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Meta-analysis assessing potential of steady-state chlorophyll fluorescence for remote sensing detection of plant water, temperature and nitrogen stress

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ABSTRACT

Many laboratory studies investigating chlorophyll fluorescence (F) of plants have provided sufficient evidence of the functional link between dynamic changes in photosynthetic activity and F emissions. Far fewer studies, however, have been devoted to detailed analysis of F emission under steady-state conditions, which may be amenable to measurement by passive spectroradiometers onboard airborne or satellite missions. Here, we provide a random-effects meta-analysis of studies using both passively (sun-induced) and actively (e.g. laser-induced) measured steady-state F for detecting stress reactions in terrestrial vegetation. Specifically, we review behaviour of F in red and far-red wavelengths, and also the red to far-red F ratio, for plants physiologically stressed by water deficit, temperature extremes, and nitrogen insufficiency. Results suggest that water stress is, in general, associated with a decline in red and far-red F signal intensity measured at both leaf and canopy levels, whereas the red to far-red F ratio displays an inconsistent behaviour. Chilling, for which only studies with active measurements at the leaf level are available, significantly increased red and far-red F, whereas heat stress produced a less convincing decrease in both F emissions, notably in canopies measured passively. The clearest indicator of temperature stress was the F ratio, which declined significantly and consistently. The F ratio was also the strongest indicator of nitrogen deficiency, revealing a nearly uniformly increasing pattern driven by predominantly declining far-red F. Although significant knowledge gaps were encountered for certain scales and F measurement techniques, the analyses indicate that future airborne or space-borne acquisitions of both red and far-red F signals would be beneficial for timely detection of plant stress events.

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1. Introduction

The Earth's environment is increasingly exposed to multiple stress agents, due to a combination of exponentially growing human population and associated energy needs (Hughes, Carpenter, Rockstrom, Scheffer, & Walker, 2013), as well as naturally occurring stress episodes. Under such conditions, the ability to detect timely stress responses of vegetation at regional and also global scale is necessary for successful mitigation of adverse and potentially irreversible negative impacts.

For over three decades, remote sensing has provided essential inputs for estimation of carbon fluxes and vegetation productivity at various spatial scales (e.g. Running et al., 2004). Increasing spectral resolution and accuracy of instruments has opened up possibilities to assess new characteristics associated with dynamic vegetation functioning (Grace et al., 2007; Rascher et al., 2007; Suarez et al., 2008). One such characteristic is the emission of chlorophyll fluorescence (F) under steady-state light conditions, which provides information on the functional status of photosynthetically active leaves (Papageorgiou & Govindjee, 2004). Steady-state F measured by active (laser or pulse-amplitude modulation) fluorometers, commonly termed F_s, and solar-induced steady-state F measured by passive systems (SIF), are the subject of intensive research in recent years (Malenovský, Mishra, Zemek, Rascher, & Nedbal, 2009). Reliable estimates of global SIF observed from space (Joiner, Yoshida, Vasilkov, Corp, & Middleton, 2011) are expected to reduce uncertainties associated with modelling of gross primary production (GPP) using terrestrial carbon fluxes (Frankenberg et al., 2011; Guanter et al., 2014). Our study investigates another possible use of the steady-state F as an indicator tracking development of vegetation stress reactions and providing early identification of physiological strain prior to appearance of visual symptoms.

Upon absorption of incoming photosynthetically active radiation (PAR) between 400 and 700 nm, the energy of photons is converted into: i) photochemical energy of photosynthesis, ii) heat dissipation related to photoprotection, and iii) F emissions (Maxwell & Johnson, 2000; Demmig-Adams & Adams, 2000; Demmig-Adams & Adams, 2006). In general, the magnitude of F emission during photosynthesis is inversely related to the efficiency of energy transfer between antenna pigments and electron acceptors (Kok, 1965). Under steady-state light conditions, chlorophyll fluorescence usually constitutes only around 2–3% of red (684–695 nm) and far-red (730–760 nm) light reflected by leaves (e.g. Zarco-Tejada, Pushnik, Dobrowski, & Ustin, 2003), which is a small yet measurable quantity, if sufficiently sensitive instrumentation and appropriate signal retrieval methods are used. While hundreds of laboratory studies using well established active F measurement methods and protocols proved the functional link between various F features and photosynthesis (e.g. Papageorgiou & Govindjee, 2004), the information content of the steady-state F signal, especially from passive detectors measuring SIF, is yet to be fully understood and exploited.

