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Relationships between net photosynthesis and steady-state chlorophyll fluorescence retrieved from airborne hyperspectral imagery

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ABSTRACT

Previous studies have demonstrated the link between leaf chlorophyll fluorescence and photosynthesis, mainly at the leaf level and under controlled laboratory conditions. The present study makes progress in demonstrating the relationship between steady-state fluorescence and net photosynthesis measured under natural light field conditions both at the leaf and image levels. Ground measurements and airborne campaigns were conducted over two summers to acquire hyperspectral imagery at 40 cm resolution and 260 spectral bands in the 400–885 nm spectral region. This enabled the identification of pure vegetation pixels to extract their radiance spectra. The datasets were collected in August 2010 and 2011 in the western part of the area included in the Ribera del Duero Designation of Origin (*Denominación de Origen*), in northern Spain. The experiments were conducted in twelve full production vineyards where two study plots per field were selected to ensure adequate variability in leaf biochemistry and physiological condition. The vineyard fields were selected on the basis of their gradient in leaf nutrition and plant water status and showed variability in leaf pigment values and stomatal conductance. Leaves were collected for destructive sampling and biochemical determination of chlorophyll $a+b$, carotenoids and anthocyanins in the laboratory. Leaf steady-state and dark-adapted fluorescence parameters, net photosynthesis (P_n) and stomatal conductance (G_s) were measured in the field under natural light conditions. Such data were used as a validation dataset to assess fluorescence–photosynthesis relationships both at the leaf and the image level. The Fraunhofer Line Depth (FLD) principle based on three spectral bands (FLD3) was the method used to quantify fluorescence emission from radiance spectra extracted from pure vegetation pixels identified in the hyperspectral imagery. Fluorescence retrievals conducted using the FLD3 method yielded significant results when compared to ground-measured steady-state F_s ($r^2 = 0.48$; $p < 0.01$) and F_v'/F_m' ($r^2 = 0.53$; $p < 0.01$). The two-year assessment yielded consistent results on the relationship between P_n and F_s both at the leaf level and based on the airborne hyperspectral imagery. At the leaf level, significant relationships were found between leaf F_s and P_n ($r^2 = 0.55$; $p < 0.001$ for 2010; $r^2 = 0.59$; $p < 0.001$ for 2011). At the hyperspectral image level, the agreement between leaf P_n and airborne F was consistent for both years separately, yielding significant relationships at $p < 0.01$ for 2010 ($r^2 = 0.54$) and 2011 ($r^2 = 0.41$) and a significant relationship at $p < 0.001$ for the aggregated years ($r^2 = 0.52$). Results show the link between net photosynthesis and steady-state fluorescence obtained under natural sunlight conditions at both leaf and airborne hyperspectral imagery levels.

1. Introduction

A number of studies have demonstrated the link between leaf chlorophyll fluorescence and photosynthesis (Krause & Weis, 1984; Larcher, 1994; Lichtenthaler, 1992; Lichtenthaler & Rinderle, 1988; Papageorgiou, 1975; Schreiber & Bilger, 1987; Schreiber et al., 1994). In particular, experiments conducted at the leaf and laboratory level in controlled environments have shown that fluorescence and reflectance indices were able to track diurnal changes caused by heat and water stress (Dobrowski et al., 2005). Under water deficit conditions, red edge indices measured at the canopy level have shown sensitivity to temperature and stress through steady-state fluorescence (F_s), tracking CO_2 assimilation. Such findings confirm earlier results obtained at the leaf level by a study comparing fluorescence and net photosynthesis relationships at the leaf level under water stress in grapevines (Flexas et al., 2000). In that study, leaf measurements showed a link between gas-exchange rates of CO_2, H_2O and chlorophyll fluorescence data.

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Although such studies have clearly shown the interest of monitoring chlorophyll fluorescence as an indicator of photosynthesis, several earlier studies focused instead on the Photochemical (or Physiological) Reflectance Index (PRI) (Gamon et al., 1992) as a proxy for photosynthesis. In particular, they evaluated the potential for measuring terrestrial photosynthesis from space (Grace et al., 2007) using reflectance (PRI) and fluorescence (F) indices. Specific assessments of the dynamic changes in chlorophyll fluorescence vs. the PRI and photosynthesis were conducted in grapevines (Evain et al., 2004), Scots pine (Louis et al., 2005), experimental mangrove canopies (Nichol et al., 2006) and coastal shrubs (Naumann et al., 2008). In natural vegetation developed under salt and drought stress, both dark-adapted and steady-state chlorophyll fluorescence measures were used to detect effects on physiology before they were evident (Naumann et al., 2007).

Despite the successful results obtained in some cases with the PRI as a proxy for photosynthesis, some studies have shown that this index is highly affected by the canopy structure, leaf pigments and background (Suárez et al., 2008, 2009). In fact, this can prevent the successful monitoring of photosynthesis (Rascher & Pieruschka, 2008). In this latter study, the PRI failed to monitor photosynthetic light conversion due to the effects of the canopy structure on the index, suggesting the use of fluorescence as a better indicator of photosynthesis. The modeling study conducted by Zarco-Tejada et al. (2009) showed that fluorescence estimations using *in-filling* methods were little affected by structural changes of the canopy such as leaf area density. On the other hand, other *standard* indicators suggested in the past for canopy monitoring such as the NDVI or leaf chlorophyll content are highly affected by the canopy medium and fail to track photosynthesis (Stylinski et al., 2002). This confirms the need for sensitive indices related to short-term physiological changes.

