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

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## ARTICLE INFO

## ABSTRACT

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

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## 1. Introduction

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

2014; Osada et al., 2014) at multiple scales, from individual leaves to entire canopies (Field et al., 1995; Goetz and Prince, 1999). Many of these studies analyze the patterns of individual components in isolation, while fewer evaluate the combination of a limited number of components for assessing synergistic relations and trade-offs (Karlsson, 1994; Herppich et al., 2002; Ali et al., 2012; Xu et al., 2013). However, a thorough understanding of the processes behind these optimization patterns is still elusive, mainly due to limitations in the scaling of photosynthesis models from individual leaves to entire canopies (Kull, 2002; Niinemets and Anten, 2009), as well as trade-offs in the use of different resources that may prevent plants from optimizing their efficiencies of use simultaneously (Hirose and Bazzaz, 1998).

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

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

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

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

## 2. Concept of chlorophyll efficiency

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

$$GPP = (fAPAR_{green} \times PAR_{in}) \times LUE \tag{1}$$

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

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

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

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

$$GPP = F(Chl \times PAR_{in}) \tag{2}$$

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

$$ChlE = GPP/(PAR_{in} \times Chl) \tag{3}$$

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

$$ChlE = (fAPAR_{green}/Chl) \times LUE \tag{4}$$

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

## 3. Methods

### 3.1. Study area

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

### 3.2. GPP measurements

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