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Sun-induced chlorophyll fluorescence is more strongly related to absorbed light than to photosynthesis at half-hourly resolution in a rice paddy

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ABSTRACT

Sun-induced chlorophyll fluorescence (SiF) is increasingly used as a proxy for vegetation canopy photosynthesis. While ground-based, airborne, and satellite observations have demonstrated a strong linear relationship between SiF and gross primary production (GPP) at seasonal scales, their relationships at high temporal resolution across diurnal to seasonal scales remain unclear. In this study, far-red canopy SiF, GPP, and absorbed photosynthetically active radiation (APAR) were continuously monitored using automated spectral systems and an eddy flux tower over an entire growing season in a rice paddy. At half-hourly resolution, strong linear relationships between SiF and GPP ($R^2 = 0.76$) and APAR and GPP ($R^2 = 0.76$) for the whole growing season were observed. We found that relative humidity, diffuse PAR fraction, and growth stage influenced the relationships between SiF and GPP, and APAR and GPP, and incorporating those factors into multiple regression analysis led to improvements up to $R^2 = 0.83$ and $R^2 = 0.88$, respectively. Relationships between LUE_p (=GPP/APAR) and LUE_f (=SiF/APAR) were inconsistent at half-hourly and weak at daily resolutions ($R^2 = 0.24$). Both at diurnal and seasonal time scales with half-hourly resolution, we found considerably stronger linear relationships between SiF and APAR than between either SiF and GPP or APAR and GPP. Overall, our results indicate that for subdiurnal temporal resolution, canopy SiF in the rice paddy is above all a very good proxy for APAR at diurnal and seasonal time scales and that therefore SiF-based GPP estimation needs to take into account relevant environmental information to model LUE_p. These findings can help develop mechanistic links between canopy SiF and GPP across multiple temporal scales.

1. Introduction

Measuring sun-induced chlorophyll fluorescence (SiF) using remote sensing platforms has opened up new opportunities to quantify the photosynthetic activity of terrestrial ecosystems (Frankenberg et al., 2011; Porcar-Castell et al., 2014). SiF is emitted from the photosynthetic machinery in the spectral range of about 650 to 800 nm, with two peaks in the red and far-red spectral regions (Buschmann et al., 2000; Meroni et al., 2009). It is driven by absorbed photosynthetically active radiation (APAR), and shares the same excitation energy with photochemistry and non-photochemical quenching (NPQ) (Baker, 2008). Therefore, the magnitude of SiF is not only closely related to the amount of APAR but also to the actual light use efficiency of photosynthesis (LUE_p), which are two crucial factors in remote sensing-based estimations of gross primary production (GPP) (Jiang and Ryu, 2016; Monteith, 1972; Ryu et al., 2011; Sellers, 1985).

Recently, strong empirical linear relationships between canopy SiF and GPP have been widely reported at seasonal scales. These studies include retrievals from satellite (Frankenberg et al., 2011; Guanter et al., 2012; Guanter et al., 2014; Joiner et al., 2014; Verma et al., 2017; Wagle et al., 2016; Zhang et al., 2016b), airborne (Zarco-Tejada et al., 2013a; Zarco-Tejada et al., 2013b), and ground- based measurements (Rossini et al., 2010; Yang et al., 2017; Yang et al., 2015; Zhang et al., 2016a). Furthermore, as the revisit frequencies of satellite SiF

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observation increase, studies on short time scales are needed to verify results from satellite observations. The Tropospheric Emissions: Monitoring of Pollution geostationary mission, for instance, will be able to provide hourly SiF observations from space (Zoogman et al., 2017). In this case, the relationship between SiF and GPP on a diurnal time scale actually matters.

When relating canopy SiF to GPP on short temporal scales (e.g., subdaily), however, their relationships remain unclear. First, studies on short time scales found weaker empirical linear relationships between SiF and GPP compared with seasonal scales (Cheng et al., 2013; Goulas et al., 2017; Liu et al., 2017). Cheng et al. (2013), for instance, compared GPP estimates from flux tower records with SiF retrievals from ground-based spectral measurements over four growing seasons. They found that when linking half-hourly SiF with GPP using linear regression, values of the coefficient of determination (R^2) were much lower ($R2 \leq 0.3$) compared with values found in seasonal scale studies. Second, both model simulations (van der Tol et al., 2014; Zhang et al., 2016a) and ground based (Zhang et al., 2016a) as well as airborne measurements (Damm et al., 2015; Zarco-Tejada et al., 2016) have demonstrated that the relationship between SiF and GPP can be nonlinear on short temporal scales. Zarco-Tejada et al. (2016), for example, assessed the relationships between SiF from airborne observations and field-measured leaf CO_2 assimilation over two years in a citrus crop field. They found statistically significant ($p < 0.05$) relationships between SiF and leaf carbon assimilation on a diurnal scale using second order polynomial regressions at different phenological stages throughout the season.

Observed relationships between SiF and GPP can be explained with the formulation based on the concept of light use efficiency (Monteith, 1972):

$$GPP = APAR \times LUE_p \tag{1}$$

where LUE_p is the light use efficiency of photosynthesis, which represents the efficiency of energy conversion for gross CO_2 assimilation. Similarly, SiF can be expressed as:

$$SiF = APAR \times LUE_f \tag{2}$$

where LUE_f is the effective light use efficiency of canopy fluorescence, which accounts for both the fluorescence yield and the fraction of emitted photons escaping the canopy (Damm et al., 2015).

