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Far-red sun-induced chlorophyll fluorescence shows ecosystem-specific relationships to gross primary production: An assessment based on observational and modeling approaches



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ABSTRACT

Sun-induced chlorophyll fluorescence (SIF) is a radiation flux emitted from chlorophyll molecules and is considered an indicator of the actual functional state of plant photosynthesis. The remote measurement of SIF opens a new perspective to assess actual photosynthesis at larger, ecologically relevant scales and provides an alternative approach to study the terrestrial carbon cycle. Recent studies demonstrated the reliability of measured SIF signals and showed significant relationships between SIF and gross primary production (GPP) at ecosystem and global scales. Despite these encouraging results, understanding the complex mechanisms between SIF and GPP remains challenging before SIF can be finally utilized to constrain estimates of GPP. In this study, we present a comprehensive assessment of the relationship between far-red SIF retrieved at 760 nm (SIF₇₆₀) and GPP, and its transferability across three structurally and physiologically contrasting ecosystems: perennial grassland, cropland and mixed temperate forest. We use multi-temporal imaging spectroscopy (IS) data acquired with the Airborne Prism EXperiment (APEX) sensor as well as eddy covariance (EC) flux tower data to evaluate the relationship between SIF760 and GPPEC. We use simulations performed with the coupled photosynthesis-fluorescence model SCOPE to prove trends obtained from our observational data and to assess apparent confounding factors such as physiological and structural interferences or temporal scaling effects. Observed relationships between SIF₇₆₀ and GPP_{EC} were asymptotic and ecosystem-specific, i.e., perennial grassland ($R^2 = 0.59$, rRMSE = 27.1%), cropland $(R^2 = 0.88, rRMSE = 3.5\%)$ and mixed temperate forest $(R^2 = 0.48, rRMSE = 15.88\%)$. We demonstrate that asymptotic leaf level relationships between SIF₇₆₀ and GPP_{EC} became more linear at canopy level and scaled with temporal aggregation. We conclude that remote sensing of SIF provides a new observational approach to decrease uncertainties in estimating GPP across ecosystems but requires dedicated strategies to compensate for the various confounding factors impacting SIF-GPP relationships. Our findings help in bridging the gap between mechanistic understanding at leaf level and ecosystem-specific observations of the relationships between SIF and GPP.

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1. Introduction

Plant photosynthesis is a key process in terrestrial ecosystems, mediating gas and energy exchanges in the atmosphere–biosphere system (Baldocchi et al., 2001; Ozanne et al., 2003). Products of photosynthesis provide a wealth of ecosystem services that are essential for human well-being, including food, fiber, energy and oxygen (Imhoff et al., 2004; Krausmann et al., 2013; Schroter et al., 2005). Photosynthesis as the underlying process for plant growth is a particularly interesting

* Corresponding author. E-mail address: alexander.damm@geo.uzh.ch (A. Damm). indicator of crop efficiency and agricultural management practices (Falloon & Betts, 2010; Guanter et al., 2014; Trnka, Dubrovsky, & Zalud, 2004), both of which having important implications for yield forecasts and for the implementation of climate change adaptation strategies (IPCC, 2013).

Observing the highly dynamic process of photosynthesis beyond the level of individual leaves or plants in-situ is based on measuring the carbon dioxide (CO₂) exchange between vegetation and atmosphere with eddy-covariance (EC) flux towers, and partitioning it into gross primary production (*GPP*) and ecosystem respiration (Baldocchi et al., 2001). Measurements of plant–light interactions using spectrometers installed on, for example, EC towers allow deriving information about the

pigment status and provide an alternative approach to estimate GPP (Balzarolo et al., 2011; Gamon et al., 2010; Hilker, Gitelson, Coops, Hall, & Black, 2011). At landscape scale, photosynthesis can be assessed using process-based models (Sitch et al., 2003), greenness-based satellite observations (Running et al., 2004), or hybrid approaches combining in-situ observations and statistical modeling (Jung et al., 2011). All these approaches provide important insights to study photosynthesis but usually do not allow assessing photosynthesis at larger scales while preserving the high spatial variability present in ecosystems. EC flux tower measurements represent only smaller areas in preselected ecosystems (Drolet et al., 2008; Turner et al., 2005), are not spatially distributed according to carbon stocks (Schimel et al., 2014), and do not allow spatial differentiations within the measured footprint (Barcza, Kern, Haszpra, & Kljun, 2009; Kljun, Rotach, & Schmid, 2002). Combined large scale modeling and observational approaches based on vegetation greenness are spatially contiguous but face the complexity of naturally varying systems, including diverse interactions and complex feedbacks, which limits their predictive capabilities (Beer et al., 2010; Goetz & Prince, 1999; Turner et al., 2005).

Over the last decade, significant progress has been made in measuring plant-light interactions and the process of photosynthesis. Remote measurements of sun-induced chlorophyll fluorescence (SIF), in particular, open a new perspective to assess photosynthesis at ecosystem scale. SIF is a radiation flux emitted from plant chlorophyll molecules a few nanoseconds after light absorption in the wavelength range from 600 to 800 nm and is considered an indicator for the functional status of actual plant photosynthesis (Baker, 2008). Various studies demonstrated the possibility to measure SIF at certain wavelengths on ground (Guanter et al., 2013; Rascher et al., 2009), from airborne platforms (Damm et al., 2014; Guanter et al., 2007; Zarco-Tejada, Gonzalez-Dugo, & Berni, 2012), and from satellites (Frankenberg et al., 2011; Guanter et al., 2014; Joiner et al., 2013). Recent research demonstrated SIF being sensitive to changes in photosynthesis, showing strong links to GPP at the level of leaves (Meroni et al., 2008; Middleton et al., 2002), plants (Damm et al., 2010; Rossini et al., 2010), canopies (Zarco-Tejada, Morales, Testi, & Villalobos, 2013), and ecosystems (Frankenberg et al., 2011; Guanter et al., 2012).