The pulse amplitude modulation (PAM) method, developed by Schreiber, Schliwa, and Bilger (1986), is the most commonly used active method to measure F of single leaves in laboratory and also field experiments. The PAM approach enables discrimination of F from extraneous reflected light via selective amplification (Roháček & Barták, 1999). However, the strong saturation flashes applied in high-frequency time series might induce a non-natural behaviour of the plant photosynthetic apparatus altering possibly plant F responses. Other active remote sensing F methods used either pulsed (i.e. laser-induced fluorescence — LIF) (Buschmann et al., 1996; Cerovic et al., 1996; Lavrov et al., 2012) or non-pulsed light sources (Kim et al., 2001) for excitation of F. While LIF has the advantage of measuring F in the presence of sunlight, the non-pulse methods tend to acquire more stable F signals, which enable better characterization of F emission peaks. LIF methods can induce F emissions of different intensities depending on the excitation wavelengths of laser sources, which typically range between 300 and 700 nm (Chappelle & Williams, 1987; Middleton, Corp, & Campbell, 2008). Apart from the excitation wavelength, selection of optical filters and detectors with appropriate spectral resolution affects the quality (i.e. intensity, amplitude, accuracy and signal-to-noise ratio) of the acquired F signal. Recently, a laser or light-emitting diode induced fluorescence transient (LIFT) system, which is based on a fast repetition rate (FRR) fluorometry, was applied for remote sensing of photosystem II fluorescence of tree crowns or small canopies from a distance up to 50 m (Kolber et al., 2005; Pieruschka et al., 2014).

Passive remote sensing methods retrieving the steady-state F signal from air-/space-borne data can be divided into: i) reflectance-based (relative unit) and ii) radiance-based approaches (in physical unit of $W \cdot m^{-2} \cdot sr^{-1} \cdot \mu m^{-1}$). Reflectance-based approaches utilize F signal integrated in vegetation reflectance measured between 650 and 800 nm. According to Meroni et al. (2009), twenty-four F indices based on reflectance differences, reflectance ratios or reflectance derivatives of 2 to 3 spectral bands have been proposed. The rationale behind these indices is to normalize reflectance of F-sensitive wavelengths by the closest F insensitive wavelength (Perez-Priego, Zarco-Tejada, Miller, Sepulcre-Canto, & Fereres, 2005). Radiance based F quantities were derived using the Fraunhofer Line Discriminator (or Fraunhofer Line Depth, FLD) technique (Plascyk, 1975), which requires measurements of total solar irradiance (reference standard) and the sample radiance (leaf or canopy) inside and outside the atmospheric oxygen absorption bands or solar Fraunhofer lines located in the red and/or far-red parts of the spectrum (Theisen, 2002). Recently Joiner et al. (2011), Frankenberg et al. (2011), and Guanter et al. (2012) presented global maps of vegetation SIF using Fraunhofer lines at 755 and 770 nm acquired by the high spectral resolution Fourier Transform Spectrometer (FTS) aboard of the Japanese Greenhouse Gases Observing Satellite (GOSAT). Lee et al. (2013) used F estimates from GOSAT to detect drought stress in the Amazon forest. Other satellite platforms usable, but not purposely designed for F observations, include the Global Ozone Monitoring Experiment-2 (GOME-2; Joiner et al., 2013), the Scanning Imaging Absorption Spectrometer for Atmospheric Chartography (SCIAMACHY; Köhler et al., 2014), and the Orbiting Carbon Observatory-2 (OCO-2; Frankenberg et al., 2014).

Mapping terrestrial photosynthetic activity from space is the main objective of one of the current candidate missions for the European Space Agency's (ESA) 8th Earth Explorer programme (Kraft et al., 2012). The Fluorescence Explorer (FLEX) satellite is proposed as a tandem mission with ESA's Sentinel-3 operational mission. FLEX would measure red and far-red vegetation F as a potential key input into GPP modelling of ecosystem vegetation canopies, and also as an indicator of actual vegetation stress status (Rascher et al., 2008). This study aims to contribute to filling current knowledge gaps about use of