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Remote sensing-based estimation of gross primary production in a subalpine grassland

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Abstract

This study investigates the performances in a terrestrial ecosystem of gross primary production (GPP) estimation of a suite of spectral vegetation indexes (VIs) that can be computed from currently orbiting platforms. Vegetation indexes were computed from near-surface field spectroscopy measurements collected using an automatic system designed for high temporal frequency acquisition of spectral measurements in the visible near-infrared region. Spectral observations were collected for two consecu-

tive years in Italy in a subalpine grassland equipped with an Eddy Covariance (EC) flux tower which provides continuous measurements of net ecosystem carbon dioxide (CO_2) exchange (NEE) and the derived GPP.

Different VIs were calculated based on ESA-MERIS and NASA-MODIS spectral bands and correlated with biophysical (Leaf Area Index, LAI; fraction of photosynthetically active radiation intercepted by green vegetation, $fIPAR_g$), biochemical (chlorophyll concentration) and ecophysiological (green light-use efficiency, LUE_g) canopy variables. In this study, the normalized difference vegetation index (NDVI) showed better correlations with LAI and $fIPAR_g$ (r = 0.90 and 0.95, respectively), the MERIS terrestrial chlorophyll index (MTCI) with leaf chlorophyll content (r = 0.91) and the Photochemical Reflectance Index (PRI₅₅₁), computed as $(R_{531} - R_{551})/(R_{531} + R_{551})$ with LUE_g (r = 0.64).

- ²⁰ Subsequently, these VIs were used to estimate GPP using different modelling solutions based on the light-use efficiency model describing the GPP as driven by the photosynthetically active radiation absorbed by green vegetation (APAR_g) and by the efficiency (ε) with which plants use the absorbed radiation to fix carbon via photosynthesis. Results show that GPP can be successfully modelled with a combination of VIs
- and meteorological data or VIs only. Vegetation indexes designed to be more sensitive to chlorophyll content explained most of the variability in GPP in the ecosystem investigated, characterized by a strong seasonal dynamic of GPP. Accuracy in GPP estimation slightly improves when taking into account high frequency modulations of



GPP driven by incident PAR or modelling LUE_g with the PRI in model formulation. Similar results were obtained for both measured daily VIs and VIs obtained as 16-day composite time series and then downscaled from the compositing period to daily scale (resampled data). However, the use of resampled data rather than measured daily input data decreases the accuracy of the total GPP estimation on an annual basis.

1 Introduction

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The availability of simultaneous acquisition of near-surface spectral observations and gas flux measurements quantified with the eddy covariance (EC) technique (Baldocchi et al., 1996) has notably increased in recent years (Sims et al., 2006a; Nakaji et al., 2007, 2008; Hilker et al., 2008a; Cheng et al., 2009; Middleton et al., 2009; Rossini et al., 2010) due to its potential to identify effective links between optical signals and photosynthesis at canopy level (Gamon et al., 2006, 2010). Currently, several research groups have developed different automatic devices to collect canopy spectral properties (Leuning et al., 2006; Hilker et al., 2007; Nakaji et al., 2007, 2008; Daumard et al., 2010; Hilker et al., 2010; Relzarela et al., 2011; Marchi et al., 2011) for

- ¹⁵ 2010; Hilker et al., 2010; Ide et al., 2010; Balzarolo et al., 2011; Meroni et al., 2011) for the purpose of gaining new insights in the quantification and monitoring of plant photosynthesis on a temporal scale. Such devices are generally operated automatically for long periods in the sampling area of flux towers. The increased availability of coupled spectral and flux measurements acquired with comparable temporal and spatial scales
- has encouraged the revision of existing approaches to modelling photosynthesis and the assessment of the potential for using remotely sensed inputs to spatially extrapolate at landscape level predictions of carbon exchange from information acquired at tower sites.

One of the most widely applied approaches to modelling gross primary production (GPP) based on remote sensing (RS) data is the light-use efficiency (LUE) model proposed by Monteith (1972, 1977), in which GPP is modelled as a function of the incident photosynthetically active radiation absorbed by vegetation (APAR), determined as the



product of the fraction of photosynthetically active radiation absorbed by vegetation (fAPAR) and the incident photosynthetically active radiation (PAR), and the conversion efficiency of absorbed energy to fixed carbon (light-use efficiency, ε).

Different studies have used RS derived quantities to feed the LUE model (Hilker ⁵ et al., 2008b; Coops et al., 2010; Rossini et al., 2010; Penuelas et al., 2011).

fAPAR is usually modelled as a function of VIs. Besides the normalized difference vegetation index (NDVI, Rouse et al., 1974), several recent satellite products or indexes (e.g., Enhanced Vegetation Index, EVI, Huete et al., 2002) have been explored to estimate fAPAR. With the advent of hyperspectral RS and the availability of commercial sensors and field instruments the exploration of a number of different wavelengths and VIs has been promoted to estimate *f*APAR (Inoue et al., 2008).

A more challenging component of the Monteith model to be inferred from RS is ε . In most LUE models, ε is expressed as a biome-specific constant at its potential maximum, adjusted for unfavorable environmental conditions (e.g., limitations of tempera-

ture, humidity, soil moisture, etc.) (Nouvellon et al., 2000; Veroustraete et al., 2002; 15 Heinsch et al., 2006). Some attempts have recently been made to directly infer ε from RS data by exploiting variations in vegetation spectral properties resulting from photoprotection, a process closely linked to photosynthesis. For this purpose, Gamon et al. (1990) originally proposed to exploit changes in reflectance in a narrow-waveband interval centered at 531 nm to track the xanthophyll de-epoxidation state and formulated 20 the Photochemical Reflectance Index (PRI, Gamon et al., 1992) as:

$$\mathsf{PRI} = \frac{R_{531} - R_{\mathsf{ref}}}{R_{531} + R_{\mathsf{ref}}}$$

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where R_{ref} is a xanthophyll-insensitive reference band. Several studies have demonstrated that ε can be successfully estimated with PRI at leaf (Meroni et al., 2008a), canopy (Evain et al., 2004; Meroni et al., 2008b) and ecosystem (Drolet et al., 2005, 2008; Middleton et al., 2009) scale.

An alternative approach recently proposed to directly infer ε from RS exploits the link between carbon fixation and sun-induced chlorophyll fluorescence, derived from the



(1)

BGD



oxygen absorption band located at 760 nm (Meroni et al., 2009). Tests of this method have been limited to few studies (Damm et al., 2010; Rossini et al., 2010; Frankenberg et al., 2011) and consequently, the potential of this approach has not yet been fully evaluated.

- ⁵ Another approach to estimating GPP proposed in recent years builds on a simplified version of Monteith's model, which does not need independent estimates of the *f*APAR and the ε terms. Based on the assumption that chlorophyll is related to the presence of photosynthetic biomass, which is essential for primary production and thus conceptually related to GPP (Sellers et al., 1992), recent studies (Gitelson et al., 2008;
- ¹⁰ Harris and Dash, 2010) suggest that GPP can be estimated through direct correlation with chlorophyll-related indexes. Successful results have been obtained in agricultural crops (Gitelson et al., 2008). In these ecosystems, in fact, chlorophyll-related VIs can be considered as a proxy of photosynthesis or primary productivity because, in unstressed conditions, ε tends to be correlated with chlorophyll content, thus making an independent actimate of a unpresence (Sime et al., 2006a). However, these models
- ¹⁵ independent estimate of ε unnecessary (Sims et al., 2006a). However, these models are unable to model high frequency GPP variations due to changing illumination conditions. To take into account these variations, several studies modelled GPP as the product of VIs and the incident PAR (Gitelson et al., 2006; Wu et al., 2009; Peng et al., 2011).
- In this study two years of field spectroscopy measurements acquired with an automatic spectral system (Meroni et al., 2011) on a subalpine grassland equipped with an EC tower have been analyzed to: (1) evaluate the potential of automatic continuous spectral measurements to monitor the seasonal development of a grassland ecosystem; (2) test the performances of different LUE model formulations driven by remote consisting indexes and metagralaginal data to actimate CDP. While several studies have
- 25 sensing indexes and meteorological data to estimate GPP. While several studies have evaluated the possibility of modelling grassland GPP based on remote sensing indexes derived from satellite data (Sims et al., 2006b; Li et al., 2007; Harris and Dash, 2010), we are aware of only one study, by Wohlfahrt et al. (2010), that investigated the relationship between EC-derived carbon fluxes and ground measurement of NDVI collected at



similar temporal (i.e. daily) and spatial scale in a mountain grassland. In this study, near-surface spectral measurements were resampled at the same spectral and temporal resolution as the NASA's Moderate Resolution Imaging Spectrometer (MODIS) and the European Space Agency's (ESA) Medium Resolution Imaging Spectrometer

