Radiative transfer Vcmax estimation from hyperspectral imagery and SIF retrievals to assess photosynthetic performance in rainfed and irrigated plant phenotyping trials

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Abstract

Plant photosynthetic traits may be indicative of stress tolerance and performance in the field, making their accurate assessment critical in phenotyping trials. The maximum rate of carboxylation (V_{cmax}) is a key parameter for estimating CO_2 assimilation (A), as it controls the CO_2 fixation rate. This study demonstrates the utility of combining airborne-based solar-induced chlorophyll fluorescence (SIF) and hyperspectral imagery through the inversion of the Soil-Canopy Observation of Photosynthesis and Energy (SCOPE) model to estimate V_{cmax} , using sensor resolutions available in precision agriculture technologies. V_{cmax} was quantified in three wheat phenotyping experimental fields during the 2015-2018 growing seasons, comprising both rainfed and irrigated conditions. Airborne campaigns were carried out with two hyperspectral sensors, covering the 400–850 nm (20 cm resolution) and 950–1750 nm (70 cm resolution) spectral regions, and with a thermal camera (25 cm resolution) in the 8–14 μm region. Validation between model-estimated and field-measured V_{cmax} was statistically significant ($r^2 = 0.77$; $p\text{-value} \leq 2.2\text{e-}16$), and V_{cmax} was reliably associated with net assimilation both in irrigated and rainfed conditions ($r^2 = 0.65$ and 0.5 , respectively). By contrast, simulated chlorophyll content (C_{ab}) and airborne-derived structural and chlorophyll indicators (NDVI and PSSRb) lacked significant correlations with assimilation rate in irrigated plots, while the relationship between assimilation rate and the crop water stress index (CWSI) was not significant in rainfed plots. The superior sensitivity of remotely-sensed V_{cmax} under irrigated conditions was likely related to its robustness to distortions from high canopy densities observed in other indices. The remote sensing retrieval of V_{cmax} , and the methodology demonstrated in this study is directly relevant for high-throughput plant phenotyping and for precision agriculture applications.

24 **Keywords:** Sun-induced chlorophyll fluorescence, SCOPE, high-resolution hyperspectral,
25 leaf maximum carboxylation rate (V_{cmax}), water stress

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1. Introduction

CO₂ assimilation (A) occurs in the chloroplasts and involves light biochemical reactions (Quebbeman and Ramirez, 2016). Environmental conditions such as light intensity and temperature, biophysical processes such as CO₂ transport through the leaf and stomata, and leaf biochemistry determine the assimilation rate (Sharkey *et al.*, 2007). At the leaf level, the photosynthetic capacity is defined by the maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}). V_{cmax} is the maximum rate of Ribulose-1,5-Bisphosphate (RuBP) carboxylation, which controls CO₂ fixation (Farquhar *et al.*, 1980). J_{max} is the maximum rate of electron transport, which limits the supply of ATP and NADPH during the carboxylation and the regeneration of RuBP in the Calvin-Benson cycle (Quebbeman and Ramirez, 2016). Wullschleger (1993) demonstrated that J_{max} should follow V_{cmax} across plant species, a relationship not affected by nitrogen content within leaves (Walker *et al.*, 2014).

The most common biochemical photosynthesis model for estimating the CO₂ assimilation at leaf level is the Farquhar–von Caemmerer–Berry (FvCB) model (Farquhar *et al.*, 1980). The FvCB model and its subsequent variants (Caemmerer and Farquhar, 1981; Farquhar and Wong, 1984; Collatz *et al.*, 1992; Harley *et al.*, 1992a) relate the kinetic properties of Ribulose-1,5-Bisphosphate Carboxylase-Oxygenase (RuBisCo) to photosynthetic capacity (Caemmerer, 2000). The FvCB model is typically embedded in terrestrial biosphere models (TBM), which have been used to estimate photosynthetic carbon uptake (Norton *et al.*, 2017), gross primary productivity (Sellers, 1987; Koffi *et al.*, 2015) and leaf respiration (Sitch *et al.*, 2003; Oleson *et al.*, 2013). In recent years, progress has been made to quantify photosynthetic capacity from hyperspectral satellite imagery, enabling the development of TBMs at new

spatial scales. In the context of a plant phenotyping study, Silva-Perez *et al.* (2018) demonstrated the use of hyperspectral reflectance to estimate V_{cmax} and other physiological traits in wheat crops. However, imagery was obtained at the leaf level, where the remote sensing signal was not affected by canopy structure, as it is for larger-scale applications. For images at the canopy level, standard reflectance indices such as the normalized difference vegetation index (NDVI) (Rouse *et al.*, 1973) have been widely used for detecting vigor, growth, yield and senescence patterns from airborne and near-field scales in maize and wheat crops (Cairns *et al.*, 2012; Kipp *et al.*, 2014). However, NDVI has well-known disadvantages associated with its saturation at high biomass levels, its sensitivity to canopy background, and the inability to track short-term physiological changes due to its strong relationship with tissue structure (Huete, 1988; Huete *et al.*, 2002). Despite these disadvantages, NDVI is still one of the most widely used indicators for the remote assessment of canopy characteristics by plant breeders.

Several studies have demonstrated that canopy temperature can be related to physiological processes (Gonzalez-Dugo *et al.*, 2015) or even used to detect nutritional deficiencies (Rodriguez *et al.*, 2006). The thermal-based Crop Water Stress Index (CWSI) developed by Idso *et al.* (1978) and Jackson *et al.* (1981) is inversely related to transpiration and stomatal conductance, and therefore a potentially good proxy for estimating crop photosynthesis rates under stress. However, a range of environmental factors may affect the relationship between stomatal closure and canopy temperature, such as changes in radiation exposure, nutrient deficiency or soil water deficit (Radin *et al.*, 1985; Jones *et al.*, 1995; Zweifel *et al.*, 2002).

In the last twenty years the quantification of sun-induced chlorophyll fluorescence (SIF) through hyperspectral imaging has provided a new tool for monitoring crop photosynthetic activity and vegetation functioning (Frankenberg *et al.*, 2011; Houborg *et al.*, 2013; Zarco-Tejada *et al.*, 2016; Norton *et al.*, 2017). Chlorophyll fluorescence is closely related to the electron transport rate and hence to photosynthetic activity (Genty *et al.*, 1989; Weis and Berry, 1987). Chlorophyll fluorescence may therefore be useful for detecting nutrient-limitation in crops (Camino *et al.*, 2018a). Chlorophyll fluorescence may also be used to estimate V_{cmax} since both are linked with chlorophyll content (Houborg *et al.*, 2013; Croft *et al.*, 2017) and therefore photosynthetic activity (Rascher *et al.*, 2015; Yang *et al.*, 2015).

Recent studies have successfully estimated V_{cmax} from satellite SIF retrievals (Guan *et al.*, 2016; Zhang *et al.*, 2014, 2018) using the Soil Canopy Observation, Photochemistry and Energy fluxes (SCOPE) model (Guanter *et al.*, 2014; Koffi *et al.*, 2015; Zhang *et al.*, 2014, 2018). Nevertheless, further progress is needed for the assessment of V_{cmax} under both water and nutrient-limited conditions (i.e. under stress) and in the context of plant phenotyping experiments with high-resolution imagery. In some cases, SIF retrievals have been performed using cost-effective hyperspectral imagers with broader spectral resolutions (i.e. 2–7 nm FWHM) (Damm *et al.*, 2015; Zarco-Tejada *et al.*, 2016; Camino *et al.*, 2018b). Although offsets in the fluorescence retrievals may occur due to the broader spectral resolutions used in these imagers, the consequences may be negligible for most precision agriculture applications since emphasis is on relative spatio-temporal variability of stress rather than absolute fluorescence emission levels.

