). NDVI was very sensitive to chlorophyll content below 1.5 g/m² and lost sensitivity to chlorophyll content above 2 g/m². EVI2 and WDRVI with $\alpha = 0.1$ were much more sensitive than NDVI to moderate to high chlorophyll contents, and exhibited non-linear relationships. SR, CIgreen and CIred edge were linearly related to chlorophyll content, remaining sensitive to the wide range of chlorophyll content. However, the relationship of SR with chlorophyll content was less close than that of Clgreen and Clred edge due to the very low values of red reflectance (not exceeding 2–3%).
Fig. 5. Temporal behavior of total canopy chlorophyll content and GPP in maize during the growing seasons 2001 through 2005.

\[ y = 0.92 - \frac{10.2}{1 + e^{(x + 2.74)/1.04}} \]
\[ R^2 = 0.92 \]

Fig. 6. Relationship between total chlorophyll content and (a) NDVI, (b) WDRVI with \( \alpha = 0.1 \), (c) EVI2, (d) SR, (e) CI\text{green} and (f) CI\text{red edge}.

\[ y = 0.63 - 1.43 \times 0.66^x \]
\[ R^2 = 0.92 \]

\[ y = 0.43 \times 0.43 \]
\[ R^2 = 0.90 \]

\[ y = 5.29x + 0.41 \]
\[ R^2 = 0.87 \]

\[ y = 2.31x + 1.29 \]
\[ R^2 = 0.92 \]

\[ y = 2.08x + 0.19 \]
\[ R^2 = 0.92 \]
in maize with moderate to high chlorophyll content. The use of a low value of the red reflectance in the denominator makes SR quite noisy.

The CIgreen index (Eq. (9)) was related closely to maize GPP, as it changed in accord with the growing season cycle (Fig. 7a). Low frequency variations in GPP responded mainly to changes in canopy phenological and physiological status, which are closely related to canopy chlorophyll content and, thus, to CIgreen. However, there is another type of GPP variation, which occurs at a much higher frequency, and it is caused by the variation of incoming PAR. Under overcast conditions and associated low values of PARin, the crop absorbed less incoming light, thus resulting in less production. Moreover, there is a significant decline in PARin beyond the 200th day of year (DOY), which leads to a decline in production and is the cause of the discrepancy between CIgreen and GPP for DOY > 200 (Fig. 7a). Thus, while the vegetation index (VI) alone responds well to low frequency GPP variations, it does not capture GPP variations that are caused by changes in the high frequency of PARin variation, which do not produce an immediate direct change in Chl content, as well as in low frequency of PARin variation which occurs after DOY 200. The product of VI and the incoming PAR, in accord with Eq 4, relates more closely to GPP than does the VI alone because it accounts for the modulation of GPP by changes in radiation conditions (Fig. 7b).

To study how the model (Eq. (4)) works in estimating GPP by different VIs in each site from 2001 through 2008 (12 site-years all together), we established quadratic polynomial relationships between daytime GPP and the product VI×PARin for six vegetation indices (SR, NDVI, EVI2, WDRVI with α = 0.1, CIgreen, and CIred edge). Table 2 summarizes the root mean square error (RMSE) and the coefficients of variation (CV=RMSE/mean GPP) of these relationships, as well as minimum, maximum, and median GPP values in each site and year.

Daytime GPP measured in the growing season varied widely, ranging from 0 to 35 gC/m²/d. For each site from 2001 through 2008, NDVI was consistently less accurate as a GPP predictor with the mean CV>25%, and it was saturated as GPP exceeded 15 gC/m²/d. The last row in Table 2 shows mean values of the coefficient of variation for each index, which are quite informative for comparing the performances among indices regardless of the different dynamic ranges of GPP. Overall, CI and SR were the most accurate in GPP estimation except for site 3 in 2001 and site 1 in 2002 where EVI2 performed the best. The same pattern of VI performance was found for the estimation of total crop chlorophyll content (Fig. 6). Therefore, the indices that are the most accurate in estimating crop chlorophyll content are likely to work the best for GPP estimation.

