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Application of the photosynthetic light-use efficiency model in a northern Great Plains grassland

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ABSTRACT

The light-use efficiency (LUE) model of photosynthesis is widely used to estimate ecosystem photosynthesis and net primary production from remote sensing measurements. The fraction of absorbed photosynthetically active radiation (f_{APAR}) is a dominant term in this model, and it is fundamentally important for model calculations of ecosystem productivity across large areas. The LUE term is sometimes considered a constant, but may be best represented as a variable scalar under stress conditions. The main objective of this study was to better understand factors influencing f_{APAR}, its relationship with seasonal variation in canopy greenness (Normalized Difference Vegetation Index (NDVI)), and the consequences of potential seasonal changes in the NDVI-f_{APAR} relationship for LUE model calculations of ecosystem photosynthesis in a semi-arid grassland. We used two approaches to determine f_{APAR}, (i) direct incoming and outgoing radiation measurements above and below the canopy, and (ii) an inversion approach based on incident photosynthetically active radiation and the light response curve of net ecosystem productivity measured by eddy covariance at low light levels. The two approaches resulted in f_{APAR} values that were very strongly correlated during the initial development of the canopy until peak leaf area index (LAI) was reached. During this time, a strong linear relationship also occurred between f_{APAR} and NDVI calculated from spectral reflectance measurements of the grassland canopy. After peak LAI, there was hysteresis in the NDVI–f_{APAR} relationship, and the two f_{APAR} estimates diverged. Light-use efficiency model calculations of ecosystem photosynthesis made using f_{APAR} values were strongly correlated with chamber CO_2 exchange measurements during the initial development of the canopy leaf area. After peak LAI, a stress function, based on either soil moisture or vapour pressure deficit (VPD) measurements, was necessary to reduce quantum yield and model calculations of ecosystem photosynthesis during periods of relatively low soil moisture and higher VPD later in the growing season. Both stress functions were similarly effective in improving the correlation between modeled and measured ecosystem photosynthesis values, and indicated reduced LUE under late season conditions. Modulating LUE based on the Photochemical Reflectance Index or the Water Band Index (both proposed as possible indicators of LUE) was not effective to improve the correlation between modeled and measured ecosystem photosynthesis values in this ecosystem.

1. Introduction

The light-use efficiency (LUE) model originally described by J.L. Monteith (Kumar & Monteith, 1981; Monteith, 1972, 1977) has been widely used for estimating gross ecosystem productivity (GEP) at regional and global scales (Ogutu et al., 2013; Running et al., 2004). Over the years, this model has evolved into many permutations based on operational definitions of the component model terms. A fundamental concept of this model in its current form, is that GEP should be linearly related to the product of (i) the incident photosynthetically active photon flux density (PPFD), (ii) the fraction of photosynthetically active radiation absorbed by the photosynthetic canopy (f_{APAR}), and (iii) the efficiency of converting the absorbed radiation into carbon during photosynthesis (Running et al., 2004). While the LUE model has been widely applied in regional and global scale calculations of productivity, model inter-comparison studies have shown uncertainties in the calculations associated with a variety of errors including how the light-use efficiency term is calculated and determination of the amount of radiation absorbed by plant canopies (Gitelson & Gamon, 2015; Keenan et al., 2012; Schaefer et al., 2012).

Direct estimates of f_{APAR} can be obtained at a specific research site from measurements of incident and reflected radiation above and below plant canopies. However, these radiation measurements are often impractical and can be quite difficult in low-statured plant canopies where below canopy light measurements are hard to obtain. In addition, the presence of non-photosynthetic plant parts and dead organic matter (litter) on the soil surface can make it difficult to obtain accurate

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estimates of f_{APAR} using radiation measurements. A common solution is to correct f_{APAR} by the fraction of green/total vegetation to calculate a "green f_{APAR}" that captures the fraction of radiation absorbed by green vegetation only (Gamon et al., 1995; Gitelson & Gamon, 2015), but this requires tedious harvesting and sorting of plant tissue, and can easily introduce additional errors. Hanan et al. (2002) pioneered an alternative approach to obtain estimates of f_{APAR} based on incident PPFD and the light response curve of net ecosystem productivity (NEP) at low light levels. This inversion approach assumes a fixed quantum yield and results in a physiologically-based estimate of the fractional light absorption efficiency of canopy chlorophyll (f_{CHL}) that can be compared with calculations of f_{APAR} from radiation measurements, and provides an alternate estimate of green f_{APAR}.

In regional- and global-scale calculations of GEP, f_{APAR} is often estimated for a given area based on empirical or theoretical relationships between f_{APAR} and vegetation greenness indices (e.g. normalized difference vegetation index, NDVI or MERIS terrestrial chlorophyll index, MTCI) (Ogutu et al., 2013; Running et al., 2004). Empirical relationships between NDVI and f_{APAR} are often reported as linear (Daughtry, 1988; Gitelson et al., 2014b; Sims et al., 2006), but recent studies in crop ecosystems have demonstrated that the linear relationship observed during the initial stages of plant development changes as the crop matures and switches to reproduction and seed development (Gitelson et al. 2014ab). The resulting hysteresis in the NDVI–f_{APAR} relationship requires separate equations to be used to obtain accurate GEP calculations at different times of the growing season, complicating the application of the LUE model. A few major factors can contribute to hysteresis in the NDVI–f_{APAR} relationship. First, variation in canopy structure due to contrasting leaf inclination angle distributions can produce separate non-linear relationships between NDVI–f_{APAR} (Huemmrich, 2013). The characteristics of the leaves may also vary seasonally as leaves mature, alter their chlorophyll and nitrogen content and then senesce (Gitelson et al., 2014a). In addition, the optical characteristics of the surface can be different and this background can change over time as the surface litter and soil vary in association with water content, ongoing decomposition processes, or fire cycles. In grassland ecosystems, the amount of standing dead biomass, or "carryover" from the previous year can add further complexity to the NDVI–f_{APAR} relationship by obscuring varying amounts of green canopy leaf area from the view above. Additionally, seasonal increases in water stress and/or high vapour pressure difference (VPD), particularly in arid land ecosystems, can result in reduction in stomatal conductance and associated changes in leaf/canopy photosynthetic activity even while canopy greenness is apparently unchanged, at least during the early stages of stress. This is another factor that could contribute to hysteresis in the NDVI–f_{APAR} relationship, particularly when f_{APAR} is based on a physiological assessment of canopy light absorption (Hanan et al., 2002). Finally, plant canopies can alter both their physiology and green canopy structure when exposed to water stress (via leaf movement or rolling), which can affect the NDVI–f_{APAR} relationship (Garbulsky et al., 2011).