The remote assessment of plant photosynthesis requires careful attention to the influence of stress. Photosynthesis is strongly affected by stress, with assimilation affected by water deficit (Chaves, 1991) and carboxylation capacity sensitive to leaf nitrogen levels (Walker *et al.* 2014). However, under drought conditions, water deficit may alter the nitrogen balance as growth rate diminishes (Gonzalez-Dugo *et al.*, 2010). In bread wheat, populations display heritable variation in photosynthetic traits, amenable to artificial selection (Carmo-Silva *et al.* 2017). As a result, remotely sensed chlorophyll fluorescence may be useful for phenotyping photosynthetic traits desirable for breeding. In this study we quantify V_{cmax} as a proxy for photosynthetic activity in wheat phenotyping trials using airborne hyperspectral-based SIF retrievals through SCOPE model inversions. Specifically, we evaluated airborne estimates of V_{cmax} under both well-watered and water-limited regimes.

2. Material and Methods

2.1 Study area

Experiments took place at three field trial sites for bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* L. var. *durum*) in Southern Spain in 2015, 2016 and 2018 (Fig. 1). The regional climate is Mediterranean, characterized by mild winters, warm and dry summers and with annual rainfall averages around 600 mm. The first trial site was located in Ecija (37°32'17"N, 5°06'57"W), which was managed under rainfed conditions in 2015 and 2018. The plot size was 12.5 m² (10 m×1.25 m) with a spacing of 1 m x 1.25 m between plots (Fig. 1a and 1d).

The second site trial was located in Carmona (37°30'29"N, 5°34'42"W) in 2015, which was managed under both rainfed and irrigated conditions. Severe drought at the Carmona

experimental site during the spring of 2015 (precipitation < 30 mm in preceding months of the airborne campaign) prompted irrigation in rainfed plots the week before the flights to partially recover the experiment and to avoid damage. At Carmona, 882 individual plots (7.5×1.25 m) were divided across two blocks according to water regime. There was a space of 1.50 m x 0.25 m between plots (Fig. 1b). Forty-nine varieties of durum or bread wheat were replicated three times per block.

The third trial site was located in Santaella (37°31'34"N, 4°50'40"W) , which was also managed under rainfed and irrigated conditions in 2016. Twenty varieties of durum wheat and 20 varieties of bread wheat were replicated three times across a total of 120 plots (Fig. 1c). The plot size was 15 m² (10×1.5 m) with a spacing of 2.50 m x 0.50 m between plots.

At all trial sites, plots consisted of five rows of wheat with a spacing of 0.25 m per row. Physiological measurements and spectral reflectance were taken from the three central rows. The remaining two rows were excluded from analysis. The soil in the three trial sites was dominated by vertisols (FAO classification), which ranged in texture from clay, clay loam to silt. Slope across sites ranged from 2 to 4%. Vertisols are often poor in organic matter and associated with nitrogen and phosphorus deficiencies. Fertilization with diammonium phosphate and urea was carried out in early November to ensure fertility levels.

The wheat growth stage during the airborne campaigns corresponded to i) stem elongation stage, and ii) the grain filling (milking stage) (Table 1). All flights were performed under clear sky conditions. Average meteorological conditions during each flight (ERA-Interim atmospheric reanalysis data; <http://www.ecmwf.int>) are presented in Table 1.

Table 1. Flight dates and field measurements collected during the airborne campaigns. The meteorological conditions at the time of the flights are included.

Year	Site	Flight dates	Growth Stage	Airborne imagery	Field measurements	Meteorological conditions		
						T _a	RH	R _{in}
2015	Ecija	28/05	Grain filling	T + VNIR + NIR	ψ_L , A, C _{ab} , N	295.1	38.0	944.2
	Carmona	30/05	Grain filling	T + VNIR + NIR	ψ_L , A, C _{ab} , N	296.8	38.8	935.8
2016	Santaella	17/03	Stem elongation	T + VNIR + NIR	ψ_L , A, C _{ab} , N	289.6	49.2	558.2
	Santaella	26/04	Grain filling	T + VNIR + NIR	ψ_L , A, C _{ab} , N	297.5	42.5	933.3
2018	Ecija	18/04	Stem elongation	T + VNIR + NIR	A, C _{ab} , N, Curve A/C _i	297.1	43.6	924.8

T= thermal, VNIR = hyperspectral visible and infrared region, NIR = hyperspectral near-short wave infrared region, ψ_L = leaf water potential (MPa), A = net assimilation rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), C_{ab} = chlorophyll content ($\mu\text{g}\cdot\text{cm}^{-2}$), N= nitrogen concentration (%), Curve A/C_i = response curves of A to the intercellular CO₂ concentration, T_a= air temperature (K), RH= relative humidity (%) and R_{in}= Incoming shortwave radiation ($\text{W}\cdot\text{m}^{-2}$).

2.2 Field physiological measurements and leaf gas exchange curves

A summary of the physiological variables measured for each site and sampling date is included in Table 1. Field measurements of assimilation rate (A; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and leaf water potential (ψ_L ; MPa) were made at the same time (± 1 hour) as acquisition of high-resolution airborne imagery over the experimental field sites. These measurements were performed on leaves at the top of the canopy at noontime, under clear skies and with photosynthetically active radiation (PAR) values ranging from 1700 to 2200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. To assess the physiology and nutritional status of the wheat plots under different water regimes, some additional leaf measurements were made at the trial sites (Table 1). Leaf photosynthesis was measured with a photosynthesis measurement system (LC pro- SD, ADC Bioscientific Ltd., Herts, UK) on two leaves per plot. The LCpro-SD plant leaf photosynthesis chamber has a flow rate accuracy of $\pm 2\%$ of its range. Leaf water potential (ψ_L) was measured on two sunlit leaves per plot with a pressure chamber (Model 600 Pressure Chamber Instrument, PMI Instrument Company, Albany, NY, USA). Chlorophyll content was measured on 10–15

leaves per plot using a hand-held chlorophyll meter (SPAD-502, Minolta Corp., Ramsey, NJ, USA). The SPAD-502 chlorophyll meter has an accuracy of ± 1 SPAD units. In 2018, leaf chlorophyll content was measured with the Dualex instrument (FORCE-A, Orsay, France), which has an accuracy of 5%. The SPAD and Dualex readings were converted to chlorophyll content ($\mu\text{g}\cdot\text{cm}^{-2}$) according to Uddling *et al.* (2007). Total N concentration (%) was determined by the Kjeldahl method (Kjeldahl, 1883) in random samples of 20-25 leaves from the top of the canopy in select plots. This value was demonstrated to be a good proxy of the crop nutritional status (Farruggia *et al.*, 2004).

Fig. 1. Overview of the field trial sites at Ecija (a and b), Carmona (c) and Santaella (d). Figures a and c were obtained with a CIR camera (a: 800 (R), 670 (G) and 550 (B) nm; d: true color). Figure b shows a sample of the thermal imagery. Figure d was obtained with a VNIR hyperspectral imager (composite: 706 (R), 679 (G) and 520 (B) nm).

The response of assimilation to intercellular CO₂ concentration was measured using the portable LCpro-SD photosynthesis measurement system during the field campaign at Ecija in 2018. To assess variability in CO₂ response curves, six wheat varieties (W_I to W_{VI}) displaying contrasting nutritional and physiological statuses were selected across the trial site (Fig. 2). Varieties were selected based on patterns in chlorophyll content, nitrogen, and assimilation rate (red asterisks in Fig. 2). The photosynthetic photon flux density was kept constant at 1900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during measurements. Prior to sampling, selected leaves were adapted to the chamber light conditions, humidity and temperature for about 5 minutes. CO₂ concentration was then ramped in steps of 100 ppm, with each step lasting a minimum of 1 minute and a maximum of 3 minutes.

Fig. 2. Leaf physiological measurements on durum wheat plots (in blue) and bread wheat plots (in grey) carried out during the field campaign in Ecija 2018 under rainfed conditions: a) the nitrogen balance index (NBI) in dimensionless units (d.u.), b) chlorophyll content (C_{ab}) in Dualux units (both measurements were collected with the hand-held Dualux device) and c) assimilation rate (A) in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, measured with the plant leaf photosynthesis chamber. The red asterisks indicate wheat plots selected for A/Ci curves. In the box plots, the black line within the box is the median, and the top and bottom of the box represent the 75th and 25th quartiles, respectively. The whiskers represent the upper and lower range. The average values are shown with a white point over each box plot.