From 2006 through 2008, in site 1 the conservation-plow tillage operation was initiated while site 2 was under no-till management. The reflectance of residue was much higher than that of bare soil; thus, in 2006 through 2008, soil reflectance in site 1 was significantly lower than that in site 2. Another difference between sites 1 and 2 was a difference in maize hybrids planted from year to year (Table 1, see also Suyker and Verma, 2010). These differences may affect the relationship between GPP and chlorophyll content. To answer the question as to whether the relationship, GPP vs. VI×PARin, is statistically significantly different for sites 1 and 2, we applied an F-test comparing two groups of datasets: site 1 (all measurements taken from 2001 to 2008) and site 2 (all measurements taken in 2001, 2003, 2005, and 2007). We found no statistically significant difference between the two irrigated sites for all vegetation indices (P-value was 0.2 for NDVI, 0.03 for EVI2, 0.45 for WDRVI, 0.12 for CIgreen, 0.06 for CIred edge, and 0.1 for SR). This means that differences in management practices between the two sites, soil reflectance and the maize hybrids planted did not affect the relationship, GPP vs. chlorophyll content, and the model does not need re-parameterization for GPP estimation in irrigated sites.

Site 3 relies entirely on rainfall and is under maize-soybean rotation and no-till management. Importantly, the density of planting in sites 1 and 2 was approximately 80,000 to 85,000 plants per hectare, while only 60,000 to 65,000 plants per hectare in site 3 (at least 25% lower). To understand how this factor affects the relationship, GPP vs. VI×PARin, we compared two datasets: (1) irrigated sites with higher density of planting (site 1 — 2001 through 2008 and site 2 — 2001, 2003, 2005, and 2007) and (2) rainfed sites with lower density of planting (site 3 — 2001, 2003, 2005, and 2007). We did find a statistically significant difference in the relationship between sites with all VIs except NDVI (P-value was 0.84 for NDVI, 0.0033 for EVI2, 0.0007 for WDRVI, 0.12 for CIgreen, 0.06 for CIred edge, and 0.1 for SR). A rather wide scattering of points in the relationship NDVI×PARin vs. GPP makes it impossible to distinguish between irrigated and rainfed sites. For other indices tested, the slopes of the VI×PARin vs. GPP relationships for irrigated sites were consistently higher than those for rainfed sites (Fig. 8 for CIgreen and CIred edge). The reason for this difference is likely the variable planting densities, because the distance between plants affects the fAPAR value. For the same VI×PARin (i.e., total chlorophyll content), GPP was higher in rainfed site 3 than in the more densely planted sites 1 and 2. So, in crops with the same total chlorophyll content and similar PARin, more light was absorbed and used for photosynthesis by the sparsely distributed plants in site 3 than the densely distributed plants in sites 1 and 2. In other words, maize planted at a low density can produce more GPP per total chlorophyll content than maize planted at a high density due to the availability of more open area for absorbing light as well as the higher efficiency of light absorption in sparse vegetation than in dense vegetation. So, specific absorption (fAPAR/chlorophyll) is higher in sparse vegetation than in dense vegetation.

In odd years (2001, 2003, 2005 and 2007), all three sites were planted with maize. In these years, sites 1 and 2 were irrigated while site 3 relied entirely on rainfall. Irrigation provided about 40-50% of the total water received by maize (Suyker and Verma, 2010). Among these four years of observation, two years (2003 and 2005) were

Fig. 7. Temporal change in (a) GPP, the CIgreen and incident PAR and (b) GPP and product of CIgreen and incident PAR (CIgreen×PARin) for maize in the growing season of 2004.
especially dry with annual precipitation 25.6 and 23.9 inches compared to the 40.4 inches in 2007, a "normal" year. The rainfall obviously affected soil moisture and grain yield at the rainfed site. During dry periods over the rainfed site in 2003, soil moisture at 10 cm depth dropped more than 40% compared to that in the irrigated site. Obviously affected soil moisture and grain yield at the rainfed site.

Table 2

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<th>Year</th>
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<th>WDRVI</th>
<th>EVI2</th>
<th>SR</th>
<th>CIgreen</th>
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Fig. 8. Best fit functions of the relationships between daytime gross primary production and (a) CIgreen×PARin and (b) CIred edge×PARin. Solid line: 12 irrigated sites in 2001 through 2008, dotted line: 4 rainfed sites in 2002, 2004, 2006 and 2008.
at the three sites and the daytime GPP measured on the same days when the reflectance was measured (314 samples altogether) were sorted in ascending order of GPP. Samples with odd numbers (157 samples) were used for algorithm calibration, and samples with even numbers (157 samples) were used for algorithm validation. To exclude outliers in the calibration data set, which may significantly affect the accuracy of the algorithms, all samples for which the deviation from the best fit function exceeded two standard deviations were removed (e.g., Zibordi et al., 2004). There were 5 such outliers for NDVI, 9 for WDRVI, 6 for EVI2, and 7 for SR and CIs. Then the relationships, GPP vs. VI×PARin, were established (Table 3).

