



The need for a common basis for defining light-use efficiency: Implications for productivity estimation



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ABSTRACT

A primary focus of this short communication is to show how the operational definition of light use efficiency (LUE) influences the results and interpretation of the LUE model. Our study was motivated by the observation that multiple LUE definitions are reported in the literature. The temporal behavior of three operational definitions of LUE, based on (i) incident radiation, (ii) total absorbed radiation and (iii) radiation absorbed by photosynthetically active/green vegetation was examined for two contrasting crops (soybean and maize) having different physiologies, leaf structures and canopy architectures. Over the course of a growing season, the behavior of these three contrasting LUE definitions was strikingly dissimilar, and the degree of dissimilarity varied with contrasting crops (corn and soybean). This demonstrates that LUE model behavior would vary strongly with the LUE definition used, with resulting implications both for the estimated seasonal productivity, and for the interpretation of the underlying mechanism. Based on these findings, we recommend a standard definition of the LUE model based on radiation absorbed by green vegetation. We also discuss the practical and theoretical implications of using this simple conceptual model on a dynamic biological system.

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1. Introduction

The LUE model originated with the work of Monteith (1972, 1977), and has since been adopted by many in the remote sensing and carbon flux communities. While it can be viewed as a conceptual model, the LUE model can also be expressed in explicit, mechanistic terms, based on the underlying physical and physiological processes of light absorption and conversion. Conceptually, the amount of photosynthesis or primary production is largely determined by the amount of photosynthetically active radiation (PAR) absorbed by vegetation (APAR). This is further modified by the efficiency with which this absorbed light is converted to fixed carbon, light use efficiency (LUE). Loosely speaking, the absorbed radiation relates to vegetation structure and pigment pools, and the efficiency term relates to physiology. In reality, the absorption and efficiency terms can be confounded to varying degrees depending on the underlying dynamic biological processes, and on the exact operational definition of APAR and LUE.

Mechanistically, the APAR term is affected by a number of factors that include PAR irradiance, canopy structure and photosynthetic pigment content, including leaf area index (LAI), leaf angle distribution, and PAR absorptance. This absorption term tends to vary slowly over

long (seasonal) time spans and is affected by the growth and senescence of vegetation, and can also be influenced over the short term (e.g. diurnally) via changing leaf display in the case of plants exhibiting leaf movement, leaf wilting, or chloroplast movement (Björkman & Demmig-Adams, 1994). The efficiency term is affected by a number of processes that affect the energy distribution within the photosynthetic system, ranging from pigment composition (chlorophyll and carotenoid content, and the relative levels of xanthophyll cycle pigments), to enzyme kinetics (e.g. xanthophyll cycle de-epoxidase) (Björkman & Demmig-Adams, 1994; Gamon & Qiu, 1999). Together, these comprise the physiological response, which varies dynamically over short (diurnal) and long (seasonal) time scales, based on changing environmental conditions and ontogeny.

While we often think of APAR and LUE as distinct aspects of the model operating over different time scales, they are also linked in several ways, and this relationship may vary with the exact definitions used and the dynamics of changing structure and physiological state as a plant grows. The underlying explanation for this linkage lies in the tendency for plants to follow coherent rules of resource acquisition and distribution. For example, nitrogen constraints not only limit photosynthetic physiology, but also ultimately limit plant growth, resulting in coherence between plant physiological performance (affecting LUE) as well as leaf and plant structure and pigment content (affecting light absorption). This coordinated response, has been called *functional*

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convergence, provides a useful framework for understanding plant optical behavior (Field, 1991; Ollinger, 2010). The beauty of the LUE model is that it can be parameterized with metrics that are widely available from remote sensing and other sources (e.g. meteorological stations). The challenge is that the measurements can only approximate the complex and dynamic system that they are meant to represent.

One of the difficulties of the LUE model is that various operational definitions exist for its component terms. For example, the APAR term can be measured on the basis of incident irradiance, absorbed irradiance, or the irradiance absorbed only by green (photosynthetically active) vegetation. This variation typically results from the different measurement approaches at different sites, which range from simple PAR irradiance (PPFD), to total PAR absorbed ($PPFD \times fPAR$), to PAR absorbed by green vegetation ($PPFD \times fPAR_{green}$). Similarly, LUE has been defined in the plant physiological literature as the initial slope (quantum yield) of the light response curve (Björkman, 1981), whereas in remote sensing literature as the carbon uptake (variously defined as the photosynthetic rate, the gross primary production, GPP, or the net primary production, NPP) divided by the irradiance (variously defined as one of the three ways described above). Additionally, while some models infer a constant LUE for all vegetation (Myneni, Los, & Asrar, 1995), some vary the LUE based on an assumed (fixed) LUE value for each vegetation type (Ruimy, Saugier, & Dedieu, 1994), and others allow LUE to vary dynamically with vegetation type and stress level as affected by internal or external (environmental) factors (Potter et al., 1993; Prince & Goward, 1995; Running et al. 2004). These differences are often defined by operational challenges that force the usage of a particular tractable definition, regardless of whether that definition is theoretically optimal.

Here we argue that the lack of standard definitions limits our understanding of mechanism, and confounds comparative analyses (meta-analyses) across studies and ecosystems. We discuss the implications of various LUE definitions and present recommendations emerging from this analysis.