Leaf V_{cmax} was estimated from assimilation-intercellular CO_2 concentration ($A-C_i$) curves (Fig. 3) using the C_3 FvCB photosynthesis model (Farquhar *et al.*, 1980). Photosynthetic response $[\text{CO}_2]$ curves developed by Sharkey *et al.* (2007) were used to estimate V_{cmax} according to the FvCB model. Following this method, field measurements with intercellular CO_2 partial pressure between 20 to 30 Pa were excluded to reduce errors associated with the interface between the RuBisCo-limited and RuBP-regeneration-limited state.

Fig 3. Relationship obtained between assimilation rate (A ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and intercellular CO_2 partial pressure (Pa). Each colour is associated with different wheat varieties (W_n). The dashed lines represent the RuBisCo-limited (left) and RuBP-regeneration-limited (right) state according to Sharkey *et al.* (2007).

Kinetic parameters for respiration (R_d) and the mesophyll conductance (g_m) were estimated for each wheat variety following the nonlinear curve fitting procedures outlined in Sharkey *et al.* (2007). The temperature dependence of the Michaelis-Menten constant of RuBisCo (K_c) for CO_2 , inhibition constant (K_o), photorespiratory compensation point (Γ^*), R_d , g_m , V_{cmax} , rate of photosynthetic electron transport (J) and triose phosphate use (TPU) were estimated using exponential functions of temperature responses described in Harley *et al.*

(1992b). The scaling constant (c), enthalpies of activation (ΔH_a), deactivation (ΔH_d) and entropy (ΔS) were taken from Sharkey *et al.* (2017) in Table 1.

The retrievals of V_{cmax} were adjusted to 25°C using the FvCB model. Only measurements where leaf temperatures were $\pm 0.5^\circ\text{C}$ of the average were used in generating these estimates. Atmospheric pressure and intercellular concentration of oxygen (O_i) for all collected wheat varieties were set to 21 kPa and 99.75 kPa, respectively. R_d and g_m values used to estimate V_{cmax} are provided in Table 2.

Table 2. Input parameters and constants (adjusted to 25°C), maximum carboxylation rate (V_{cmax}), photosynthetic electron transport rate (J) and triose phosphate use (TPU) obtained from the A/C_i curves shown in Fig. 3 for six wheat varieties using exclusively measures with a leaf temperature equal to the average $\pm 0.5^\circ\text{C}$. The kinetic parameters include the Michaelis constant of RuBisCo for carbon dioxide (K_c), the inhibition constant (K_o), and the photorespiratory compensation point (Γ^*). Day respiration (R_d) and the mesophyll conductance (g_m) were used for adjusting estimates to 25°C. Temperature responses were estimated using the equations described in Harley *et al.* (1992b). The specific kinetic constants [scaling constant (c), enthalpies of activation (ΔH_a), deactivation (ΔH_d) and entropy (ΔS)] were taken from Sharkey *et al.* (2007).

Parameters	W _I	W _{II}	W _{III}	W _{IV}	W _V	W _{VI}
Temperature leaf ($^\circ\text{C}$)	32.6 $\pm$ 0.2	24.12 $\pm$ 0.5	25.2 $\pm$ 0.2	26.2 $\pm$ 0.2	26.42 $\pm$ 0.5	23.5 $\pm$ 0.5
Constants for fitting						
K_c (Pa)	61.87	24.73	27.84	31.05	31.82	23.09
K_o (kPa)	21.08	16.12	16.69	17.23	17.35	15.80
Γ^* (Pa)	4.79	3.63	3.77	3.89	3.92	3.56
Constant for adjusting to 25°C						
R_d (mmol·m ⁻² ·s ⁻¹)	1.601	0.947	1.013	1.078	1.094	0.910
g_m (mmol m ⁻² s ⁻¹ ·Pa ⁻¹)	1.611	0.943	1.014	1.083	1.100	0.904
Outputs adjusting to 25°C						
V_{cmax} (μmol·m ⁻² ·s ⁻¹)	109	118	106	109	101	104
J (μmol·m ⁻² ·s ⁻¹)	201	292	275	259	227	299
TPU (μmol·m ⁻² ·s ⁻¹)	18.6	24.1	23.1	21.2	2.5	25.0

2.3 Airborne campaigns

Five airborne campaigns were conducted using an aircraft operated by the Laboratory for Research Methods in Quantitative Remote Sensing (QuantaLab), Consejo Superior de

Investigaciones Científicas (IAS-CSIC, Spain). Flights occurred at 250 m above ground level (AGL) with heading on the solar plane. Images were acquired concurrently with field data acquisitions (Table 1) between 12:00 and 13:00h (local time) under clear sky conditions and free of coarse aerosol (i.e.: dust mineral, biomass burning). To minimize differences due to sun angle effects, the flights were performed at solar zenith angle between 45° and 60°, which varied according to the day, place and the exact flight time. The viewing zenith angle was 0° for all flights. Images were collected with a micro-hyperspectral imager (Micro-Hyperspec VNIR model, Headwall Photonics, Fitchburg, MA, USA), a Micro-Hyperspec NIR-100 (Headwall Photonics) and a thermal infrared camera (FLIR SC655, FLIR Systems, Wilsonville, OR, USA). The Micro-Hyperspec VNIR was configured to acquire 260 spectral bands with a light dispersion of 1.85 nm/pixel with 12-bit radiometric resolution in the 400–885 nm spectral region, yielding a 6.4 nm full width at half maximum (FWHM) with an entrance slit width of 25- μ m. The acquisition and storage module obtained 50 frames per second at 25 ms integration time. The 8-mm focal length lens yielded an IFOV of 0.93 mrad and an angular FOV of 50° with a spatial resolution of 20 cm (Fig. 1c). The micro-hyperspec NIR-100 sensor was configured for 165 spectral bands at 16-bit radiometric resolution covering the 950–1750 nm spectral region, yielding 6.05 nm FWHM with a spatial resolution of 70 cm. Radiometric calibration of the VNIR and NIR-100 cameras was performed with an integrating sphere (CSTM-USS-2000C LabSphere, North Sutton, NH, USA) using four levels of illumination and six integration times.

Hyperspectral imagery was atmospherically corrected using incoming irradiance measured with a field spectrometer (FieldSpec Handheld Pro, ASD Inc., Longmont, Colorado, USA) for the VNIR sensor, and simulated by the SMARTS model (Gueymard, 1995; Gueymard *et*

al., 2002) for the NIR-100 sensor. In addition, the view and illumination angle effects were corrected using a bidirectional reflectance distribution function (BRDF) in the VNIR and NIR-100 hyperspectral imagery. Irradiance measurements were interpolated and convoluted to the bandwidth of each sensor. To simulate incoming irradiance, aerosol optical measurements (Table 3) were acquired at flight time with a Microtops II handheld multichannel sunphotometer (Solar Light, Philadelphia, USA) connected to a GPS-12 model (Garmin, Olathe, KS). The aerosol measurements carried out with the sunphotometer instrument at flight-time confirmed the absence of dust mineral, biomass burning ($AOD_{500nm} \leq 0.25$ and Ångström exponent ($AE \geq 0.6$, according to Cuevas *et al.* (2015)) and other extinction aerosols which could affect the reflectance and radiance spectrum during the airborne campaign. A portable weather station (Transmitter PTU30, Vaisala, Helsinki, Finland) was used for simultaneous readings of the relative humidity, temperature and pressure at the time of hyperspectral and thermal acquisitions. Ortho-rectification of hyperspectral imagery was performed following Zarco-Tejada *et al.* (2016). Sample average radiance and reflectance spectra of wheat plots obtained with the VNIR hyperspectral sensor at the Ecija trial site in 2018 are shown in Fig. 4.