(MERIS) onboard Envisat to evaluate the usefulness of currently available global satellite mission observations for modeling GPP by means of the LUE approach. Thus, the research presented in this paper is expected to advance our current ability to monitor and model grassland photosynthesis and it should be useful for the future application of these models to better quantify CO₂ fluxes in different terrestrial ecosystems.

10 2 Materials and methods

2.1 Experimental site

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The study site is an unmanaged grassland of the subalpine belt located in the North-Western Italian Alps (45°50′40″ N, 7°34′41″ E, Torgnon, Aosta Valley) at 2160 m a.s.l. (Migliavacca et al., 2011). The vegetation of the site is composed mainly of matgrass and the dominant species are *Nardus stricta, Arnica montana, Trifolium alpinum* and *Carex sempervirens*. The area is classified as an intra-alpine region with semicontinental climate with an annual mean temperature of 3.1 °C and mean annual precipitation of about 920 mm (Mercalli and Berro, 2003). The snow-free period lasts generally from late May to early November.

20 2.2 Biochemical and structural field data

Leaf Area Index (LAI) was determined destructively every two weeks during the two growing seasons (2009 and 2010) at 12 plots of 30 × 30 cm. Collected phytomass was kept on ice and transported to the laboratory. Sample leaves were run through an area meter (Model LI-3100, Li-Cor, Inc., Lincoln NE) and the leaf area index was determined. Total LAI for the 12 plots were then averaged to obtain a site-level value.



Furthermore, in correspondence to the 12 plots identified for LAI estimation, a nadiral picture of an area of 50 × 50 cm of the canopy (identified by a square positioned on the ground) was acquired every week. The collected images were then analyzed with the Wincam software (Regent Instruments Inc., Quebec, Canada) to classify the per ⁵ centage of photosynthetic (green) and non-photosynthetic components of the canopy during the growing season. The percentage of green components of the canopy derived from image classification was fitted with a 4th order polynomial to obtain a daily time series.

The fraction of photosynthetically active radiation intercepted by vegetation (*f*IPAR) was computed using measurements from four LI-190 PAR sensors (Li-Cor, Inc., Lincoln NE): one sensor was installed above the canopy at a height of 2.20 m while three sensors were positioned on ground below the canopy at a distance of approximately 2 m one from the other. fIPAR was then computed as:

 $f | \mathsf{PAR} = \frac{\mathsf{PAR}_i - \mathsf{PAR}_t}{\mathsf{PAR}_i}$

In the grassland studied, yellow and/or dead biomass represented a significant fraction of the above-ground biomass during much of the growing season. To adjust the interception of this non-photosynthetic biomass in the calculation of fIPAR, the fraction of standing green vegetation derived from the analysis of nadiral pictures was multiplied by fIPAR to give an estimation of "green" or photosynthetic fIPAR (fIPAR_g, Hall et al., 1992).

Furthermore, in 2010, leaf samples were collected every ten days at the 12 plots used for LAI estimation. Leaf samples were immediately stored in sealed plastic bags, kept fresh in an ice chest until transported to the laboratory and stored at -80 °C. Leaf pigments were extracted in the following days with *N*,*N*-dimethylformamide (DMF) from

100 mg of fresh biomass. The tissue samples were crushed by adding liquid nitrogen, ground in 10 ml DMF for 2 h and then centrifuged (Thermo Electron Corporation Mod. PK110) at 4000 rpm for 25 min to remove particulates. The absorbance of the extracted solutions was measured at 663.8 and 646.8 nm by a Varian UV-Visible Cary100



(2)

spectrophotometer. Chlorophyll-*a* and chlorophyll-*b* concentrations per unit leaf mass $(\mu g g^{-1})$ were then calculated using the extinction coefficients derived by Porra et al. (1989).

2.3 Eddy covariance and meteorological data

The turbulent vertical fluxes of CO₂ and latent and sensible heat were measured us-5 ing the eddy covariance technique (Baldocchi et al., 1996), according to EUROFLUX methodology (Aubinet et al., 2000). To evaluate temporal variations of CO₂ fluxes and compare these data with spectral measurements, half-hourly measurements of NEE were partitioned to derive GPP. For the gap-filling and partitioning, the marginal distribution sampling (MDS) method and the partitioning method described in Reichstein et al. (2005), implemented in the online tool (http://www.bgc-jena.mpg.de/bgc-mdi/ html/eddyproc/), were used. Different CO_2 flux metrics were used in the analyses: midday mean GPP (GPP_m) for the same time period used for calculating spectral properties (11:00-13:00 local solar time) and daily sums of GPP (GPP_d). A detailed description of the EC flux measurements and flux footprint is reported in Migliavacca 15 et al. (2011). Since only PAR absorbed by photosynthetic pigments (approximated with IPAR_a in this study) enables photosynthesis processes, to provide more realistic LUE estimates, a "green" LUE (LUE_a, Zhang et al., 2009) was computed as:

$$LUE_{g} = \frac{GPP}{fPAR_{g} \times PAR} = \frac{GPP}{PAR_{g}}$$

Along with EC fluxes, the main meteorological variables were measured with a time step of 30 min, among these the incident photosynthetically active radiation (PAR) and air temperature were measured above the grassland by means of a quantum sensor (LI-190s, LI-COR Inc.) and a shielded thermo-hygrometer (HMP45C, Vaisala Inc., Woburn MA, USA), respectively. Precipitation was measured using a tipping bucket rain gauge (CS700, Campbell Scientific, Logan, Utah, USA); soil water content (SWC)



(3)

was measured with water content reflectometers (CS-616, Campbell Scientific, Logan, Utah, USA) installed at two different depths (5–30 cm).