There are at least three commonly used definitions of photosynthetically LUE based on: (a) incident radiation (LUE_{inc}); (b) total absorbed light (LUE_{total}); and (c) radiation absorbed by photosynthetically active vegetation (LUE_{green}) (e.g., Garbulsky, Peñuelas, Papale, et al., 2010; Hall, Huemmrich, Goetz, Sellers, & Nickeson, 1992; Lindquist, Arkebauer, Walters, Cassman, & Dobermann, 2005; Nichol et al., 2000; Norman & Arkebauer, 1991; Suyker et al., 2004). Consequently, LUE values reported do not have a common basis, bringing confusion and limiting the utility of reported LUE values for comparative analyses. Not surprisingly, the value of LUE reported in the literature varies by a factor of three (Garbulsky, Peñuelas, Gamon, Inoue, & Filella, 2010; Nichol et al., 2000; Norman & Arkebauer, 1991; Peng, Gitelson, Keydan, Rundquist, & Moses, 2011; Rosati & Dejong, 2003; Suyker et al., 2004). Similarly, the Photochemical Reflectance Index (PRI), which is sometimes considered as a proxy of LUE (Gamon, Penuelas, & Field, 1992), has different operational definitions, resulting in a wide range of reported values for comparable conditions (Garbulsky, Peñuelas, Gamon, et al., 2010). This is further confounded by variation in the responses of optical sensors from different instruments and manufacturers; true standards in instrumentation are lacking (Balzarolo et al., 2010; Gamon, Rahman, Dungan, Schildhauer, & Huemmrich, 2006; Gamon et al., 2010).

The initial objective of this short communication was to investigate the seasonal behavior of each definition of LUE in two contrasting crops (soybean, a C3 species; and maize, a C4 species) having different physiologies, leaf structures and canopy architectures. In both crops, green leaf area index (LAI) was closely tied to the seasonal dynamics of gross primary production (GPP), providing a simple experiment examining how the behavior of the LUE model varied depending upon how the APAR and LUE terms were defined. Consequently, a primary focus was the effect of the operational definition of LUE on the results and interpretation of the LUE model. In particular, we examined the consequences of incorporating canopy structure (and green canopy

structure) into the APAR term for the behavior of both APAR and LUE. We then discuss the practical and theoretical implications of using these different versions of this simple conceptual model on a dynamic biological system. The ultimate goal of this analysis is to draw attention to the need for standard operational definitions within the remote sensing community when using the LUE model.

2. Methods

The study took place during the growing seasons of 2001 to 2008 at a University of Nebraska-Lincoln research facility located 58 km northeast of Lincoln NE, U.S.A., and consisted of three agricultural sites; the first two were 65-ha fields equipped with center pivot irrigation systems. The third site was of approximately the same size, but relied entirely on rainfall. Site 1 was under continuous maize, while sites 2 and 3 had been under maize–soybean rotation. Soils of the study area are deep silty clay loam (Suyker et al., 2004).

Each study site was equipped with an eddy covariance tower and meteorological sensors, with which the continuous measurements of CO_2 fluxes, water vapor and energy fluxes were obtained every hour. Daytime net ecosystem exchange (NEE) values were computed by integrating the hourly CO_2 fluxes collected during a day when PAR_{in} exceeded $10^{-3} MJ/m^2/s$. Daytime estimates of ecosystem respiration (Re) were obtained from the night CO_2 exchange–temperature relationship (e.g., Xu & Baldocchi, 2003). The GPP was then obtained by subtracting Re from NEE as: $GPP = NEE - Re$. Daily GPP values were presented in the units of $gC/m^2/d$, and the sign convention used here was such that CO_2 flux to the surface was positive so that GPP was always positive and Re was always negative (details are in Verma et al., 2005).

Daily measurements of photosynthetically active radiation (PAR) were obtained using the following procedures: incoming PAR (PAR_{inc}) was measured with point quantum sensors (190-SB LI-COR, Lincoln, NE) pointing to the sky, and placed at 6 m from the ground. PAR reflected by the canopy and soil (PAR_{out}) was measured with the LI-COR point quantum sensors pointing down, and placed at 6 m above the ground. PAR transmitted through the canopy (PAR_{transm}) was measured with line quantum sensors (LI-191, LI-COR, Lincoln, NE) placed at about 2 cm above the ground, looking upward. PAR reflected by the soil (PAR_{soil}) was measured with LI-COR line quantum sensors placed about 12 cm above the ground, looking downward (details by Hanan et al., 2002; Burba, 2005). Daily absorbed PAR (APAR) was computed by integrating the hourly PAR values collected during a day when PAR_{in} exceeded $10^{-3} MJ/m^2/d$ and calculated as (Goward & Huemmrich, 1992):

$$APAR = PAR_{inc} - PAR_{out} - PAR_{transm} + PAR_{soil}$$

$fAPAR$ was calculated as $APAR/PAR_{inc}$.

To obtain a measure of the $fAPAR$ absorbed only by the photosynthetic component of the vegetation, we calculated $fAPAR_{green} = fAPAR \times (green\ LAI/total\ LAI)$ (sensu Hall et al., 1992; Hanan et al., 2002).

Within each of the study sites, six small (20 m × 20 m) plot areas were established for detailed process-level studies. These intensive measurement zones (IMZ) represented all major occurrences of soil and crop production zones within each site. Plant populations were determined (by counting plants) for each IMZ. On each sampling date, plants from a 1 m length of either of two rows within each IMZ were collected and total number of plants recorded. Collection rows were alternated on successive dates to minimize edge effects on subsequent plant growth. Plants were transported on ice to the laboratory. In the lab, plants were dissected into green leaves, dead leaves, stems, and reproductive organs. The green 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 green leaf area per plant was

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