Fig. 4. Mean radiance ($\text{W}\cdot\text{sr}^{-1}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$) (a) and reflectance spectra (b) retrieved from the VNIR hyperspectral camera at the Ecija site in 2018. The black lines correspond to the average spectra of all wheat plots. Shaded areas comprise the ± 1 standard deviation of the average radiance and reflectance profiles.

Table 3. Average values of aerosol optical depth (AOD) at 500 nm, the Ångström exponent (AE) at 440–936 nm, air mass and the precipitable water vapor column (in cm) measured using a hand-held sun photometer (MicroTops-II) instrument. The sun photometer measurements were performed at each trial site during the airborne campaigns of 2015–2018.

Year	Site	Flight dates	AOD _{500 nm}	AE _{440-936nm}	Air mass	H ₂ O atm (in cm)
2015	Ecija	28/05	0.09	0.84	1.30	1.05
	Carmona	30/05	0.07	0.75	1.28	1.30
2016	Santaella	17/03	0.13	0.69	1.31	1.06
	Santaella	26/04	0.09	0.65	1.27	1.22
2018	Ecija	18/04	0.12	0.61	1.25	0.98

253 The FLIR SC655 thermal camera used in this study had a resolution of 640×480 pixels with
254 a 13.1 mm focal length at 16 bits, providing an angular FOV of $45 \times 33.7^\circ$ and a ground
255 resolution of 25 cm at the flight altitude (Figure 1d). Thermal imagery was calibrated using
256 ground temperature data collected with a handheld infrared thermometer (LaserSight, Optris,
257 Germany) on each flight date.

2.4 Fluorescence retrieval and calculation of narrow-band indices and CWSI from hyperspectral and thermal imagery

According to the method developed by Camino *et al.* (2018b), an automatic segmentation based on quartile breaks was applied to the high-resolution hyperspectral imagery for minimizing the effect of the soil background inside wheat plots. The average radiance and reflectance spectra (Fig. 4) were extracted from the high-resolution hyperspectral imagery using the segmented areas, which corresponded with the central region of each wheat plot. Using the same scheme as for the hyperspectral imagery, the watershed segmentation method was applied to high-resolution thermal imagery for separating the vegetation from the soil background.

Solar induced fluorescence (SIF) was quantified from radiance spectra (Fig. 4a) by the *in-filling* method using the Fraunhofer Line Depth (FLD) principle (Plascyk and Gabriel, 1975). The FLD method compares canopy radiance to incoming irradiance at the 760.5 nm atmospheric O₂-A oxygen absorption Fraunhofer Line, as described in Moya *et al.* (2004) and Meroni *et al.* (2010). We compared the radiance values L_{in} (L_{762} nm) and L_{out} (L_{750} nm) extracted from the VNIR hyperspectral imagery, to incoming irradiances E_{in} (E_{762} nm) and E_{out} (E_{750} nm) measured at the time of the flights. Reasonable SIF retrieval via the FLD method using broader spectral bandwidths (i.e., 5–7 nm FWHM) has been demonstrated in a simulation study (Damm *et al.*, 2011) and experimentally (Zarco-Tejada *et al.*, 2012, 2016; Damm *et al.*, 2015; Hernandez-Clemente *et al.*, 2017). The configuration of the hyperspectral imager during the airborne campaigns carried out in this study (1.85 nm sampling interval, 6.4 nm bandwidths and SNR of 300:1 with spatial binning) is comparable to that of Zarco-Tejada *et al.* (2012), and observations with the Airborne Prism EXperiment (APEX) sensor

in Damm *et al.* (2015). In addition, NDVI and the pigment-specific simple ratio chlorophyll *b* index (PSSR_b) proposed by Blackburn (1998) were calculated from the average reflectance values for each experimental plot (Fig. 4b).

The Crop Water Stress Index (CWSI) was calculated from the thermal imagery according to the methodology proposed by Idso *et al.* (1981, Eq. 1). For the assessment of CWSI, the average canopy temperature (*T_c*) retrieved from the top of the wheat canopy at sunlit conditions and the air temperature (*T_a*) registered at the flight time were used.

$$CWSI = \frac{(T_c - T_a) - (T_c - T_a)_{LL}}{(T_c - T_a)_{UL} - (T_c - T_a)_{LL}} \quad (1)$$

(*T_c*-*T_a*)_{LL} represents the canopy-air temperature differential of a canopy transpiring at the maximum rate, and (*T_c*-*T_a*)_{UL} represents this temperature differential when transpiration is completely halted. The Non-Water-Stress-Baseline (NWSB) was used to derive (*T_c*-*T_a*)_{LL}, defined as the relationship between the *T_c*-*T_a* of a well-irrigated wheat plot at a given vapour pressure deficit (VPD). The NWSB used in this study (*T_c*-*T_a*=3.38-3.25·VPD) was obtained by Idso (1982), while the upper limit was calculated according to the methodology proposed by Idso *et al.* (1981).

2.5 Modelling methods

V_{cmax}, standardized to a reference temperature at 25 °C (hereinafter referred to *V_{cmax}*), was estimated by inversion of the SCOPE model v1.70 (van der Tol *et al.*, 2009a) using biophysical parameter retrievals and SIF quantification for each wheat plot. SCOPE is a vertical (1-D) integrated radiative transfer and energy balance model.

SCOPE models the relationship between chlorophyll fluorescence and photosynthesis at the leaf level as a function of environmental conditions (van der Tol *et al.*, 2009b). Photosynthesis and chlorophyll fluorescence simulations are carried out in SCOPE with meteorological forcing inputs (incoming shortwave and long-wave radiation, air temperature, humidity, wind speed and CO₂ concentration) and four kinds of parameters: i) leaf parameters including leaf mesophyll structure (N-struct), leaf chlorophyll content (C_{ab}), dry matter content (C_m), leaf equivalent water thickness (C_w), senescent material (C_s) and anthocyanins (C_{ant}); ii) vegetation structural parameters, including the leaf area index (LAI), leaf angle distribution, leaf size and canopy height (h_c); iii) optical parameters, including vegetation emissivity and soil reflectance in the visible, near infrared and thermal bands; and iv) physiological parameters, including stomatal conductance (m) and maximum carboxylation capacity. A summary of the relevant SCOPE inputs for this study is given in Table 4.

The canopy geometry effects on the outgoing spectrum and on the heterogeneity of net radiation are treated stochastically with 60 elementary layers, with a maximum LAI of 0.1 each, 13 discrete leaf zenith inclinations and 36 leaf azimuth classes for shaded and sunlit leaves. The fluorescence contributions from individual leaves are integrated over the canopy layer to calculate top of canopy (TOC) fluorescence in the viewing direction of the hyperspectral sensor based on absorbed fluxes over the photosynthetic active radiation (PAR) region (400–700 nm). The chlorophyll fluorescence at leaf level is computed as a product of the FvCB photosynthesis model, stomatal resistance (Cowan, 1978), the Ball–Berry stomatal conductance model (Ball *et al.*, 1987), the coupled photosynthesis-stomatal model (Collatz *et al.*, 1991), and the emission of chlorophyll fluorescence. The SCOPE model combines the Collatz *et al.* (1991) model and the Farquhar *et al.* (1980) photosynthesis model for retrieving

the V_{cmax} , taking into account the stomatal conductance and assimilation rate. For further details see van der Tol *et al.* (2009b) and van der Tol *et al.* (2014).

2.5.1 Ancillary climatic data

The meteorological inputs required for SCOPE simulations were extracted from ERA-Interim atmospheric reanalysis data (Dee *et al.*, 2011) produced by the European Centre for Medium-Range Weather Forecasts (ECMWF). The ERA-Interim is the latest global atmospheric reanalysis produced by the ECMWF (<http://www.ecmwf.int>). Surface parameters extracted from 3-hourly time step ERA-Interim reanalysis included 2-meter air temperature, air pressure, water vapour pressure, incoming shortwave and long-wave downward radiation, and 10-meter wind speeds. The data from ERA-Interim atmospheric reanalysis was spatially interpolated from their native spatial grid (0.75° by 0.75°) to a finer 0.25° by 0.25° resolution using nearest-neighbour resampling. To assess the meteorological variables retrieved from ERA-Interim atmospheric reanalysis, data were compared with observations from the nearest meteorological stations in the regional agro-climatic network (Consejería de Agricultura y Pesca, Junta de Andalucía). Errors associated with convective processes at surface level were reduced using wind speed at 2 meters from this network.