2.4 Radiometric measurements and spectral index computation

Canopy radiance spectra were collected using the HyperSpectral Irradiometer (HSI,
Meroni et al., 2011). This instrument is designed for unattended high temporal frequency acquisition of high spectral resolution radiometric measurements. HSI employs a rotating arm equipped with a cosine-response optic to observe alternately the sky and the target surface, thus allowing the computation of the Bi-Hemispherical Reflectance factor (BHR, Schaepman-Strub et al., 2006). HSI uses two HR4000 (OceanOptics, USA) spectrometers sharing the same optical signal, one covering the visible and near-infrared range (400–1000 nm) with a full width at half maximum (FWHM) of 1 nm, and the other providing higher spectral resolution (0.1 nm FWHM) within a narrower spectral interval (700–800 nm) in the near-infrared. In this study only the visible and near-infrared spectrometer was used. The spectrometer was spectrally calibrated

- ¹⁵ with a source of known characteristics (CAL-2000 mercury argon lamp, OceanOptics, USA), while the radiometric calibration was inferred from cross-calibration measurements performed with a calibrated FieldSpec FS FR spectrometer (ASD, USA). This spectrometer is calibrated by the manufacturer with yearly frequency. Furthermore, the stability of the spectral calibration is regularly assessed during the season using field
- ²⁰ measured data and the SpecCal algorithm (Meroni et al., 2010; Busetto et al., 2011). The instrument was installed in the proximity of the EC tower at a height of 3.5 m above the investigated surface using a dedicated tower, thus allowing the measurement of the BHR with a nadiral viewing geometry. With this configuration, 97% of the total signal comes from a circular ground area with a radius of about 20 m.
- ²⁵ Unattended operations were carried out during the snow-free season in 2009 and 2010. During 2009, the instrument was operated between 9 June and 17 October and in 2010 from 20 May to 15 October. Spectral measurements were acquired every 5 min during daylight hours. Only data collected close to solar noon (between 11:00



and 13:00 local solar time) were used for the analyses to minimize changes in solar angle. The spectral system was operated automatically through dedicated software (Meroni and Colombo, 2009). For each acquisition session the following spectra were collected: spectrometer dark current, incident irradiance, upwelling irradiance and fi-

⁵ nally incident irradiance again. The target measurement was "sandwiched" between two downwelling irradiance measurements collected some seconds apart. The incident irradiance at the time of target measurement was then computed by linear interpolation. For every acquisition, ten scans were averaged and stored as a single file.

Collected data were processed with a specifically developed IDL (ITTvis IDL 7.1.1) application. This application allowed the basic processing steps of raw data necessary for the computation of BHR and the application of a set of quality criteria for automatic data selection, described in Meroni et al. (2011). These criteria are intended to identify poor-quality data due to unfavourable meteorological conditions (e.g. clouds, rain or fog) or instrumental causes (e.g. problems in the optimization procedure). Whenever one of the quality criteria is not satisfied, the measurement is rejected and excluded from further analyses.

For each retained measurement, canopy reflectance spectra were used to simulate MERIS and MODIS spectral bands, on the basis of the spectral bandwidths and spectral response functions of the two sensors. The list of spectral indexes investigated in this study is reported in Table 1. The NDVL EVL and PPL spectral indexes were semi-

this study is reported in Table 1. The NDVI, EVI and PRI spectral indexes were computed from MODIS simulated data, while the MTCI index was computed from MERIS simulated data. In particular, the MODIS PRI was calculated using the MODIS band 11, centered at 531 nm, which is affected by the xanthophyll de-epoxidation state, and the spectral bands 1 (620–670 nm) (PRI₆₄₅), 4 (545–565 nm) (PRI₅₅₅), 12 (546–556 nm)
 (PRI₅₅₁), and 13 (662–672 nm) (PRI₆₆₇) as potential reference bands, in accordance

with recent studies (Drolet et al., 2005, 2008; Goerner et al., 2011).

Daily time series of solar-noon spectral indexes were then computed by daily averaging the values of the indexes collected between 11:00 and 13:00 local solar time. Sixteen-day composite time series of the different indexes were finally derived from



the daily data using the maximum value composite technique to simulate the 16-day dataset routinely produced from MODIS NDVI and EVI and MERIS MTCI acquisitions. The 16-day composite VIs time series were then smoothed with a cubic smoothing spline to downscale from the compositing period to daily VI values (Bradley et al., 2007). We will refer to this VI time series as resampled VIs hereafter in this paper.

2.5 Testing of different RS models to estimate GPP

Four groups of models with an increasing data requirement and complexity (i.e. number of model parameters) were tested to estimate GPP:

i. model 1, direct linear relationship between GPP and a VI related to canopy greenness (VI_{α})

 $GPP = aVI_g + b \tag{4}$

ii. model 2, direct linear relationship between GPP and the product of a VI related to canopy greenness and incident photosynthetically active radiation

 $GPP = a(VI_q \times PAR) + b$

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iii. model 3, LUE model assuming constant ε and fAPAR estimated as a linear function of a VI related to canopy greenness

 $GPP = \varepsilon \times (aVI_{g} + b) \times PAR$

Finally, to overcome the limitation of a constant ε , a fourth set of models in which ε is estimated as a linear function of PRI was tested:

iv. model 4, assuming ε and *f*APAR estimated as a linear function of PRI and VI_g, respectively

$$GPP = (a_0PRI + b_0) \times (aVI_q + b) \times PAR$$



(5)

(6)

(7)

Finally, the widely used LUE model MOD17 (Heinsch et al., 2006), which is the algorithm used for the MODIS gross primary production product, was also included in model comparison. MOD17 is driven by meteorological variables (air temperature and VPD), PAR and *f*APAR. In this study, *f*APAR is estimated as a linear function of VI_g, so the resulting model formulation is:

$$\mathsf{GPP} = \varepsilon_{\max} \times (a\mathsf{VI}_{\mathsf{g}} + b) \times \mathsf{PAR} \times f(\mathsf{VPD}) \times f(\mathcal{T}_{\min})$$

where ε_{max} is the maximum radiation use efficiency (g C MJ¹); *f* (VPD) and *f*(T_{min}) varied linearly between 0 and 1 as a consequence of suboptimal temperatures and water availability for photosynthesis. We use site measurements of PAR, VPD and T_{min} to feed the MOD17 algorithm. To take into account the nonlinear relationship between GPP and the incident PAR (Gilmanov et al., 2007), the inclusion of In(PAR) instead of PAR in model formulations was also tested. Models 1 to 4 were tested using both the measured and resampled VI time series and midday average or daily value of the measured meteorological variables. The performances of MOD17 were evaluated using measured and resampled VI time series and daily meteorological variables.

2.6 Statistical analysis

Pearson's correlation analysis was used to test the significance of relationships of VIs and biochemical and structural field data. Model coefficients were derived by fitting each model against both the daily midday average GPP estimated with the eddy covariance technique (GPP_m, µmol CO₂ m⁻² s⁻¹) and the daily cumulated GPP (GPP_d, g C m⁻² d⁻¹) for each day where HSI data were available and for the resampled VI time series. Model coefficients and their relative standard errors were estimated using the Gauss-Newton nonlinear least square optimization method (Bates and Watts, 1988), implemented in the R standard package (R, version 2.6.2, R Development Core Team, 2011). The main fitting (determination coefficient r² and root mean square error RMSE) and cross-validated statistics (r_{cv}^2 and RMSE_{cv}) obtained with the *k*-fold crossvalidation procedure were computed to compare performances of different groups of



(8)

models. The *k*-fold cross-validation approach (Hastie et al., 2001) divides the data into k subsets, then the model is fitted using (k - 1) subsets as the training set and the validation is conducted using the omitted subset. In this study, the *k* subsets were defined by partitioning the dataset into 10 ordinal subsets of equal length (each subset corre-

⁵ sponds to 1-month data). This approach is more restrictive than the random definition of the *k* subsets and was chosen to assess the model performances when large gaps occurred in the data time-series (Richardson et al., 2006). Finally, the Akaike information criterion (AIC, Akaike, 1973) was adopted to compare performances of the various model formulations.

10 3 Results

3.1 Seasonal variation of meteorological and biophysical variables

During the snow-free period (DOY 146–306 and DOY 143–303 in 2009 and 2010, respectively), the average midday PAR was 1390 and 1305 μ mol m⁻² s⁻¹ in 2009 and 2010, respectively, having maximum values of about 2050 μ mol m⁻² s⁻¹ (Fig. 1a).

