

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Variations in the influence of diffuse light on gross primary productivity in temperate ecosystems



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ARTICLE INFO

Article history: Received 15 May 2014 Received in revised form 28 October 2014 Accepted 1 November 2014

Keywords: Net ecosystem exchange Diffuse PAR Carbon cycling Land–atmosphere interactions

ABSTRACT

The carbon storage potential of terrestrial ecosystems depends in part on how atmospheric conditions influence the type and amount of surface radiation available for photosynthesis. Diffuse light, resulting from interactions between incident solar radiation and atmospheric aerosols and clouds, has been postulated to increase carbon uptake in terrestrial ecosystems. However, the magnitude of the diffuse light effect is unclear because existing studies use different methods to derive above-canopy diffuse light conditions. We used site-based, above-canopy measurements of diffuse light and gross primary productivity (GPP) from 10 temperate ecosystems (including mixed conifer forests, deciduous broadleaf forests, and croplands) to quantify the GPP variation explained by diffuse photosynthetically active radiation (PAR) and to calculate increases in GPP as a function of diffuse light. Our analyses show that diffuse PAR explained up to 41% of variation in GPP in croplands and up to 17% in forests, independent of direct light levels. Carbon enhancement rates in response to diffuse PAR (calculated after accounting for vapor pressure deficit and air temperature) were also higher in croplands (0.011-0.050 µmol CO2 per µmol photons of diffuse PAR) than in forests ($0.003-0.018 \mu$ mol CO₂ per μ mol photons of diffuse PAR). The amount of variation in GPP and carbon enhancement rate both differed with solar zenith angle and across sites for the same plant functional type. At crop sites, diffuse PAR had the strongest influence and the largest carbon enhancement rate during early mornings and late afternoons when zenith angles were large, with greater enhancement in the afternoons. In forests, diffuse PAR had the strongest influence at small zenith angles, but the largest carbon enhancement rate at large zenith angles, with a trend in ecosystem-specific responses. These results highlight the influence of zenith angle and the role of plant community composition in modifying diffuse light enhancement in terrestrial ecosystems, which will be important in scaling this effect from individual sites to the globe.

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1. Introduction

Forests are estimated to remove up to 27% of human-emitted CO_2 annually $(2.6 \pm 0.8 \text{ Gt C yr}^{-1})$, with temperate forests responsible for about half of this uptake globally (Le Quéré et al., 2013; Sarmiento et al., 2010). It is uncertain how this amount of carbon uptake will change in the future because forest carbon processes are affected by complex interactions driven by changes in climate and

http://dx.doi.org/10.1016/j.agrformet.2014.11.002 0168-1923/© 2014 Elsevier B.V. All rights reserved. natural- and human-caused shifts in plant species composition and canopy structure. Isolating and quantifying the impacts of individual drivers of land-atmosphere CO_2 exchange could improve these calculations of the future terrestrial carbon sink.

One important factor influencing photosynthesis and hence forest CO_2 uptake is light availability. Rates of leaf-level CO_2 uptake increase with solar radiation until leaves are light saturated (Mercado et al., 2009). This implies that forest CO_2 uptake is greater on sunny days when leaves are fully exposed to direct light. However, increases in diffuse light, which is produced when clouds and aerosols interact with and scatter incoming solar radiation, may be even more beneficial than equal increases in direct light. At the

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ecosystem level, key processes related to photosynthesis, including gross primary productivity (GPP), net ecosystem exchange (NEE), and light-use efficiency (LUE), can increase in magnitude when the proportion of light entering a forest canopy is more diffuse (Gu et al., 1999; Hollinger et al., 1994; Jenkins et al., 2007; Oliphant et al., 2011; Urban et al., 2012; Zhang et al., 2011). In addition, global simulations from 1960 to 1999 indicate that increases in the proportion of diffuse light reaching plant canopy surfaces may have amplified the global land carbon sink by 24% (Mercado et al., 2009).

Several mechanisms have been proposed to explain how diffuse light increases ecosystem CO₂ uptake and LUE. First, diffuse light can penetrate deeper into a forest canopy and reach lower canopy leaves that would normally be light-limited on clear days when light is mostly direct (Hollinger et al., 1994; Oliphant et al., 2011). Second, the same amount of light is distributed across more leaves when diffuse light is dominant, which can minimize light saturation and photo-inhibition of upper canopy leaves and increase canopy LUE or photosynthesis (Gu et al., 2002; Knohl and Baldocchi, 2008). Third, diffuse light can create conditions favorable for photosynthesis by reducing water and heat stress on plants (Steiner and Chameides, 2005; Urban et al., 2012). Finally, a fourth hypothesis suggests that diffuse light has a higher ratio of blue to red light, which may stimulate photochemical reactions and stomatal opening (Urban et al., 2012).