Table 4. Range of the PROSPECT-SAILH and SCOPE parameters used in this study.

Parameters	Definition	Unit	Range	Step
PROSPECT				
Leaf biophysical				
N-struct	Leaf mesophyll structure parameter	[-]	1.25–1.85	0.1
C _{ab}	Chlorophyll a +b content	$\mu\text{g}\cdot\text{cm}^{-2}$	10–70	0.5
C _w	Equivalent water thickness	$\text{g}\cdot\text{cm}^{-2}$	0.001–0.05	0.0005
C _m	Dry matter content	$\text{g}\cdot\text{cm}^{-2}$	0.001–0.05	0.0005
C _s	Senescence factor	[-]	0	...
FLUSPECT (integrated into SCOPE model)				
C _{ant}	Anthocyanin content	$\mu\text{g}\cdot\text{cm}^{-2}$	3,5,10	...
SAILH				
Canopy				
LAI	Leaf area index	$\text{m}^2\cdot\text{m}^{-2}$	2–5	0.1
LADF	Leaf inclination distribution function	[-]	1,2,3 and 4 ^(a)	...
TV	Solar zenith angle	deg	45,60,85	5
Ph _i	Viewing zenith angle	deg	0	...
PSR	Relative azimuth angle	deg	0	...
S _i	Hot-spot parameter	[-]	0 ^(d)	...
SCOPE				
Leaf biochemistry				
V _{cmax}	Maximum carboxylation capacity at 25°C	$\mu\text{mol}\cdot\text{m}^{-1}\cdot\text{s}^{-1}$	0–260	10
m	Ball-Berry stomatal conductance	[-]	8	...
Rdparam	Parameter for dark respiration	[-]	0.015	...
K _v	Extinction coefficient for vertical V _{cmax} profile	[-]	0.64	...
K _c	Cowan's water use efficiency	[-]	700	...
$\rho(\text{thermal})$	Leaf thermal reflectance	[-]	0.01	...
$\tau(\text{thermal})$	Leaf thermal transmittance	[-]	0.01	...
$\rho_s(\text{thermal})$	Soil thermal reflectance	[-]	0.06	...
Stressfactor	Stress multiplier for V _{cmax}	[-]	1	...
kNPQs	Rate thermal dissipation	[-]	0	...
qLs	Fraction active photosystems	[-]	1	...
fge	Fraction of photons partitioned to PSII	[-]	0.02	...
Canopy				
l _w	Leaf width	m	0.1	...
LIDF _a	Leaf inclination distribution of leaves	[-]	-1–1	0.05
LIDF _b	Variation in leaf inclination	[-]	-1–1	0.05
hc	Canopy height	m	1.2	...
Micrometeorological				
p	Air pressure	hPa	988–997 ^(b)	...
u	Wind speed	$\text{m}\cdot\text{s}^{-1}$	2.2–2.8 ^(c)	...
O _a	O ₂ concentration in the air	per mille	209	...
e _a	Atmospheric vapor pressure	hPa	15	...
C _a	CO ₂ concentration in the air	ppm	392.2	...
T _a	Air temperature	°C	18–25 ^(b)	...
R _{in}	Incoming shortwave radiation	$\text{W}\cdot\text{m}^{-2}$	500–950 ^(b)	...
R _{li}	Incoming longwave radiation	$\text{W}\cdot\text{m}^{-2}$	70–150 ^(b)	...

a) Canopy types proposed to define LADF: planophile (1), erectophile (2), plagiophile (3) and spherical (4).

b) Meteorological variables retrieved from hourly ERA-Interim reanalysis dataset for each trial sites.

c) Wind speed at 2-meter from a weather station located close to each trial sites.

d) Leaves were under sunlit conditions without shadowing effects on the bidirectional reflectance

2.5.2 Leaf biophysical and structural parameters

The leaf and canopy parameters needed for SCOPE simulations were estimated using a multi-step PROSPECT-SAILH model inversion scheme from reflectance in the 400–1700 nm spectral region. A look-up table (LUT) of 200,000 simulations was built to minimize the *ill-posed inversion* problem (Combal *et al.*, 2003; Li and Wang, 2011; Yebra and Chuvieco, 2009). The range of variation for C_{ab} was determined based on prior field information. The main input parameters were calculated using specific spectral ranges (Table 4) where the biophysical parameters are known to have the greatest influence on reflectance and transmittance spectra. The iterative-optimization numerical (I-optN) approach was used to invert the PROSPECT-SAILH model for the estimation of leaf traits and canopy parameters from reflectance across the observed spectrum. The I-optN method estimates the set of parameters, symbolized by the vector $\theta = [LADF, LAI, N, C_{ab}, C_m, C_w]$ which minimizes Δ^2 (Eq. 2). The method calculates the root mean square error (RMSE) between the simulated reflectance and the hyperspectral image reflectance by successive input parameter iteration.

$$\Delta^2 = \sum_n [\rho_{\lambda,obs} - \rho_{\lambda,sim}]^2 \quad (2)$$

Where $\rho_{\lambda,obs}$ is the image (canopy level) spectral reflectance, and $\rho_{\lambda,sim}$ is the modeled canopy spectral reflectance with a set of parameters defined in the LUT for each wavelength n . The procedure was conducted in several steps: 1) a leaf angle distribution function (LADF) was estimated over the VNIR and SWIR spectral range (400–1750 nm) with variables C_{ab} , C_w and C_m . LADF was first retrieved by model inversion, given its key role in canopy structure; 2) the mesophyll structural parameter (N-struct) and the leaf area index (LAI) were simultaneously determined over the range 960–1300 nm using the LADF from step 1, and variable C_{ab} , C_w and C_m inputs; 3) C_{ab} was then calculated using reflectances in the 455–

690 nm range, where chlorophyll absorption has the strongest effect, with fixed LADF, LAI and N estimated in previous steps; 4) Finally, C_m and C_w were estimated over 900–1700 nm, where dry and water matter have the largest absorption effects (Baret and Fourty, 1997; Feret *et al.*, 2008; Fourty *et al.*, 1996; Jacquemoud *et al.*, 2009, 1996), fixing C_{ab} , LADF, LAI and N obtained previously.

2.5.3 SCOPE iterative-optimization for LIDF_s and R_{in} parameters

After meteorological, leaf, and canopy parameters had been obtained, the SCOPE model was run using an I-optN approach with a LUT table of 27,500 simulations for optimizing the LADF and the broadband incoming shortwave radiation (R_{in}). The LADF retrievals derived from PROSPECT-SAILH were optimized with SCOPE iterative-optimization using the radiance spectrum, varying the leaf inclination angle distribution function (LIDF) parameters. The LIDF_a and LIDF_b parameters mathematically describe the LAD function estimated using PROSPECT-SAILH inversions, where LIDF_a determines the average leaf inclination and LIDF_b describes the variation in leaf inclination, controlling the distribution's bimodality.