- For the same period, the average midday air temperature was 19.2 and 19.7 °C in 2009 and 2010, respectively (Fig. 1b). The total amount of precipitation (Fig. 1c) during the snow-free period markedly differed in the two years: 172 mm in 2009 and 362 mm in 2010. The precipitation amount recorded in 2010 was similar to the long-term average (400 mm, 1927–2001) in the same area (Mercalli and Berro, 2003), while 2009 was particularly dry. Soil water content (SWC) was strongly related to precipitation inputs during the growing season. As a consequence, the average seasonal SWC in 2010 was higher (24.6 mm³ mm⁻³) than in 2009 (15.0 mm³ mm⁻³). In particular, in 2010 there was a precipitation event exceeding 65 mm (DOY 226) which considerably affected SWC. Leaf area index increased from May and reached its annual maximum in mid July in both years (Fig. 2a). The maximum LAI in 2009 was 2.7 m² m⁻² (DOY 194).
- slightly lower than the $3 \text{ m}^2 \text{ m}^{-2}$ in 2010 (DOY 201). LAI decreased earlier and steeper



in 2010 than in 2009 autumn. The variation of leaf chlorophyll content during the growing season was measured only in 2010 (Fig. 2b). The first available sampling was on DOY 176, when the chlorophyll content was already high. It peaked at around DOY 201, as did LAI, and after that it started to decrease. The seasonal pattern of IPAR_m

- ⁵ (Fig. 2c) showed an increasing trend at the beginning of the growing season, it reached a maximum in about early August and then remained quite stable, with a slightly decreasing course. Therefore, IPAR_m failed to detect the reduction of PAR absorbed by the canopy and thus used for CO₂ fixation at the end of the growing season when the canopy was dominated by yellow and dead material. This trend was instead captured
 ¹⁰ by (IPAR_g)_m (Fig. 2d). Both IPAR_m and (IPAR_g)_m were also characterized by consider-
- able day-to-day oscillations due to variations in the ratio of direct to diffuse radiation.

3.2 Seasonal variability of spectral data

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HSI was operated for 130 days in 2009 (9 June-17 October) and 148 days in 2010 (20 May-15 October). A total of 7331 spectra were collected in the time-window used

in the present study. Of these, 32.5 % was not considered in the following analyses since they did not fulfil the data-quality criteria. Most data were rejected due to instable meteorological conditions, typical of the study site, while only a small percentage was rejected due to instrument failures (Table 2).

Figure 3 shows the daily time series of midday (11:00–13:00) VIs computed from HSI data.

In both years, measurements started about two weeks after snow melting when the grassland was already greening. As the growing season proceeded, all the vegetation indexes except PRI_{555} and PRI_{551} increased as a result of green biomass accumulation, reaching maximum values in July (around DOY 190) at the same time as maximum

LAI and (IPAR_g)_m. Then, in the senescent phase of the grassland (from August on), indexes decreased due to plant yellowing and wilting. The patterns of MTCI resembled that of NDVI but, due to the higher sensitivity of MTCI to chlorophyll content with respect to NDVI (Dash and Curran, 2004), it started to decrease earlier. The EVI dynamics,



as compared with other VIs, showed a higher scatter, in particular for high EVI values. This result confirmed a previous study by Miura et al. (2000) which demonstrated that EVI uncertainties tended to increase with increasing VI values and attributed this uncertainty to the inclusion of the blue band in VI formulation for EVI values above 0.4

⁵ (between DOY 180 and 225 in our study). PRI₆₄₅ and PRI₆₆₇ exhibited a pattern similar to other VIs, while PRI₅₅₅ and PRI₅₅₁ showed an opposite trend characterised by a progressive decrease at the beginning of the growing season up to maximum canopy development and a slower increase in the senescent phase. The most notable differences between the two years analysed were observed in the seasonal dynamics of MTCI and PRI_{645/677} between DOY 220 and 250.

3.3 Retrieval of biochemical, biophysical and ecophysiological variables from HSI data

The higher sensitivity of MTCI to chlorophyll content was confirmed by the correlation analysis. MTCI correlated with ChI content with an *r* of 0.91 (*p* < 0.001), followed by NDVI (*r* = 0.80, *p* < 0.01) and EVI (n.s.) (Table 3). NDVI was the VI that related best to total green LAI (*r* = 0.90, *p* < 0.001) and *f*IPAR_g (*r* = 0.95, *p* < 0.001). PRI₅₅₁ was instead the index best related to LUE_g (*r* = 0.64, *p* < 0.001). The correlation between PRI using reference band 4 at 555 nm (PRI₅₅₅) and LUE_g was similar to that obtained for a PRI using reference band 12 at 551 nm (PRI₅₅₁); while the correlations between PRI using reference band 1 at 645 nm (PRI₆₄₅) or band 13 at 645 nm (PRI₆₆₇) and LUE_g were weaker.

3.4 Comparison of VIs and micrometeorological measurements

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The comparison between seasonal variations of VIs and variables derived from EC measurements (Fig. 4) showed that the temporal behaviour of VIs related to canopy chlorophyll content (i.e. MTCI, Fig. 3) tracked quite well the one of GPP_m (Fig. 4a).



In 2010, both MTCI and GPP_m tracked a rebound around DOY 240, probably caused by a rain pulse that occurred on DOY 226 (Fig. 1c). Seasonal courses of PRI₆₆₇ and PRI₆₄₅ were more similar to those of MTCI than PRI₅₅₅ or PRI₅₅₁. Although PRI₆₆₇ and PRI₆₄₅ were supposed to be a proxy for (LUE_g)_m the correlation analysis confirmed that in this study they were correlated most with leaf chlorophyll content and fIPAR_g. The different concavity of PRI₅₅₅ or PRI₅₅₁ compared to PRI₆₆₇ or PRI₆₄₅ can be explained by the different position of the reference bands on the grassland spectra (Fig. 5). Bands 4 and 12 (551 and 555 nm band center wavelength, respectively) fell on the peak of vegetation reflectance in the green region while bands 1 and 13 (645 and 667 nm, respectively) were in the chlorophyll absorption well in the red region of the spectrum. Thus, bands 4 and 12 always had a higher value than band 11 (531 nm) during the growing season. On the contrary, bands 1 and 13 were much higher than band 11 at the beginning and end of the growing season, while they had similar values during maximum canopy development (July and August).

 $(LUE_{a})_{m}$ (Fig. 4b) showed high values at the beginning of the growing season, with 15 a maximum around DOY 165, corresponding to a LAI of $1.5 \text{ m}^2 \text{ m}^{-2}$ in both 2009 and 2010, and then it suddenly started to decrease. In both years, $(LUE_{\alpha})_{m}$ exhibited indistinct seasonality from around DOY 190 to 250, but day-to-day fluctuation, especially on cloudy and partly cloudy days (Fig. 1b) and in correspondence of sharp meteorological events. As an example, the 68 mm precipitation event that occurred on DOY 226 in 2010 caused a sudden increase in SWC and appeared to stimulate $(LUE_{\alpha})_m$ which started to increase and reached a value of 0.048 μ mol CO₂ μ mol⁻¹ photon on DOY 236. From DOY 250 on, $(LUE_{a})_{m}$ started to increase probably due to the reduction of the incoming PAR (Fig. 1b). Finally, LUE_a dropped after DOY 280, when the canopy was composed almost entirely by yellow and dead material. A similar seasonal course was 25 observed for both PRI555 and PRI551, thus suggesting that these PRI formulations were the best suited to track $(LUE_{\alpha})_m$ in this ecosystem. Better performances of these reference bands confirmed previous studies by Middleton et al. (2009) on a Douglas-fir



the hypothesis that the suitability of different reference wavelengths may depend on species composition and stand structure (Gamon et al., 1992; Goerner et al., 2011).

3.5 Evaluation of different RS models to estimate GPP

3.5.1 Measured time series

⁵ The summary statistics in fitting and cross-validation of different models tested in this study for GPP estimation starting from HSI data are shown in Tables 4 and 5. All different VIs combinations were tested and are discussed in the following sections.