In recent years, increasing attention has been given to chlorophyll fluorescence for global monitoring of vegetation physiology. Specific studies have explored the technical aspects and challenges of retrieving fluorescence to monitor global photosynthesis (Malenovsky et al., 2009). They have discussed scaling issues from the leaf to the region level using O_2 bands for fluorescence quantification (Rascher et al., 2009) and modeled gross primary production (GPP) from fluorescence/assimilation rates in diurnal patterns (Damm et al., 2010). These efforts related to global photosynthesis mapping through fluorescence quantification have received much attention as part of the FLuorescence EXplorer FLEX mission (FLEX) supported by the European Space Agency (ESA) Earth Explorer program. Under such scope, earlier modeling work was conducted as part of the Vegetation Fluorescence Canopy Model (FluorMOD project) (Miller et al., 2004), which served to develop a leaf model named FluorMODleaf (Pedrós et al., 2004, 2008, 2010) and a canopy model named FluorSAIL (Verhoef, 2004). These models were used as a first tool to explore the feasibility of retrieving the fluorescence signal superimposed on the leaf and canopy reflectance spectra. These earlier efforts were critical for the simulation work conducted later to assess F retrieval accuracy in response to relevant sensor properties, including the spectral sampling interval, spectral resolution, signal to noise and spectral shift, along with different fluorescence retrieval methods (Damm et al., 2011). These experimental and modeling advances enabled the development of SCOPE (Van der Tol et al., 2009a,b), an integrated leaf-canopy fluorescence-temperature-photosynthesis model. The abovementioned modeling studies are critical to understand the feasibility of fluorescence retrieval at both leaf and canopy levels. They have shown that it is a challenging task since the contribution to the radiance signal is estimated to be about 2–3%. Thanks to these efforts, several methods have been reported to extract the fluorescence signal at the leaf and canopy levels with very narrow spectral bands (Meroni et al., 2004, 2008a,b, 2009; Moya et al., 2004; Pérez-Priego et al., 2005), proving the feasibility of fluorescence retrieval using the O_2-A band feature. Recently, global maps of chlorophyll fluorescence have been published (Frankenberg et al., 2011; Joiner et al., 2011) using the Thermal And Near infrared Sensor for carbon Observation sensor (TANSO) on board GOSAT (Kuze et al., 2009). The fluorescence retrievals and global maps obtained from GOSAT were discussed by Guanter et al. (2012), who found overall good agreement between fluorescence quantification by the satellite sensor and annual and seasonal patterns of vegetation.

Although these recent advances in the global mapping of fluorescence are a major step forward, progress in leaf-canopy fluorescence modeling and near-field validation experiments is critical to understand the fluorescence signal linked to photosynthesis under natural sunlight conditions in pure vegetation pixels. This is particularly important as vegetation structure, background, illumination and atmospheric effects play a critical role at larger scales where the fluorescence signal is quantified in mixed pixels that aggregates shadows, pure vegetation and the background. Few published validation studies have addressed the retrieval of fluorescence at the image level and the relationships between fluorescence retrieved and field-measured photosynthesis under natural light conditions. This is due to the lack of appropriate imagery acquired at high spatial and spectral resolutions and the complexity of the field validation required. Recent studies (Zarco-Tejada et al., 2009) applying the *in-filling* method to 1 nm FWHM airborne multispectral imagery acquired over crops for stress detection have shown the feasibility of mapping fluorescence at 40 cm resolution using a micro-hyperspectral imager on board an unmanned aerial vehicle (UAV) (Zarco-Tejada et al., 2012).

Despite the improvements in high-resolution fluorescence retrieval from pure vegetation pixels under varying physiological conditions, studies focused on the link between fluorescence quantification from high-resolution imagery and field photosynthesis data are still lacking. In the present study, field photosynthesis and fluorescence data and high-resolution airborne hyperspectral imagery were collected over two summers. The aim was to explore the relationships between fluorescence, pigment content and net photosynthesis in pure vegetation pixels extracted from the imagery. Leaf and canopy level fluorescence and hyperspectral radiance images were used to explore i) the relationships between leaf fluorescence measures and photosynthesis data during two consecutive years, assessing steady-state and dark-adapted fluorescence parameters as well as leaf chlorophyll, carotenoid and anthocyanin pigment data; and ii) the link between airborne F quantification extracted from pure vegetation pixels and photosynthesis data in a validation study conducted over two summers.

2. Materials and methods

2.1. Field experiments and airborne campaigns

2.1.1. Study site description

The study was conducted in 2010 and 2011 in the western part of the area included in the Ribera del Duero Designation of Origin (*Denominación de Origen*), in Peñafiel, Valladolid, northern Spain, at an altitude of 800 m above sea level. A group of non-irrigated full production vineyards were selected to ensure adequate variability in soil background and physiological status according to the purposes of the study. This resulted in 24 different 10 × 10 m study plots. All the vineyards had been planted between 1983 and 1994 with cv. Tempranillo grafted on 110-Richter rootstock. The vines, spaced 3 × 1.5 m apart, were trained to double cordons and spur pruned, with an average bud count of 16 buds per plant. Shoots were maintained in a vertical position (trellis). The main wire was 0.70 m above the soil surface.

Soils were calcareous (up to 58.8% total carbonate content) and poor in organic matter (about 0.76%), with an average pH of 8.6. Texture ranged from medium to medium-weighted. Concentrations of active carbonate (3.3–15.5%) and DPTA extractable iron (2.3–6.4 mg kg^{-1}) were highly heterogeneous within the area. Such soil properties along with the presence of a sensitive rootstock (110-Richter) led to different levels of iron deficiency chlorosis in the vineyards of the area. The study plots had high variability of soil concentrations of extractable potassium (86–345 mg kg^{-1}), phosphorus (4.6–31.8 mg kg^{-1}) and magnesium (120–663 mg kg^{-1}). The area has Mediterranean climate, with low