The I-optN method minimizes a cost function (Eq. 3) to estimate the set of parameters symbolized by the vector $\theta = [R_{in}, LIDF_a, LIDF_b]$. In this step, the I-optN method was based on the calculation of the RMSE between the *at-sensor* canopy spectral radiance and the SCOPE-simulated spectra by successive input parameter iterations over the spectral region used for the SIF retrievals (740–780 nm).

$$\Delta^2 = \sum_n [L_{\lambda,obs} - L_{\lambda,sim}]^2 \quad (3)$$

Where $L_{\lambda\text{obs}}$ is the measured canopy spectral radiance, and $L_{\lambda\text{sim}}$ is the canopy spectral radiance modeled by SCOPE with the set of parameters defined in the LUT for a given wavelength λ . The LUT was built varying R_{in} and LIDF_s , but keeping the V_{cmax} constant at $80 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and the remaining default values fixed, as shown in Table 1. R_{in} varied $100 \text{ W}\cdot\text{m}^{-2}$ with a step of $5\text{--}10 \text{ W}\cdot\text{m}^{-2}$ from the incoming shortwave radiation from the ERA-Interim reanalysis for each trial site. The leaf inclination distribution factors (LIDF_a and LIDF_b) varied according to the LADF obtained from PROSPECT-SAILH inversions, using a total of 500 variations. Among the canopy structural variables, LIDF_a , representing the inclination distribution of leaves, had the greatest effect on SIF variability. In fact, LIDF_a had a large influence on modeled reflectance with a contribution of over 20% of the variation between 720–1150 nm, while the LAI parameter governed over $\geq 50\%$ of variation in reflectance at wavelengths longer than 1400 nm. The remaining structural inputs used in SCOPE (leaf width, LIDF_b , and canopy height) had a marginal impact on the modeled reflectance (Verrelst *et al.*, 2015). Recent studies (Koffi *et al.*, 2015; Verrelst *et al.*, 2016, 2015) have demonstrated the importance of R_{in} , since the fluorescence spectrum is proportional to the absorbed PAR.

2.5.4 V_{cmax} estimation from SCOPE model inversion

Once the leaf, canopy and meteorological parameters were obtained following the I-optN approaches using the PROSPECT-SAILH and SCOPE simulations, the relationships between V_{cmax} and canopy fluorescence ($V_{\text{cmax}}=f(\text{SIF})$; Fig 5b) were established for all wheat plots. For this purpose, the SCOPE model was run in forward mode with the V_{cmax} range set to $0\text{--}260 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, divided into 27 intervals. As an additional step, the simulated radiance spectra from SCOPE at 1 nm resolution in the 640–800 spectral windows

412 was convoluted using the Whittaker-Shannon interpolation, as described in Butzer *et al.*
413 (2011). Fig. 5a shows the comparison between the radiance retrieved with the VNIR
414 hyperspectral sensor, the original radiance simulated by SCOPE at 1nm, and the simulated
415 SCOPE radiance spectra convoluted to match the airborne hyperspectral data. The spectral
416 convolution of the radiance simulated by SCOPE was critical to match the broader resolution
417 of the hyperspectral imager, and therefore to obtain comparable SIF values. Fig. 5b shows
418 the effect of the convoluted radiance signal when applied to the SCOPE simulations,
419 observing the relationship between SIF and V_{cmax} .

Fig. 5. Radiance spectra obtained by the VNIR hyperspectral sensor (in grey), the radiance simulated by SCOPE model at 1 nm (in black) and the convoluted SCOPE-simulated radiance using Whittaker and moving average filters (in red) (a). For the same wheat plot, the SCOPE-simulated SIF (black line) and the SIF obtained after convolution (red line) are shown as a function of V_{cmax} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (b) for simulations with $C_{ab}=33 \mu\text{g}\cdot\text{cm}^{-2}$, $\text{LAI}=2$ and $R_{in} = 575 \text{ W}\cdot\text{m}^{-2}$.

3. Results

3.1 Nutrient and water-stress variability in rainfed and irrigated study sites

Field-based leaf physiological measurements (net assimilation, N concentration and water potential), V_{cmax} estimated by SCOPE inversions, C_{ab} estimated by PROSPECT-SAILH inversions, and CWSI for the entire experiment comprising rainfed and irrigated plots are shown in Fig. 6. There were large differences in the crop photosynthesis, water and nitrogen status between water regimes. As expected, irrigated plots had better water and nutritional status compared to rainfed plots overall. Irrigated plots had higher assimilation rates, N concentrations, V_{cmax} , and C_{ab} (Fig 6a, b, d and e) than rainfed plots. ANOVA analysis confirmed statistically significant differences between the means of the two water stress regimes for all field physiological measurements (all p-values ≤ 0.0036).

Fig. 6. Leaf- and canopy-level physiological data acquired in plots under rainfed (red) and irrigated (blue) conditions: a) assimilation rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); b) leaf N concentration (%); c) water potential (MPa); d) V_{cmax} estimated by SCOPE ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); e) chlorophyll content estimated by PROSPECT-SAILH ($\mu\text{g}\cdot\text{cm}^{-2}$); and f) CWSI calculated from high-resolution thermal imagery. In the box plots, the horizontal line represents the median, and the top and bottom are the 75th and 25th quartiles, respectively. The whiskers represent the upper and lower range. Average values shown with a white point over the box plot.

There was a significant correlation between CWSI and water potential in rainfed plots ($r^2 = 0.30$, $p\text{-value} = 0.7e-4$), although the correlation was stronger for irrigated plots ($r^2 = 0.72$, $p\text{-value} = 1.7e-5$). The high variability in N concentration for both treatments (Fig. 6b) suggests that rainfed plots were also affected by N deficit. Assimilation rate was significantly correlated with the N concentration ($r^2 = 0.51$ and 0.56 for irrigated and rainfed, respectively) indicating that the N concentration also affected the photosynthetic capacity in both water regimes.

3.2 Effects of the biochemical and environmental parameters on SIF and V_{cmax} estimation

The sensitivity of the convoluted radiance signal simulated with SCOPE to chlorophyll content, LAI and the broadband incoming shortwave radiation are shown in Figure 7. Variation in C_{ab} had a relatively small effect on radiance at the spectral region typically used to quantify chlorophyll fluorescence (750–775 nm), particularly as compared to LAI and R_{in} (Fig 7b and c). In general, for the same value of C_{ab} , the radiance significantly increased with the increase of LAI and R_{in} in the $O_2\text{-A}$ region. However, large differences were observed as a function of R_{in} variation, reaching more than $30 \text{ W} \cdot \text{sr}^{-1} \cdot \text{m}^{-2} \cdot \text{nm}^{-2}$. These results showed that R_{in} was a key micrometeorological variable in driving SIF variability simulated by the SCOPE model.

Figure 8 shows the relationship between SCOPE-simulated SIF and V_{cmax} , as a function of LAI, C_{ab} and R_{in} . At constant radiation ($R_{\text{in}} = 800 \text{ W} \cdot \text{m}^{-2}$) and LAI (2), fluorescence increased with increasing values of C_{ab} and V_{cmax} . The largest increase in the SIF retrievals occurred

454 for V_{cmax} between $10\text{--}60\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. For larger V_{cmax} values ($\geq 150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), SIF
 455 retrievals remained steady, with a tendency to increase with C_{ab} .

Fig. 7. Sensitivity of SCOPE radiance profiles convoluted to match the FWHM of the hyperspectral imager used in the study, as a function of chlorophyll content (C_{ab}) in $\mu\text{g}\cdot\text{cm}^{-2}$ (a), leaf area index (LAI) (b) and the broadband incoming shortwave radiation (R_{in}) in $\text{W}\cdot\text{m}^{-2}$ (c) for $V_{\text{cmax}} = 80\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. CO_2 and O_2 concentration at the interface of the canopy were set to 382.17 ppm and 200×10^3 ppm, respectively.

456 At constant C_{ab} , there were dramatic changes in the relationship between simulated SIF and
 457 V_{cmax} with increased with LAI and R_{in} (Fig. 9b and c). SIF significantly increased with LAI,
 458 nearly doubling with an increase in LAI from 1 to 5 (Fig 8b). Unsurprisingly, SIF increased
 459 proportionally to R_{in} (Fig 8c).

Fig. 8. Relationships between SIF estimated from SCOPE radiance simulations and V_{cmax} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) as a function of chlorophyll content (C_{ab}) in $\mu\text{g}\cdot\text{cm}^{-2}$ (a), LAI (b) and the broadband incoming shortwave radiation (R_{in}) in $\text{W}\cdot\text{m}^{-2}$ (c).