The regression analysis (model 1) confirmed that vegetation indexes averaged over midday hours explained most of the variability in GPP averaged over that same period (GPP_m) and in daily GPP (GPP_d). MTCI was the best predictor for both GPP_m 10 and GPP_d with a RMSE_{cv} of 1.50 μ mol CO₂ m⁻² s⁻¹ and 0.74 g C m⁻² d⁻¹, respectively, followed by NDVI and EVI. The inclusion of incident PAR as a multiplicative term of VI_a in model formulation (model 2) decreased model performances in GPP_m estimation up to a RMSE_{cv} of almost double relative to the corresponding model 1. As an example, RMSE_{cv} of the model fitted against MTCI increased from 1.50 up to 3.30 μ mol CO₂ m⁻² s⁻¹ and AIC increased from 157 to 417. Similar results were obtained on including the PAR in the form of model 3 when the model was fitted against GPP_m, thus yielding a RMSE_{cv} between 2.99 and 3.53 μ mol CO₂ m⁻² s⁻¹ (depending on the vegetation index used). The same occurred for GPP_{d} estimation with an increase of RMSE_{cv} of the model driven by MTCI (the best-performing index) from 20 $0.74 \text{ g Cm}^{-2} \text{ d}^{-1}$ to $1.17 \text{ g Cm}^{-2} \text{ d}^{-1}$ (model 2) and $0.99 \text{ g Cm}^{-2} \text{ d}^{-1}$ (model 3). Thus, in the majority of cases PAR did not appear to be a useful model component in estimating GPP. On the contrary, results obtained with model 2 including the logarithm of the incident PAR in the model, as the product between VI and In(PAR), showed an improvement of the performances in both GPP_m and GPP_d estimation. The extent of 25 the improvement changed with the different indexes considered. Similar results were obtained with model 3 formulation.



The use of PRI to estimate ε tended to increase model performances, in particular when it was used in combination with MTCI to estimate *f*APAR. Better results in both GPP_m and GPP_d estimation were obtained when ln(PAR_m) was used instead of PAR_m. This class of models showed the best performances in estimating GPP_m with a RMSE_{cv}.

of 1.42 μmol CO₂ m⁻² s⁻¹, estimating *f*APAR as a function of MTCI and ε as a function of PRI₅₅₅. It is interesting to note that this model also showed the lowest AIC, despite the increase in the number of model variables with respect to model 1. The best-performing model in estimating GPP_d was instead model 2 with ln(PAR_d) and *f*APAR estimated as a function of MTCI. MOD17, in which ε was expressed as constant ε at its potential maximum adjusted for unfavorable *T*_{min} and VPD, showed a RMSE_{cv} between 0.78 g C m⁻² d⁻¹ for the model driven by MTCI and ln(PAR_d) and 1.57 g C m⁻² d⁻¹ for the model driven by EVI and ln(PAR_d). These results were slightly poorer than those obtained on estimating ε as a function of PRI and, due to the higher complexity of this model, it had a higher AIC.

15 3.5.2 Resampled time series

Results obtained on performing the same analysis on data aggregated at the 16-day time scale and then downscaled to a daily time step (Tables 6 and 7) confirmed overall those obtained by feeding models with data measured at a daily step. MTCI was the best estimator of *f*APAR in models 1, 2 and 3 for both GPP_m and GPP_d estimation;
²⁰ In(PAR) performed better than PAR in models 2, 3 and 4, and the improvement in using In(PAR) instead of PAR was higher for GPP_m estimation. Regarding MOD17, the use of In(PAR) instead of PAR increased the performances in GPP estimation only when it was used in combination with MTCI. Models performing better in estimating GPP_m based on the AIC value were model 1 estimating *f*APAR as a function of MTCI and model 4 performances.

estimating *f*APAR as a function of MTCI and ε as a function of PRI₅₅₅. Model 2 driven by MTCI and In(PAR) was instead the one that performed better in GPP_d estimation.



To obtain an overall view of the capability of different models to represent the seasonal time courses of GPP, we compared EC daily observations (EC-GPP) and daily model outputs obtained with the best-performing model for each class fed with both measured and resampled daily inputs (RS-based estimation of GPP, RS-GPP) (Fig. 6).

- ⁵ Both measured and resampled daily RS-GPP values agreed quite well with EC-GPP as concerns both amplitude and seasonal phase and successfully described the dynamics captured by tower fluxes. As noticeable in Fig. 6, the limitation behind the use of resampled rather than measured daily inputs to model seasonal GPP trends was their inability to model GPP day-to-day variations. Even though the statistics in fitting (r^2
- and RMSE) and cross-validation (r_{cv}^2 , RMSE_{cv} and AIC) of different models fed with resampled VIs were in most cases better than their daily counterpart, these models had poorer performances in predicting the sums of daily GPP related to the two growing seasons. Figure 7 shows the sums of daily GPP estimated using the best-performing model for each class. Considering the days for which both spectral and eddy data were
- ¹⁵ available (i.e. 130 and 148 days in 2009 and 2010, excluding a few instrumental gaps), the sums of daily GPP for the analysed periods calculated from EC-GPP were 473.8 and 421.2 g C m⁻² in 2009 and 2010, respectively. The use of RS data to estimate total GPP made it possible to obtain good estimates with both measured and resampled daily inputs. However, absolute average errors in GPP estimation using daily inputs
- ²⁰ ranged from 0.5 to 1.2 % with models 2 and 1, respectively, and from 1.8 to 2.8 % with models 3 and 1 respectively using resampled data inputs. MOD17 fed by both RS and meteorological inputs produced an average error of 2.4 % in GPP estimation using daily inputs and 1.8 % using resampled data inputs. In general, in 2009 RS-GPP_{res} tended to underestimate the EC-GPP_d. This was caused by the inability of RS- GPP_{res}
- to track the peak of EC-GPP_d occurring between DOY 180 and 210 and the recovery of EC-GPP_d at the end of the growing season (DOY 260–290). On the contrary, in 2010, RS-GPP_{res} tended to overestimate the EC-GPP_d, it being more evident at the end of the growing season.



4 Discussion

Unattended high temporal and spectral resolution canopy spectra coupled with EC data were acquired for two consecutive years on a subalpine grassland to exploit different strategies for evaluating the potential of RS in estimating carbon uptake. Collected data

- ⁵ were processed using automatic procedures which took into account a series of quality criteria related to the illumination conditions during the acquisition and the system performances and reliable time series of VIs providing useful information on the time course of different grassland variables have been obtained. In particular, MTCI was the index most related to ChI content and NDVI to *f* IPAR_g and LAI (Table 3). More-
- over, PRI computed using a reference band at 555 nm (PRI₅₅₅) and 551 nm (PRI₅₅₁) showed better correlations with LUE_g, with a coefficient of correlation of 0.63 and 0.64, respectively. This value lies in the range of previous studies at canopy level, recently reviewed by Garbulsky et al. (2011). However, these studies often analyse the relationships between PRI and light-use efficiency, computed as GPP/APAR or GPP/incident
- ¹⁵ PAR, while we are not aware of studies evaluating the relationship between PRI and ε expressed in terms of LUE_g. In this study, an attempt to estimate LUE_g was made. Due to the uncertainty in the quantification of the photosynthetically active radiation effectively used to drive photosynthesis (APAR_g) (Serrano et al., 2000; Di Bella et al., 2004), the strength of the relationship between PRI and LUE_g can be lowered with respect to
- ²⁰ previous studies. It is worth noting that, as opposed to PRI_{555/551}, PRI computed using a reference band positioned in proximity of the chlorophyll absorption well, i.e. 1 and 13 (PRI_{645/667}), were more closely related to leaf chlorophyll concentration than LUE_g (Table 3). So the choice of the reference band to be used to compute PRI appears to play a key role in the determination of the sensitivity of this index to photosynthetic
- efficiency. This result confirmed recent studies by Middleton et al. (2009) and Goerner et al. (2011), although we believe that further studies are needed to explore the best reference band for estimating PRI across vegetation types and temporal scales.