All established relationships of GPP vs. VI×PARin were non-linear, except for NDVI (Table 3). All VIs, except NDVI, displayed increased sensitivity to moderate-to-high GPP. Very importantly, the relationship, GPP vs. VI×PARin, followed the same pattern as GPP vs. Chl×PARin, with increasing sensitivity of chlorophyll content to GPP above 15 gC/m²/d (Fig. 3). It means that SR, EVI2, WDRVI with α = 0.1 and both CIs were accurate proxies of total chlorophyll content. The ratio indices, SR and CIs, which were closely related to chlorophyll content (Fig. 6), also were more accurate in estimating day time GPP.

Measured reflectances in the validation dataset were used to predict GPP values (GPPpred) in the validation data set. Then GPPpred values were compared with GPP, as measured by the eddy covariance technique (GPPmeas), in the validation dataset. Table 4 shows the accuracy of GPP prediction by the established relationships summarized in Table 3. CIs and SR were the best GPP predictors among the vegetation indices tested, with the lowest values of RMSE. The comparison of GPP predicted by CIs with GPP measured by the eddy covariance technique (GPPmeas), shown in Fig. 11, demonstrates that CIs provided a good approximation of GPP in maize. Furthermore, chlorophyll-related indices were also superior in estimating GPP in wheat (Wu et al., 2009) and in a number of AmeriFlux test sites (Harris and Dash, 2010). The first results of GPP estimation in crops using Landsat data were also very promising (Gitelson et al., 2008), confirming the validity of GPP estimation via vegetation indices related to chlorophyll content.

However, the model (Eq. (4)) would be inadequate for the estimation of GPP in shorter time steps due to the inability to track short-term (e.g., diurnal) physiological variability that does not affect chlorophyll content. Consequently, the effect of short term stresses on total cumulative GPP in crops remains unclear and it is necessary to investigate how much such stresses affect the crop carbon budget.

To track both short term and long term changes in GPP, estimation of LUE is needed. Different approaches have arisen recently to remotely estimate LUE from a wide variety of wavelengths and sensor types. Among those approaches, the use of PRI (Gamon et al., 1992) as well as the use of climatic variables, like vapor pressure deficit,

![Figure 9](image_url) GPP (a) and CIred edge × PARin (b) in three sites in 2003. Sites 1 and 2 were irrigated and site 3 relied entirely on rainfall. The model (Eq. (4)) was sensitive not only to the difference in GPP between irrigated and rainfed sites but also to small differences between GPP in irrigated continuous maze (site 1) and irrigated maize–soybean rotation (site 2).

![Figure 10](image_url) Relationship between daytime gross primary production and CIgreen × PARin (a) and CIred edge × PARin (b) for all three sites from 2001 to 2008. The solid line is the best fit function; the dashed lines represent the 95% confidence interval (i.e., two standard errors of GPP estimation).

<table>
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<th>VIs</th>
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<th>R²</th>
<th>RMSE, gC/m²/d</th>
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<td>3.36</td>
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<tr>
<td>WDRVI</td>
<td>GPP = 5E – 08 x² + 0.0013 x + 10.23</td>
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<td>2.76</td>
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<tr>
<td>EVI2</td>
<td>GPP = –1E – 07 x³ + 0.0039 x – 3.86</td>
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<td>2.75</td>
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<tr>
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<tr>
<td>CIgreen</td>
<td>GPP = –154 + 14.7 ln(x + 27900.61)</td>
<td>0.92</td>
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<tr>
<td>CIred edge</td>
<td>GPP = –121 + 12.42 ln(x + 16082.91)</td>
<td>0.93</td>
<td>2.12</td>
</tr>
</tbody>
</table>

Table 3 The results of algorithm calibration for estimating daytime gross primary production in 16 irrigated and rainfed maize sites in 2001 through 2008. Best fit functions, determination coefficients (R²) and root mean square errors (RMSE) of GPP estimation are given for six vegetation indices.
temperature, and water indices as surrogates for photosynthetic stresses (Running et al., 2004; Sims et al., 2008; Xiao et al., 2004) are widely employed. Because vapor pressure deficit, temperature and land surface water index are not always good surrogates of reduced efficiency, meteorologically based methods may not always explain efficiency variation (Garbulsky et al., 2010). While land surface temperature derived from thermal wavelengths (Sims et al., 2008) and the Vegetation Photosynthesis Model (Xiao et al., 2004) were successfully tested to estimate 16-day GPP from MODIS data, it would be inadequate, as a chlorophyll model (Eq. (4)), to track short-term physiological variability.