3.3 Validation of V_{cmax} estimated by SCOPE using leaf photosynthesis measurements

The relationship between the SCOPE-estimated V_{cmax} and the field-measured V_{cmax} is shown in Fig. 9a. There was an almost 1:1 linear relationship ($r^2 = 0.77$; $p\text{-value} \leq 2.2\text{e-}16$ and $\text{RMSE} = 2.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) between measured and estimated V_{cmax} , using the FvCB approach on the six wheat varieties from the airborne campaign in 2018. The relationships between net photosynthetic rate and both measured and simulated V_{cmax} also displayed a significant relationship for both types of V_{cmax} estimates (all $r^2 \geq 0.68$; $p\text{-value} \leq 0.005$) (Fig. 9b).

Fig. 9. a) Relationship between carboxylation maximum capacity (V_{cmax} ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) retrieved from the hyperspectral image through the SCOPE model inversion vs. field measured V_{cmax} through Farquhar–von Caemmerer–Berry (FvCB) model using the curve A/C_i (wheat Ecija plots, 2018). The black line is the fit line and the dashed line is the one-to-one line; b) relationships between the average net assimilation (A ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) measured using the photosynthesis chamber at flight time and the simulated V_{cmax} (in black dots) and the V_{cmax} calculated from FvCB model (in blue dots).

468 The relationship between V_{cmax} simulated by SCOPE model inversion and SIF quantified
 469 from the hyperspectral imagery at the different trial sites yielded a significant non-linear
 470 relationship ($r^2 = 0.84$; $p\text{-value} \leq 2.2\text{e-}16$; Fig. 11). Irrigated plots had high SIF values (≥ 4.92
 471 $\text{W}\cdot\text{sr}^{-1}\cdot\text{m}^{-2}\cdot\text{nm}^{-2}$) that were related to large values of V_{cmax} , mainly over $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.
 472 Under the severe water stress conditions in most rainfed plots, V_{cmax} was lower than 90
 473 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. However, for some rainfed plots (Ecija 2018), which were in an early growth
 474 stage and under moderate water stress, V_{cmax} and SIF retrievals were larger than $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
 475 and $5 \text{ W}\cdot\text{sr}^{-1}\cdot\text{m}^{-2}\cdot\text{nm}^{-2}$ for V_{cmax} and SIF, respectively.

Fig. 10. Relationship between carboxylation maximum capacity (V_{cmax} , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) estimated by hyperspectral imagery through SCOPE model inversion and SIF quantified from the hyperspectral imagery, displaying rainfed (red) and irrigated (blue) conditions. Each symbol corresponds with a single plot measurement.

3.4 Relationships between V_{cmax} and net assimilation under irrigation and rainfed conditions

The relationships between net assimilation and SCOPE-estimated V_{cmax} , CWSI, leaf C_{ab} , and NDVI are shown in Fig 13 and Fig 14 for each water regime. The SCOPE-estimated V_{cmax} was significantly correlated with the assimilation rate ($r^2=0.50$, $p\text{-value}=2.91\text{e-}6$) under rainfed conditions. This relationship was stronger under irrigated conditions ($r^2=0.65$, $p\text{-value}=9.31\text{e-}5$). The slightly weaker correlation obtained in rainfed plots could be associated with nutrient and water limitations, as well as an increased influence of background effects under stress conditions. In this context, variation in V_{cmax} was reduced and values were smaller ($< 90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), relative to irrigated conditions.

Fig. 11. Relationships between average assimilation (A ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) measured in leaves and V_{cmax} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) estimated by hyperspectral imagery through SCOPE model inversion under rainfed (red; $n=33$) and irrigated (blue, $n=18$) conditions. The average net assimilation per plot was obtained using two leaves from the top of the canopy and a portable photosynthesis chamber.

486 Net assimilation was significantly related to C_{ab} ($r^2=0.56$; $p\text{-value}=3.93\text{e-}7$), NDVI ($r^2=0.46$;
 487 $p\text{-value}=1.19\text{e-}5$) and PSSR_b ($r^2=0.56$; $p\text{-value}=4.21\text{e-}7$) under rainfed conditions (Fig 12b,
 488 c and d). Under rainfed conditions, chlorophyll indicators (C_{ab} and PSSR_b) had better
 489 correspondence to net assimilation than remote sensing estimates of V_{cmax} ($r^2=0.50$). By
 490 contrast, the relationship between the assimilation rate and the thermal-based CWSI (Fig.
 491 12a) was weak ($r^2 = 0.14$, $p\text{-value} < 0.03$), suggesting that the chronic water-stress may have
 492 resulted in an associated nutrient deficiency that limited assimilation rates. Indeed, net
 493 assimilation under rainfed conditions was more related to nitrogen and pigment indicators
 494 rather than to CWSI. Furthermore, after the supplemental irrigation in the Carmona plots in
 495 2015, photosynthetic rates remained low despite partially recovered water status. For these
 496 plots, CWSI reached values close to 0.4, while assimilation rates were maintained below 15
 497 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Under well-irrigated conditions, the relationships between net assimilation and C_{ab} , NDVI and PSSR_b showed weak, nonsignificant relationships ($r^2 < 0.13$; p-value = 0.83 for leaf C_{ab} content; p-value = 0.41 for PSSR_b; p-value = 0.15 for NDVI, Fig. 12). It is likely that these relationships exhibited scaling problems due to saturation effects associated with high canopy densities in irrigated plots. By contrast, the relationship between net assimilation and CWSI was strongly correlated for irrigated plots ($r^2 = 0.73$, p-value = 1.30×10^{-5}).

The estimation of V_{cmax} as a function of SIF retrievals enabled the calculation of the spatial distribution of V_{cmax} and the net assimilation in the wheat experimental plots (Fig. 15). Pixel-level estimates of V_{cmax} and assimilation (Fig 13) for rainfed and irrigated wheat varieties were retrieved using the regression between SIF and V_{cmax} shown in Fig. 10.

Fig. 12. Relationships between average net assimilation (A , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and (a) CWSI, (b) chlorophyll content (C_{ab} ; $\mu\text{g}\cdot\text{cm}^{-2}$) estimated by PROSPECT-SAILH model inversion, (c) NDVI, and (d) PSSR_b calculated from hyperspectral imagery under rainfed (red points; $n=33$) and irrigated (blue points, $n=18$) conditions. Average net assimilation per plot was obtained from two leaves at the top of the canopy with a portable photosynthesis chamber.

Fig. 13. Maps of Vcmax ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and assimilation rate (A; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) predicted from Vcmax (b), under irrigated and rainfed conditions at SA field site during 2016 airborne campaign.

4. Discussion

Several studies have shown the utility of remotely-sensed SIF as an indicator of the photosynthetic activity at across spatial resolutions (Meroni *et al.*, 2009; Porcar-Castell *et al.*, 2014; Rascher *et al.*, 2015). SIF retrieved from satellite imagery has improved estimations of gross primary productivity at ecosystem to global scales (Frankenberg *et al.*, 2011; Guanter *et al.*, 2014; Smith *et al.*, 2018). However, SIF-GPP relationships require appropriate modelling methods to compensate for structural effects of vegetation canopies (Levula *et al.*, 2019), spatial and temporal scales (Hu *et al.*, 2018), seasonal changes in photosynthetic pigments (Campbell *et al.*, 2018), environmental conditions (Verma *et al.*, 2017) and other confounding factors. In this regard, He *et al.* (2017) showed that the sun-satellite view observation geometry could produce unwanted SIF variations, affecting the

accuracy of GPP. Due to its close link to photosynthetic activity, SIF also has great potential for use in precision agriculture and plant breeding programs. At both global (satellite) and local (airborne and drone) scales, remote estimation of the maximum rate of carboxylation, V_{cmax} is thought to be a suitable proxy for photosynthesis. Zhang *et al.* (2014) demonstrated that estimation of V_{cmax} from space-based SIF retrievals combined with SCOPE simulations in corn and soybean crops was feasible. Nevertheless, further work was needed to understand if these methods are applicable to remote sensing instruments readily available in the context of routine precision agriculture operations and in plant breeding programs. In particular, it is necessary to test whether SIF and V_{cmax} retrievals are feasible with the technical constraints of the spectral resolution available for operational and commercial remote sensing work, the high spatial resolution required, and the general aim of detecting subtle physiological changes across varieties and under water and nutrient stress levels.