Most VIs peaked in the first half of July, in correspondence to maximum canopy development, attested by maximum values of LAI and GPP (Figs. 2, 3 and 4). However, due to the different sensitivity of VIs to grassland variables, their minimum and maximum values occurred at different DOYs and their slope changed in time. For example,

- ⁵ PRI₅₅₅ and PRI₅₅₁ had a less distinct seasonal course and they reached minimum values about 10–20 days after full canopy development. This time-lag observed between the peak of PRI_{555/551} and indexes using red bands can be explained by considering selective light absorption by photosynthetic pigments. Chlorophyll controls the energy flux that can be transferred to the dark reaction of photosynthesis and, because of the lower chlorophyll absorption of green light (Terashima et al., 2009), indexes based
- on green wavebands may therefore reach their peak later in the season compared to indexes involving a strong chlorophyll absorption band in the red spectral region.

The analysis conducted with LUE models indicated that GPP can be successfully modelled using RS indexes or combining RS indexes with meteorological data. Results of model 1 confirmed that VI related to canopy greenness explained most of the

- ¹⁵ sults of model 1 confirmed that VI related to canopy greenness explained most of the variability in GPP in an ecosystem characterized by a strong seasonality in green-up and senescence (Gitelson et al., 2006; Wu et al., 2009). MTCI was the best predictor for both GPP_m and GPP_d, followed by NDVI and EVI, respectively. This sequence precisely reflects the strengths of the relationship between VI_a and chlorophyll concen-
- tration. Furthermore, this result confirmed better performances of MTCI, with respect to EVI, in estimating GPP in grassland ecosystems (Harris and Dash, 2010). As observed in previous studies (Wu et al., 2009; Harris and Dash, 2010; Peng et al., 2011), chlorophyll content is a main driver of seasonal carbon dynamic and thus provides a dominant indicator of CO₂ exchange in ecosystems characterised by strong sea-
- ²⁵ sonality such as grasslands. However, as highlighted by Gitelson et al. (2008), the limitation behind this model formulation is that variations in GPP due to short-term (hours to days) variations of illumination or environmental stresses (such as temper-ature and water availability), cannot be estimated by VI alone. This limitation was overcome by exploiting models 2 and 3, which take into account variations related to



changing incident irradiance. Somewhat surprisingly, the inclusion of incident PAR in model formulation did not result in improved estimation of GPP. However, using In(PAR) instead of PAR in model parameterization, the accuracy of GPP estimation improved. This means that the grassland increases its efficiency at low values of incident PAR

- while, given its moderate LAI and erectophile leaf angle distribution, it is not able to fully exploit high radiation loads. This higher efficiency with low PAR can probably result from more diffuse light incidence within the canopy, less photoinhibition on the top of the canopy and consequently a reduced tendency toward saturation (Chen et al., 2009). Furthermore, in our case, low PAR conditions can probably be associated with
- precipitation events and associated SWC increases which stimulate photosynthetic ef-10 ficiency (Polley et al., 2011). Another possible explanation is that low PAR conditions can also be related to a decrease in temperature. Alpine plants are adapted to living in low temperatures (Billings and Mooney, 1968) and can cope with this temperature decrease by enhancing their photosynthetic systems and increasing their carbon fixation
- (Korner and Diemer, 1987). 15

To account for stress-induced changes in photosynthetic efficiency, the PRI was also tested to directly infer ε from RS data. The inclusion of PRI in model formulation showed slight improvement in GPP estimation, in particular for that of GPP_m. Physiologically, this means that in our ecosystem APAR_a is coupled with ε , and the inclusion

- of the ε term in the model slightly improves its ability to track seasonal variations. Sim-20 ilar results were obtained by Rossini et al. (2010) and Gitelson et al. (2006) in other ecosystems characterised by strong seasonal variability (crops). These results were compared with those obtained with the widely used MOD17 algorithm, in which ε is modulated as a function of meteorological conditions. Our results indicate that when
- ε and fAPAR are estimated as linear functions of PRI and VI (i.e. model 4) the GPP 25 is generally estimated with higher accuracy rather than MOD17 (Table 5) in which the ε parameter is instead modulated as a function of meteorological conditions. In this study, the vegetation indexes tested were calculated with reflectances simulated in the spectral bands of the MODIS and MERIS sensors. The temporal resolution of VI time



series can theoretically influence the ability to estimate GPP from satellite data, since the temporal dynamics inherent in plant photosynthesis requires frequent observations of vegetation status. To evaluate the effect of acquisition frequency on GPP estimation, 16-day composite time series of MODIS- (i.e. NDVI, EVI and PRI) and MERIS-derived (MTCI) products were simulated and downscaled to daily frequency and results were compared. Short-term variability (hours to days) in both VIs and flux data is damp-

- ened out by averaging data over one or two weeks, thus leading to obtain good performances when fitting GPP against resampled VIs (Tables 6 and 7). However, when these models are used to simulate annual GPP, they inevitably introduce a decrease
 in the accuracy of total GPP estimation. The results from models driven only by RS and PAR variables were as good as, and in many cases better than, the more complex
- MOD17 GPP model which requires meteorological and vegetation type data inputs in addition to remote sensing indexes.
- This study provides a conceptual background for GPP estimation using real satellite data and a better understanding the spatio-temporal variations of productivity. The choice of the index depends on the spectral characteristics of the satellite sensor being used. In particular, MTCI can be derived from satellite systems with spectral bands in the red edge region (MERIS in this study), EVI and NDVI from satellites having blue, red and near-infrared bands (MODIS in this study) and PRI from satellites with a narrow
- ²⁰ green band centered at 531 nm (MODIS in this study). Our results show that red edge indexes like MERIS can be used both as single variables or in combination with PRI and meteorological variables to obtain accurate estimations of GPP in a grassland ecosystem. Unfortunately, the computation of MTCI and PRI from a single satellite is currently not feasible because no in-orbit sensor has the right spectral bands. The
- ²⁵ launching of new image spectrometers, such as the NASA HyspIRI or the DLR EnMAP, will allow the calculation of a greater number of indexes, including MTCI and PRI, thus offering significant potential to enhance the accuracy of the assessment of CO₂ uptake in terrestrial ecosystems from space. Finally, we remark that NDVI and EVI showed poorer performances when used as single variables to predict GPP and it is preferable



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to use these indexes in combination with PRI and meteorological variables to improve accuracy in GPP estimation.

5 Conclusions

This study investigated the potential of automatic continuous near-surface spectral measurements to monitor the seasonal development of a grassland ecosystem and to evaluate different strategies for terrestrial ecosystem GPP estimation. The main outcomes of this research can be summarized as follows:

- continuous field spectroscopy measurements provided reliable information on the seasonal variations of vegetation biophysical and ecophysiological variables with daily temporal resolution. The correlation analysis between VIs and different canopy variables suggested the possibility of using NDVI as an indicator of LAI and *f*IPAR_g (*r* = 0.90 and 0.95, respectively), the MTCI of leaf chlorophyll content (*r* = 0.91) and the PRI₅₅₁ of LUE_g (*r* = 0.64);
- the spectral vegetation index designed to be more sensitive to chlorophyll content explained most of the variability in GPP in the ecosystem investigated, which was characterized by a strong seasonal dynamic of green up and senescence;
- accuracy in GPP estimation improved when taking into account high frequency modulations of GPP driven by incident PAR (in the form of In(PAR)) or modelling LUE_g with the PRI in model formulation; the model formulation which gave the best results in GPP estimation was based on *f*APAR_g estimated as a function of MTCI and ε as a function of PRI₅₅₁;
- results from models driven only by PAR and RS indexes were in many cases better than those from the MOD17 model which requires meteorological and vegetation type data inputs in addition to remote sensing indexes;



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- the use of VIs obtained as 16-day composite time series, simulating the 16-day dataset produced from satellite acquisitions, and then downscaled from the compositing period to daily scale rather than measured daily input data, decreased the accuracy of the total GPP estimation on the annual basis.
- The approach proposed in this study finds application within the framework of the established SpecNet (Gamon et al., 2010) and recent activities related to the EuroSpec COST action which propose to collect spectral data continuously, regularly and from a worldwide network in connection with the well-established network of flux towers (FLUXNET). Furthermore, improvements in operational LUE algorithms for monitoring
 global GPP are desirable in the context of efforts to understand trends in global carbon uptake.