There is no consensus regarding the magnitude of effect that diffuse light has on ecosystem carbon processing. Studies using derived values of diffuse light suggest that LUE is higher when most incident light is diffuse and can result in maximum carbon uptake under moderate cloud cover (Gu et al., 2002; Min and Wang, 2008; Rocha et al., 2004). However, studies using a three-dimensional canopy model and a land surface scheme predict that diffuse radiation will not lead to significant increases in carbon uptake on cloudy days as compared to clear days because of reductions in total shortwave radiation (Alton et al., 2005, 2007). If clouds decrease surface radiation enough to lower total canopy photosynthetic activity, this could offset any potential GPP gain resulting from increased LUE under diffuse light conditions (Alton, 2008).

Several studies using measurements of diffuse light support the hypothesis that LUE is higher under diffuse light, consistent with studies using derived diffuse light data (Dengel and Grace, 2010; Jenkins et al., 2007). In addition, total carbon uptake can be greater under cloudy, diffuse light conditions compared to clear skies in three forest types (Hollinger et al., 1994; Law et al., 2002). Aerosol-produced diffuse light also leads to an increase in the magnitude of NEE in forests and croplands (Niyogi et al., 2004). Additional observation-based analyses indicate that diffuse light increases carbon uptake when compared to the same level of direct light, but also when total light levels decrease (Hollinger et al., 1994; Urban et al., 2007, 2012).

The magnitude of the diffuse light effect on terrestrial carbon uptake may depend on ecosystem type or canopy structural characteristics. A regional modeling study suggests that diffuse light can increase net primary productivity (NPP) in mixed and broadleaf forests, but has a negligible effect on croplands (Matsui et al., 2008). Another study using derived diffuse light data suggests that LUE increases with diffuse light, and that differences among ecosystems are potentially dependent on vegetation canopy structure (Zhang et al., 2011). The influences of ecosystem type and vegetation structure are also supported by an observation-based study showing that under diffuse light, CO₂ flux into a grassland decreased, but increased by different amounts in croplands depending on the species of crop planted (Niyogi et al., 2004). However, another study using derived diffuse light data found no difference in the effect of patchy clouds on LUE among 23 grassland, prairie, cropland, and forest ecosystems in the Southern Great Plains (Wang et al., 2008). Inconsistencies among these studies may be due to differences in the methods and models used to obtain diffuse light or sky conditions and assess their impacts on ecosystem carbon processing (Gu et al., 2003).

Climate modelers have begun incorporating the influence of diffuse light on ecosystem carbon uptake into land surface schemes as more details of canopy structure are added to models (Bonan et al., 2012; Dai et al., 2004; Davin and Seneviratne, 2012). Our study provides insight into the importance of diffuse light on ecosystem carbon processing for improving projections of the terrestrial carbon sink. We seek here to (1) quantify how much variation in ecosystem GPP is explained by diffuse light, independent of direct radiation levels, (2) compare the influence of diffuse light on GPP among temperate ecosystems differing in canopy structure and species composition, and (3) determine the strength of diffuse light enhancement of GPP while accounting for its correlation with zenith angle, vapor pressure deficit (VPD), and air temperature. Unlike many previous studies (Alton, 2008; Butt et al., 2010; Gu et al., 1999; Min and Wang, 2008; Zhang et al., 2010), we drive our analyses only with direct field measurements of diffuse light, rather than with derived values from radiation partitioning models, which may be biased by incorrect representations of clouds and aerosols. Finally, our paper highlights the changes in the diffuse light effect across the diurnal cycle and the role of time of day on the diffuse light enhancement in terrestrial ecosystems, which will be important in scaling this effect from individual sites to the globe.

2. Materials and methods

2.1. Data sources

All analyzed data were collected and processed by investigators participating in the AmeriFlux program (http://ameriflux.lbl.gov/), a network of meteorological towers in the United States (U.S.) that measures net fluxes of water vapor and CO₂ between the land surface and the atmosphere and corresponding meteorological, soil, and vegetation conditions (Baldocchi, 2003). Data collection, analysis, and metadata are standardized, reviewed, and quality controlled by AmeriFlux for all sites. GPP is calculated by subtracting the modeled ecosystem respiration from observed NEE. Respiration is modeled empirically based on NEE observations during the night, when GPP is assumed to be zero. We focus our study on GPP instead of another measure of carbon processing because it describes ecosystem CO₂ uptake, is affected directly by radiation, and is the first step in processing atmospheric CO₂ into long-term storage in ecosystems.

2.2. Site selection

We selected temperate AmeriFlux sites within the contiguous U.S. with at least three years of Level 2 (processed and quality controlled) NEE and GPP. Among these, we specifically selected sites that contain equipment to measure above-canopy total and diffuse photosynthetically active radiation (PAR, 400–700 nm) and report at least three years of diffuse PAR values to AmeriFlux. For the University of Michigan Biological Station (UMBS), we obtained updated total and diffuse PAR data from site coordinators that were not yet available on the AmeriFlux website at the time of our analyses. After separating sites with crop rotations by species, there were sufficient data for ten sites covering three ecosystem types, including mixed forest (Howland Logged, Howland N Fertilized, Howland Reference), deciduous broadleaf forest (Morgan Monroe and UMBS), and cropland (Mead Irrigated Maize, Mead Irrigated Rotation: Maize, Mead Irrigated Rotation: Soybean, Mead Rainfed

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