Several applications of the LUE model for calculations of GEP make use of a stress function to modify f_{APAR} or photosynthetic light-use efficiency during times of water or temperature stress (Heinsch et al., 2006; Ogutu et al., 2013; Running et al., 2004). For research conducted at local sites where suitable meteorological measurements are made, it is possible to parameterize a water stress function (varies on a scale 0–1) to modify f_{APAR} or light-use efficiency as soil water content declines. However, for larger-scale applications detailed soil moisture content data is not usually available for all regions of interest, and so proxy water stress functions based on VPD, for which there is readily available data, have been developed and applied (Heinsch et al., 2006; Ogutu et al., 2013; Running et al., 2004). It is an open question how well a proxy stress function based on VPD compares to a stress function based on direct soil moisture measurements. Because suitable meteorological data are not always available, alternative approaches have attempted to make direct use of signals present in reflectance spectra to detect stress effects on photosynthetic light-use efficiency and to use these signals to modify the LUE model for calculations of GEP (Gamon et al., 2010). For example, the water band index (WBI) is calculated based on the ratio of reflectance at 900 and 970 nm and has been shown to record changes in leaf water content that may be correlated to seasonal changes in photosynthetic activity (Peñuelas et al., 1993, 1997). The photochemical reflectance index (PRI, a normalized-difference index based on reflectance at 531 and 570 nm) can provide a direct estimate of photosynthetic light-use efficiency based on interconversion of pigments in the xanthophyll cycle over the short-term (Demmig-Adams & Adams, 2006; Gamon et al., 1990, 1992) and based on changing chlorophyll-carotenoid ratios over longer time periods (Wong & Gamon, 2015). While the WBI and PRI indices can provide robust information at the leaf-level, their application at the canopy or larger landscape scales may be complicated by several factors such as variation in canopy structure, sun angle and view angle effects, soil background optical characteristics, and changing plant pigment pool sizes (Barton & North, 2001; Gamon et al., 2010; Garbulsky et al., 2011; Hmimina et al., 2014; Soudani et al., 2014). Because terrestrial ecosystems vary widely in these potentially confounding properties, and are subject to a wide range of environmental limitations to photosynthesis over different time scales, considerable variability exists in the behavior of the efficiency term of the LUE model. Consequently, the best way to parameterize the efficiency term of the LUE model remains an open question and a current research challenge.

In this paper we report the results of an experiment where the main objective was to better understand factors influencing f_{APAR}, its relationship with seasonal variation in canopy greenness, and the consequences of potential seasonal changes in the NDVI–f_{APAR} relationship for LUE model calculations of GEP. To do this, we first conducted estimates of f_{APAR} using radiation measurements and compared them to measurements of f_{CHL}, made using the inversion technique of Hanan et al. (2002). In addition, we quantified the relationship between NDVI–f_{APAR}, when NDVI was determined using spectral reflectance measurements along a transect above a native grassland ecosystem. The NDVI–f_{APAR} relationship was used to estimate f_{APAR} from the more frequent NDVI measurements. We then made use of the estimated f_{APAR} values to calculate GEP and compared these LUE model calculations to chamber measurements of ecosystem CO_2 exchange in burned and unburned areas of the grassland that had different amounts of standing dead and surface litter and, therefore, contrasting characteristics that could influence NDVI calculations. We also compared stress functions based on soil moisture and VPD measurements and determined their effectiveness in LUE model calculations of GEP. Finally, we measured seasonal variation in the PRI and WBI reflectance indices and tested their effectiveness for detecting stress effects on GEP and for parameterizing the efficiency term of the canopy-scale LUE model.

2. Materials and methods

2.1. Study site description, eddy covariance and meteorological measurements

The study site was located near Lethbridge, Alberta, Canada (eddy covariance tower coordinates are Lat. N: 49.470919; Long. W: 112.94025; 951 m above sea level) and it has been described in detail in several previous publications (e.g. Flanagan & Adkinson, 2011; Flanagan et al., 2013). The site is relatively undisturbed, native grassland that has not been grazed for over 35 years. It is dominated by the native grasses *Pascopyron dasystachyum* [(Hook.) Scrib.] and *Pascopyron smithii* (Rydb.), but includes several other plant species with relatively high abundance: *Vicia americana* (Nutt.), *Artemisia frigida* (Willd.), *Koeleria cristata* [(L.) Pers.], *Carex filifolia* (Nutt.), *Stipa comata* (Trin. and Rupr.), *Stipa viridula* (Trin.) (Carlson, 2000; Flanagan & Johnson, 2005). A wildfire burned about 38% of the areal extent of the site during September 2012. In addition to killing the aboveground live plant tissue, the fire