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Table 1. Spectral vegetation indexes investigated in this study: normalized difference vegetation index, NDVI; Enhanced Vegetation Index, EVI; MERIS terrestrial chlorophyll index, MTCI; photochemical reflectance index, PRI. *R* is the reflectance at the specified wavelength (nm). $R_{\rm ref}$ used in this study are 645, 555, 551 and 667 nm.

Index	Formulation	Reference
NDVI	$(R_{858.5} - R_{645})/(R_{858.5} + R_{645})$	Rouse et al. (1974)
MTCI	$(R_{753.75} - R_{708.75})/(R_{708.75} - R_{681.25})$	Dash and Curran (2004)
EVI	$2[R_{858.5} - R_{645}]/[1 + R_{858.5} + 6R_{645} - 7.5R_{460}]$	Huete et al. (2002)
PRI _{ref}	$(R_{531} - R_{ref})/(R_{531} + R_{ref})$	Gamon et al. (1992)



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 Table 2. Data collected by HSI during the study period.

Year	No. of spectra analysed	No. of retained spectra	% of rejected spectra
2009	3217	2135	33.6
2010	4114	2814	31.6

Table 3. Coefficients of correlation (*r*) between the HSI VIs and ancillary and eddy data (LUE_g) measured at the study site. *n* is the number of samples for each correlation analysis. The asterisk indicates significance of correlation: ****p* < 0.001; ***p* < 0.01; **p* < 0.05; n.s.: not significant (Pearson's correlation test). The VI best-correlated with each variable is in bold print.

Index	LAI (<i>n</i> = 16)	Chl (<i>n</i> = 11)	$f_{\rm g}~(n=162)$	LUE _g (<i>n</i> = 162)
NDVI	0.90***	0.80**	0.95***	-0.55***
MTCI	0.79***	0.91***	0.81***	-0.30***
EVI	0.78***	n.s.	0.82***	-0.37***
PRI ₆₄₅	0.83***	0.86***	0.86***	-0.39***
PRI ₅₅₅	-0.73***	n.s.	-0.71***	0.63***
PRI ₅₅₁	-0.84***	n.s.	-0.86***	0.64***
PRI ₆₆₇	0.86***	0.84***	0.89***	-0.42***



Table 4. Summary of statistics in fitting (r^2 and RMSE) and cross-validation (r_{cv}^2 , RMSE_{cv} and AIC) of different models tested in this study using average GPP_m and PAR_m data. The best-performing model in each class is in bold print.

Model	RS data	Meteo data	r ²	$r_{\rm cv}^2$	RMSE	RMSEcy	AIC
			-	-	µmol C0	O ₂ m ^{−2} s ^{−1}	-
1	MTCI	-	0.89	0.88	1.47	1.50	157
	NDVI	-	0.71	0.62	2.40	2.72	354
	EVI	_	0.44	0.31	3.32	3.68	454
2	MTCI	PAR _m	0.52	0.45	3.06	3.30	417
	NDVI	PAR _m	0.45	0.34	3.28	3.58	445
	EVI	PAR _m	0.46	0.36	3.26	3.55	442
	MTCI	In(PAR _m)	0.88	0.88	1.53	1.56	169
	NDVI	In(PAR _m)	0.71	0.64	2.37	2.64	344
	EVI	In(PAR _m)	0.54	0.43	2.99	3.35	423
3	MTCI	PAR _m	0.55	0.54	2.98	2.99	385
	NDVI	PARm	0.42	0.35	3.38	3.56	443
	EVI	PAR _m	0.49	0.36	3.18	3.53	440
	MTCI	In(PAR _m)	0.90	0.89	1.42	1.44	143
		IN(PAR _m)	0.72	0.64	2.34	2.66	347
		(1 A 1 m)	0.52	0.40	5.00	0.42	400
4	MTCI, PRI ₅₅₅	PAR _m	0.56	0.55	2.93	2.98	384
	NDVI, PRI ₅₅₅	PARm	0.54	0.39	3.01	3.46	433
			0.03	0.47	2.00	3.21	400
		In(PAR _m)	0.90	0.90	1.39	1.42	138
	EVI. PBI	$\ln(PAR_m)$	0.56	0.38	2.94	3.48	436
	MTCL PRI	PAR	0.56	0.54	2 95	3.01	387
	NDVI. PRI551	PAR	0.54	0.36	3.00	3.53	440
	EVI, PRI ₅₅₁	PARm	0.57	0.45	2.90	3.29	417
	MTCI, PRI551	In(PAR _m)	0.90	0.89	1.40	1.44	143
	NDVI, PRI ₅₅₁	In(PAR _m)	0.87	0.78	1.61	2.06	261
	EVI, PRI ₅₅₁	In(PAR _m)	0.53	0.11	3.04	4.18	496



Table 5. Summary of statistics in fitting (r^2 and RMSE) and cross-validation (r_{cv}^2 , RMSE_{cv} and AIC) of different models tested in this study using GPP_d and PAR_d data. The best-performing model in each class is in bold print.

Model	RS data	Meteo data	r ²	r _{cv} ²	RMSE	RMSE _{cv}	AIC
			_	-	gun	n u	-
1	MTCI	-	0.88	0.88	0.72	0.74	-121
	NDVI	-	0.67	0.59	1.21	1.34	157
	EVI	-	0.43	0.31	1.58	1.75	281
2	MTCI	PAR	0.71	0.69	1.12	1.17	95
	NDVI	PARd	0.67	0.62	1.21	1.30	144
	EVI	PAR _d	0.70	0.65	1.14	1.24	121
	MTCI	In(PAR _d)	0.92	0.91	0.61	0.62	-199
	NDVI	In(PAR _d)	0.73	0.67	1.08	1.21	108
	EVI	In(PAR _d)	0.54	0.45	1.42	1.56	229
3	MTCI	PAR	0.78	0.78	0.98	0.99	17
-	NDVI	PAR	0.69	0.65	1.17	1.24	122
	EVI	PARd	0.73	0.67	1.10	1.22	112
	MTCI	In(PAR _d)	0.90	0.90	0.65	0.66	-170
	NDVI	In(PAR _d)	0.71	0.64	1.13	1.26	130
	EVI	In(PAR _d)	0.51	0.40	1.47	1.63	249
4	MTCL PBI	PAR	0 79	0 78	0.95	0.99	18
	NDVI, PRI	PAR	0.78	0.76	0.98	1.03	36
	EVI, PRI ₅₅₅	PARd	0.80	0.75	0.94	1.04	41
	MTCI, PRI	In(PAR _d)	0.91	0.90	0.64	0.67	-163
	NDVI, PRI555	In(PAR _d)	0.88	0.86	0.72	0.79	-90
	EVI, PRI ₅₅₅	In(PAR _d)	0.56	0.45	1.39	1.56	227
	MTCI, PRI551	PAR _d	0.79	0.78	0.96	1.00	19
	NDVI, PRI ₅₅₁	PAR _d	0.78	0.76	0.98	1.03	34
	EVI, PRI ₅₅₁	PAR _d	0.77	0.70	1.02	1.16	88
	MTCI, PRI551	In(PAR _d)	0.91	0.90	0.64	0.68	-162
	NDVI, PRI ₅₅₁	ln(PAR _d)	0.88	0.86	0.72	0.79	-88
	EVI, PRI ₅₅₁	ln(PAR _d)	0.51	0.33	1.47	1.72	273
MOD17	MTCI	PAR _d , <i>T</i> _{min} , VPD	0.82	0.78	0.89	0.99	15
	NDVI	PAR _d , T _{min} , VPD	0.72	0.66	1.12	1.22	115
	EVI	PAR _d , T _{min} , VPD	0.74	0.62	1.07	1.29	141
	МТСІ	In(PAR _d), T _{min} , VPD	0.90	0.86	0.66	0.78	-95
	NDVI	In(PAR _d), T _{min} ,VPD	0.61	0.58	1.31	1.36	164
	EVI	In(PAR _d), <i>T</i> _{min} ,VPD	0.55	0.44	1.41	1.57	231