A recent review by Garbulsky et al. (2010) examined and synthesized the scientific literature on the relationships between PRI and several ecophysiological variables across a range of plant functional types and ecosystems at the leaf, canopy and ecosystem levels and at the daily and seasonal time scales. The authors demonstrated a consistency of the LUE–PRI relationship that suggests a surprising degree of functional convergence of biochemical, physiological and structural components affecting leaf, canopy and ecosystem carbon uptake efficiencies. It is underlined that PRI provides a useful index of seasonal carbon fluxes in evergreen plants because of its connection with LUE, whereas fAPAR as well as greenness (i.e., chlorophyll content) would presumably be less useful in this context since they change little over seasonal time scales. On the contrary, PRI may not be effective in detecting GPP in ecosystems where chlorophyll content closely follows the seasonal dynamic of CO₂ exchange. This seems to be the case in croplands, deciduous forests and grasslands. In those ecosystems, fAPAR and LUE scale well with photosynthetic rates and chlorophyll content is closely tied to seasonal carbon dynamics and thus provides a dominant indicator of ecosystem CO₂ uptake. The same probably is the case for the use of air temperature and water indices as input data to calculate LUE. As our study showed, change in chlorophyll content is the main driver of seasonal changes in crop GPP. A study is underway to assess the contribution of temperature and water content to the total CO₂ crop budget.

6. Conclusion

We showed that two key physiological properties, light capture and the efficiency of the use of absorbed light, relate closely to total maize chlorophyll content, which subsumes a broad range of processes and can be applied as an integrative diagnostic tool. Maize GPP is clearly and closely related to total canopy chlorophyll content. As a result, a procedure was suggested to remotely assess GPP in maize via estimation of total crop chlorophyll content employing vegetation indices related to canopy chlorophyll content. We justified and tested a simple model that relates GPP to a product of chlorophyll-related vegetation indices and incident PAR. The results demonstrate that this model is capable of accurately estimating GPP in maize, from both irrigated and rainfed fields. Among the vegetation indices tested, the chlorophyll indices and simple ratio appear to be the best approximations of GPP. The vegetation indices tested were calculated with reflectances simulated in the spectral bands of the Landsat and MERIS sensors. At minimum, the result provides a conceptual background for GPP estimation using real satellite data.

The choice of the index depends on the spectral characteristics of the radiometer or the specific satellite sensor being used. The CIred edge can be used for satellite systems with spectral bands in the red edge region (e.g., MERIS and Hyperion), while the CIgreen can be used in satellite systems with spectral bands in the green region (e.g., Landsat, Hyperion, 500 m and 1 km resolution MODIS, and MERIS). The EVI2, SR, and WDRVI, employing only two spectral bands, the red and NIR, can be used for crop monitoring by satellites such as AVHRR, Landsat, 250 m MODIS, and MERIS. The implications of our findings are far-reaching since the described techniques open a new possibility for an accurate estimation of crop GPP at different scales, from close-range to satellites latitude. Some of the techniques based on the red, and NIR bands allow using the extensive archive of Landsat and AVHRR imagery, acquired since the early 1970s, and the 250 m resolution MODIS imagery acquired since 2001. With these techniques, it is now possible to obtain global synoptic estimates of crop gross primary production at the 30 m spatial resolution of Landsat TM and ETM+ and the 250–300 m resolution of MODIS and MERIS.

Acknowledgments

This research was supported partially by the U.S. Department of Energy EPSCoR program, Grant Office of Science (BER), as well as the NASA NACP and NASA EPSCoR “Aerial” grant and the Nebraska Space Grant program. We acknowledge the support and the use of facilities and equipment provided by the Center for Advanced Land Management Information Technologies (CALMIT), and Carbon Sequestration Program, University of Nebraska-Lincoln. We are grateful to Shashi B. Verma and

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**Table 4**
The results of validation of algorithms in estimating daytime gross primary production in 16 irrigated and rainfed maize sites in 2001 through 2008. Slope and offset of linear relationships between predicted by algorithms (Table 3) and measured daytime GPP, and root mean square error (RMSE) are given for six vegetation indices.

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**Fig. 11.** Validation of algorithms in predicting daytime GPP in 16 irrigated and rainfed maize sites in 2001 through 2008: (a) green chlorophyll index (CIgreen) and (b) red edge chlorophyll index (CIred edge).
Andrew E. Suyker for providing data on GPP and Anthony Lawrence Nguy-Robertson for fruitful discussion and suggestions. This research was also supported in part by funds provided through the Hatch Act.

References