The work presented here demonstrates that the V_{cmax} estimated from airborne hyperspectral imagery through SCOPE model inversion was able to detect physiological changes induced by differing irrigation regimes and crop varieties. The relationships between net photosynthetic rates and both measured V_{cmax} and simulated V_{cmax} (Fig 9b) at the Ecija site were significantly correlated ($r^2 \geq 0.68$ and $p\text{-value} \leq 0.005$). The sample size used in the validation of SCOPE-simulated V_{cmax} was low due to the time-consuming nature of obtaining CO_2 response curves. Nevertheless, a larger dataset ($n > 50$) was used to demonstrate the relationship between V_{cmax} retrieved from SCOPE and plant physiological traits (Fig 11 and Fig 12). It demonstrates that V_{cmax} estimates are related to the physiological changes associated to water status. Issues related to the coarser spectral resolution of hyperspectral instruments used in precision agriculture and plant breeding

programs were evaluated with respect to SIF retrieval, and its impact on V_{cmax} estimation, as validated by field measurements of plant traits and net assimilation. In particular, the small plot sizes normally used by plant breeders during their wheat selection trials may limit the accuracy of remotely-sensed SIF. The planting-row designs with 25-cm row spacing used in this study could affect the retrievals of narrow-band and high-resolution hyperspectral (25 cm) and thermal (20 cm) imagery. When the plots are too small, soil and background effects may contaminate the signal due to the mixing of the soil and vegetation reflectance. Therefore, segmentation algorithms should be implemented to reduce soil background effects on estimates of plant physiological traits at canopy level, especially in early growth stages where these effects could significantly reduce the accuracy of retrievals. This issue is especially relevant for coarse-resolution sensors such as the SWIR camera (70 cm) and the thermal sensors. Spatial resolution issues should be considered during the experimental design in breeding programs where the remote sensing sensors are expected to be used.

The SCOPE-simulated radiance data which was convoluted to match the spectral resolution of the airborne hyperspectral imager used in our study was critical for obtaining SIF and V_{cmax} parameters within expected ranges. Analysis confirmed that the canopy structure and the incoming shortwave radiation were the main driving variables for modeled SIF emissions (Verrelst *et al.*, 2015, 2016). In particular, R_{in} had a dominant influence on SIF, as expected based on the pivotal role of PAR load on fluorescence emission. As explained in Van der Tol *et al.* (2014), PAR and V_{cmax} are the main contributors to the fluorescence yield in SCOPE. The effects of chlorophyll content, LAI and R_{in} on the relationship between SIF and V_{cmax} were also included in the sensitivity analysis reported in our manuscript, showing the large

567 impact of C_{ab} on the SIF- V_{cmax} relationships (Fig. 8a), which is in agreement with Koffi *et*
568 *al.* (2015).

569
570 Estimates of V_{cmax} from wheat plot image spectra through SCOPE model inversion were
571 within the ranges reported by other studies for wheat crops ($10\text{--}219\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$;
572 Wullschlegel, 1993; Silva-Pérez *et al.*, 2017). The relationship between the estimated V_{cmax}
573 and chlorophyll fluorescence ($r^2=0.84$; Fig. 10) differed greatly between irrigated and water-
574 stressed plots. As shown in Fig 10, the SIF and V_{cmax} are modulated by water status. In this
575 regard, Zheng *et al.* (2017) showed that photosynthesis at noon is mainly limited by V_{cmax} ,
576 further indicating that V_{cmax} may be a suitable proxy for evaluating plant stress levels. For
577 irrigated conditions, the relationship was almost linear and displayed a steeper slope with
578 larger V_{cmax} values ($\geq 100\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Under water deficit the relationship was weak. As
579 crops reduce stomatal and mesophyll conductance in response to stress, the CO_2
580 concentration within the chloroplast drops, causing a reduction in the photosynthesis capacity
581 (V_{cmax}). Under low CO_2 concentrations, plant carboxylation rates are limited by RuBisCo
582 rather than V_{cmax} (Sharkey *et al.*, 2007). Consequently, under severe water stress, both
583 V_{cmax} and SIF retrievals were suppressed, which is in agreement with the findings by Zheng
584 *et al.* (2017).

585
586 Due to the intensive field-work required to estimate the relationships between A and C_i , the
587 number of observations used to estimate V_{cmax} in the field was small. Nevertheless, our data
588 suggests that simulated V_{cmax} corresponded well with *in situ* measurements. The results
589 were satisfactory ($r^2=0.77$; $p\text{-value} \leq 2.2\text{e-}16$ and $\text{RMSE} = 2.6\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) despite the
590 limited number of leaf V_{cmax} samples, suggesting that V_{cmax} could reasonably be estimated

from SCOPE and convoluted SIF retrievals using hyperspectral imaging technology suitable for precision agriculture. Simulated V_{cmax} yielded a significant relationship with assimilation rate at the Ecija site in 2018 under non severe water stress conditions ($r^2=0.68$; $p\text{-value} \leq 0.005$). These results are in accordance with results obtained by Zhang *et al.* (2014, 2018) in soybean and corn crops. The relationships observed between V_{cmax} and the net photosynthesis (Fig. 11) supports the hypothesis that airborne-quantified V_{cmax} is a feasible indicator of crop functioning under contrasting water regimes. Moreover, we showed (Fig. 12) that in the absence of water stress, V_{cmax} was a stronger predictor of photosynthetic capacity than standard indicators such as C_{ab} , and NDVI and PSSR_b. These indicators likely performed poorly due to scaling problems related to the high canopy densities in irrigated plots. As a result, non-significant relationships were also found between net assimilation and these indices (all $p\text{-value} \geq 0.15$). In dense biomass canopies, the NIR reflectance increases greatly, reducing the sensitivity of the normalized ratios such as NDVI or PSSR_b to plant biochemical content (Thenkabail *et al.*, 2000; Gitelson, 2004).

Under rainfed conditions, i.e. in the presence of water stress, V_{cmax} , C_{ab} and reflectance indices were related to CO_2 assimilation rate, but thermal CWSI was not. Under water stress, stomatal closure reduces the CO_2 concentration inside the chloroplast, decreasing the photochemical activity and also photo-inhibition processes (Flexas and Medrano, 2002). Thus, leaf photochemistry decreases, resulting in a reduction of the chlorophyll fluorescence and RuBisCo activity. The fact that reflectance-based indicators (C_{ab} , PSSR_b, and NDVI) became significantly associated to A , under water stress, suggests that the saturation effects from canopy biomass were not present in rainfed plots. In this study, partial recovery of the water status (as happened in Carmona field in 2015) after severe water stress did not result in

elevated assimilation rates. This suggests that instantaneous assessment of water status might not track photosynthetic performance if severe water stress has affected the photosynthetic apparatus.

From an operational perspective, the remote estimation of V_{cmax} from high-resolution hyperspectral imagery through SCOPE model inversion methods provides a powerful tool to accurately assess crop assimilation rates in large plant breeding programs and in precision agriculture studies. Moreover, its robustness across both irrigated and water-stressed plots was demonstrated when compared against standard reflectance-based remote sensing indicators widely used for crop screening and high-throughput phenotyping.

5. Conclusions

The work presented in this manuscript demonstrates the estimation of maximum rate of carboxylation (V_{cmax}) using SCOPE model inversion with airborne-quantified SIF from hyperspectral imagery. Estimates suitably tracked photosynthetic rates and clearly distinguished physiological differences in irrigated and rainfed conditions. Under water stress, all plant trait indicators performed similarly (V_{cmax} , NDVI, Cab and PSSR_b) and were well related to assimilation rates. Nevertheless, estimated V_{cmax} outperformed standard remote sensing indices for the quantification of crop photosynthesis under irrigated conditions (i.e. in the absence of water stress). The methodology demonstrated in this study is directly relevant for high-throughput plant phenotyping and for precision agriculture applications.

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