Currently, it remains unclear to what extent the relationship between SiF and GPP is due to APAR and/or light use efficiency at different temporal scales (Yang et al., 2015).

The relative variabilities of APAR, LUE_p and LUE_f differ strongly at short time scales. At the diurnal time scale APAR could vary from 0 to > 2000 μmol $m^{-2} s^{-1}$ for high LAI and sunny conditions and LUE_p is known to vary by a factor of about four to eight at the leaf-level (van der Tol et al., 2009). On the other hand, LUE_f was reported to have very conservative diurnal variation with less than a factor of two between minimum and maximum values at the leaf scale (van der Tol et al., 2014). This implies that the APAR variation is expected to strongly dominate over the LUE_f variation if diurnal dynamics are included, while GPP is known to show strong saturation with high APAR (von von Caemmerer, 2000). It therefore appears plausible that for sub-diurnal temporal resolution observations at the canopy scale, SiF could show a strong linear correlation to APAR and hence the relationship between SiF and GPP could closely resemble the relationship between APAR and GPP. A consequence of this is that the slope and curvature of relationships between SiF and GPP can change on short time scales and depend strongly on the environmental conditions (Damm et al., 2015; Flexas et al., 2000) as LUE_p depends on APAR, temperature and relative humidity (Farquhar et al., 1980; van der Tol et al., 2016).

At the seasonal scale and subdiurnal temporal resolution, seasonal variation is superposed with diurnal variation which is expected to increase the dominant role of APAR due to its large seasonal changes. If seasonal observations are considered at coarser temporal resolution such as the daily scale, however, the APAR variation is considerably reduced such that the LUE_f term is expected to play a more important role in explaining GPP and SiF relationships. Nevertheless, the effects of APAR and LUE_p could still be dominant. Furthermore, based on recent theoretical and modelling results by Yang and van der Tol (2018), the seasonal variation of LUE_f is expected to be dominated by the fraction of SiF escaping the canopy although the latter was assumed constant in previous studies (Guanter et al., 2014).

Previous results from both experimental (Miao et al., 2018) and combined experimental-modelling studies (Du et al., 2017) at the canopy level seem to partly confirm the strong SiF-APAR relationship at short time scales but were limited to either part of a growing season (Miao et al., 2018) or only studied the SiF – APAR relationship without including results on the SiF-GPP relationship (Du et al., 2017). In addition, Zhang et al. (2016a) found results consistent with our above reasoning on APAR dominance using the process-based SCOPE model (van der Tol et al., 2009). To the best of our knowledge, the responses of the SiF – GPP relationship to environmental variables such as relative humidity and temperature as well as phenology have not yet been studied quantitatively using continuous, long-term, high-temporal resolution observations at the canopy scale. While effects of diffuse PAR were studied to some degree in Yang et al. (2015), Goulas et al. (2017) and Miao et al. (2018), only sunny and cloudy days or high and low diffuse PAR fraction were distinguished and possible confounding effects such as reduced APAR on cloudy days were not taken into account.

In this study, our goal is to quantify the relationships between SiF and GPP on multiple time scales in a rice paddy. For comprehensive assessment of their relationships, we integrated a range of field observation data including canopy SiF, eddy flux measurements, canopy structure, leaf gas exchange, and meteorological variables. The main scientific questions that will be addressed in this study are: 1) is the SiF-GPP relationship indeed dominated by APAR and LUE_p and is this consistent on both diurnal and seasonal time scales? 2) do environmental conditions and phenology significantly influence the relationship between SiF and GPP on the one hand, and LUE_p and LUE_f on the other hand?

2. Materials and methods

2.1. Study site

Our study site was a rice paddy located in Cheorwon, Gangwon province, South Korea (38.2013°N, 127.2506°E) registered in the Korea Flux Network (KoFlux) (Fig. 1). The region experiences a continental climate with hot humid summers and cold dry winters, which allows for only one growing season per year. In 2016, the mean annual temperature was 11.2 °C; the lowest temperature was −12.2 °C in January and the highest temperature was 31.0 °C in August (Korea Meteorology Administration). Annual precipitation was 1180.9 mm, of which two-thirds typically falls during the monsoon period from June to August (Korea Meteorology Administration).

In the rice paddy, the predominant species was *Oryza sativa* L. ssp. *Japonica* and it was grown intermittently irrigated, with a water depth of about 5 cm. Soil fertilization only occurred once along with transplantation; 12.02 g N m^{-2} fertilizer was applied at a ratio of 18:7:9 (nitrogen: phosphoric acid: potassium). The entire growing season in 2016 lasted for around four months, from transplantation at the end of April [Day of Year (DOY), 120] to harvest in early September (DOY, 248) (Huang et al., 2018). The phenology of rice is commonly divided into three growth phases: vegetative (DOY 120 to 180); reproductive (DOY 180 to 220); and ripening (DOY 220 to harvest) (Maclean et al., 2013). The vegetative phase is characterized by a gradual increase in