Observed relationships between *SIF* and *GPP* are conceptually explained using an approximation of *GPP* based on Monteith's light use efficiency concept (Monteith, 1972):

$$GPP = APAR \cdot LUE_p, \tag{1}$$

where *APAR* is the absorbed photosynthetically active radiation expressed in radiance units and LUE_p is the efficiency of light utilization for photosynthesis and allows converting measured radiances into the number of fixed CO₂ molecules. *SIF* is expressed by expanding the *GPP* notation in Eq. (1) following Guanter et al. (2014):

$$SIF = APAR \cdot LUE_f \cdot f_{esc}, \tag{2}$$

where LUE_f is the light use efficiency of *SIF* (fluorescence yield), and f_{esc} accounts for a structural interference determining the fraction of *SIF* photons escaping the canopy. Relationships between *SIF* and *GPP* are mostly driven by the common *APAR* term. In addition, a covariance between both light use efficiencies, LUE_p and LUE_f , is expected to occur in absence of the confounding impact of other protective mechanisms (Damm et al., 2010; Guanter et al., 2014).

The above outlined concept relating *SIF* and *GPP* simplifies a complex set of underlying mechanisms and violation of any assumptions made will directly confound the *SIF–GPP* relationship. In particular, the competition of three processes for de-exciting absorbed light energy, i.e., photochemistry, radiative energy loss (*SIF*), and non-radiative energy dissipation (commonly approximated as non-photochemical quenching, NPQ), causes complex and changing sensitivities of emitted SIF to actual rates of photosynthesis (Porcar-Castell et al., 2014; van der Tol, Berry, Campbell, & Rascher, 2014; van der Tol, Verhoef, & Rosema, 2009). This directly implies that the functional link between SIF and GPP depends on the rate of NPQ and, consequently, on ambient stress levels. At canopy scale, the three-dimensional structure causes gradients in light interception and light quality within canopies (Nobel, Forseth, & Long, 1993; Stewart et al., 2003), additionally altering the rate of NPQ (Demmig-Adams, 1998; Niinemets, Kollist, Garcia-Plazaola, Hernandez, & Becerril, 2003), and thus impacting the SIF-GPP relationship. Canopy structure also increases the probability for emitted SIF photons either to be re-absorbed by chlorophyll or to escape the canopy (Fournier et al., 2012; Knyazikhin et al., 2013), to some extent violating the assumption of f_{esc} to be constant. In addition to these structural and physiological effects, variations in SIF signals caused by, for example, instrumental (Damm et al., 2011) or atmospheric effects (Damm et al., 2014; Guanter et al., 2010), and retrieval uncertainties related to the estimation of surface irradiance (Damm et al., 2015) can potentially affect the apparent relationship between SIF and GPP. Proper understanding of confounding factors remains crucial to use SIF to constrain estimates for GPP at ecosystem or continental scales (Garbulsky, Filella, Verger, & Penuelas, 2014; Guanter et al., 2012; Parazoo et al., 2014).

Considering the above listed mechanisms, several aspects need to be addressed to further exploit SIF as a robust constraint for estimating GPP. We therefore aim at investigating the functional information content of SIF and its link to GPP considering three structurally and physiologically contrasting ecosystems, i.e., cropland, perennial grassland and mixed temperate forest. We use an innovative combination of multitemporal imaging spectroscopy (IS) data, EC flux tower observations, and modeling approaches at the leaf and canopy levels i) to assess the relationship between far-red SIF retrieved in the O2-A band at 760 nm (SIF₇₆₀) and GPP across ecosystems, and ii) to investigate the impact of confounding factors on the SIF₇₆₀-GPP relationship, i.e., temporal scaling effects and structural and physiological interferences. Our findings contribute to a better understanding of the information inherent in remotely measured SIF₇₆₀ and its functional relationship to GPP. Aspects discussed will help bridging the gap between small scale studies and observational attempts to estimate GPP globally.

2. Methods

2.1. Study sites

We investigated three contrasting ecosystems in terms of structure, heterogeneity, species composition, and annual productivity located on the Central Swiss Plateau. Two of these ecosystems were collocated in the agricultural area near the town of Oensingen (47°17′11″ N, 7°44′ 01" E, 452 m.a.s.l.; Fig. 1A). This area is characterized by relatively small agricultural parcels with grassland, clover fallow cropping, bean, maize, rapeseed, pea, sugar beet, winter barley, and winter wheat as dominant crops. Two grassland fields, differently managed in terms of species composition, fertilization and harvesting activities (Ammann, Flechard, Leifeld, Neftel, & Fuhrer, 2007), were investigated as representatives of the ecosystem type perennial grassland, as well as a cropland (one field with arable crop rotation) for the ecosystem type cropland. The forest area (47°28'42" N, 8°21'52" E; Fig. 1B) is located on the south-facing slope of the Laegeren mountain, northwest of the city of Zurich. The temperate mixed forest is characterized by a relatively high species diversity and a complex canopy structure, with beech, ash, sycamore, and spruce being the dominant species (Eugster et al., 2007; Schneider et al., 2014).

Both test sites are well instrumented (i.e., with eddy-covariance flux towers, micrometeorological stations) and were extensively sampled during several airborne campaigns between 2009 and 2013 (Table 1). Download English Version:

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