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Table 6. Summary of statistics in fitting (r^2 and RMSE) and cross-validation (r_{cv}^2 , RMSE_{cv} and AIC) of different models tested in this study using GPP_d and PAR_d data. The best-performing model in each class is in bold print.

Model	RS data	Meteo data	r ²	$r_{\rm cv}^2$	RMSE	RMSE _{cv}	AIC
			-	- µmorCO ₂ m s		J ₂ m ⁻s ′	-
1	MTCI	_	0.87	0.86	1.53	1.60	166
	NDVI	_	0.72	0.64	2.24	2.55	312
	EVI	_	0.62	0.49	2.63	3.04	366
2	MTCI	Par _m	0.47	0.37	3.11	3.39	400
	NDVI	Par _m	0.37	0.23	3.38	3.73	430
	EVI	Par _m	0.41	0.29	3.26	3.60	418
	MTCI	in(PAR_m)	0.85	0.84	1.63	1.70	187
	NDVI	In(PAR _m)	0.71	0.64	2.29	2.55	312
	EVI	In(PAR _m)	0.64	0.53	2.54	2.91	353
3	MTCI	Par _m	0.47	0.45	3.11	3.15	377
	NDVI	Par _m	0.36	0.30	3.40	3.56	415
	EVI	Par _m	0.32	0.24	3.51	3.70	427
	MTCI	In(PAR _m)	0.88	0.87	1.50	1.56	159
	NDVI	In(PAR _m)	0.74	0.66	2.19	2.49	305
	EVI	In(PAR _m)	0.64	0.53	2.54	2.93	355
4	MTCI, PRI ₅₅₅	PAR _m	0.47	0.43	3.11	3.21	383
	NDVI, PRI ₅₅₅	PAR _m	0.41	0.27	3.28	3.63	421
	EVI, PRI ₅₅₅	PAR _m	0.44	0.23	3.19	3.74	431
	MTCI, PRI ₅₅₅	In(PAR _m)	0.88	0.86	1.48	1.62	171
	NDVI, PRI ₅₅₅	In(PAR _m)	0.78	0.65	1.99	2.52	307
	EVI, PRI ₅₅₅	In(PAR _m)	0.79	0.35	1.97	3.43	404
	MTCI, PRI ₅₅₁	Par _m	0.47	0.43	3.10	3.21	383
	NDVI, PRI ₅₅₁	Par _m	0.41	0.29	3.27	3.59	417
	EVI, PRI ₅₅₁	Par _m	0.42	0.23	3.25	3.73	430
	MTCI, PRI ₅₅₁	In(PAR _m)	0.88	0.85	1.49	1.63	173
	NDVI, PRI ₅₅₁	In(PAR _m)	0.78	0.68	2.01	2.42	296
	EVI, PRI ₅₅₁	In(PAR _m)	0.75	0.40	2.13	3.30	391



Table 7. Summary of statistics in fitting (r^2 and RMSE) and cross-validation (r_{cv}^2 , RMSE_{cv} and AIC) of different models tested in this study using GPP_d and PAR_d data. The best-performing model in each class is in bold print.

Model	RS data	Meteo data	r ²	r ² _{cv}	RMSE	RMSE _{cv}	AIC
			-	-	gCn	$n^{-2} d^{-1}$	-
1	MTCI	-	0.89	0.88	0.69	0.72	-120
	NDVI	-	0.72	0.63	1.10	1.25	117
	EVI	-	0.69	0.60	1.15	1.31	137
2	MTCI	PAR _d	0.73	0.70	1.08	1.13	75
	NDVI	PAR _d	0.64	0.59	1.23	1.32	141
	EVI	PAR _d	0.67	0.62	1.18	1.27	125
	MTCI	In(PAR _d)	0.92	0.91	0.58	0.61	-191
	NDVI	In(PAR _d)	0.77	0.70	0.98	1.13	72
	EVI	in(PAR _d)	0.74	0.67	1.04	1.19	95
3	MTCI	PAR _d	0.77	0.77	0.98	0.99	16
	NDVI	PAR _d	0.69	0.65	1.15	1.22	108
	EVI	PAR _d	0.66	0.62	1.19	1.28	126
	MTCI	In(PAR _d)	0.91	0.90	0.61	0.64	-170
	NDVI	In(PAR _d)	0.75	0.68	1.02	1.17	89
	EVI	In(PAR _d)	0.72	0.64	1.08	1.23	111
4	MTCI, PRI ₅₅₅	PAR _d	0.77	0.77	0.98	1.00	20
	NDVI, PRI ₅₅₅	PAR _d	0.73	0.66	1.08	1.19	98
	EVI, PRI ₅₅₅	PAR _d	0.74	0.71	1.04	1.10	63
	MTCI, PRI ₅₅₅	ln(PAR _d)	0.91	0.88	0.61	0.71	-124
	NDVI, PRI ₅₅₅	In(PAR _d)	0.81	0.62	0.89	1.27	123
	EVI, PRI ₅₅₅	In(PAR _d)	0.84	0.75	0.82	1.02	31
	MTCI, PRI ₅₅₁		0.77	0.77	0.98	0.99	18
	NDVI, PRI ₅₅₁	PAR _d	0.72	0.66	1.08	1.21	102
			0.73	0.00	1.07	0.00	00
		In(PARd)	0.91	0.89	0.01	1.04	-144
	EVI PRI	In(PAR_)	0.81	0.04	0.90	1.24	79
	201,111551		0.01	0.00	0.00		10
MOD17	MTCI	PAR _d , T _{min} , VPD	0.80	0.73	0.93	1.07	49
		PAR _d , <i>I</i> _{min} , VPD	0.70	0.63	1.13	1.26	120
	EVI	PAR_d, T_{min}, VPD	0.71	0.62	1.11	1.27	120
			0.90	0.83	1.00	1.40	-45
		$\ln(PAR_d), T_{min}, VPD$	0.60	0.54	1.31	1.40	165
		$m(rAn_d), r_{min}, VFD$	0.00	0.54	1.55	1.40	103

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Fig. 1. Seasonal variation of midday average air temperature (Air T, °C) **(a)** and PAR (μ mol m⁻² s⁻¹) **(b)** in 2009 (solid line) and 2010 (dotted line); precipitation (mm) in 2009 (black bars) and 2010 (white bars) and soil water content (SWC, %) at 10 cm **(c)** in 2009 (solid line) and 2010 (dotted line).





Fig. 2. Seasonal variation of Leaf Area Index (LAI, $m^2 m^{-2}$) in 2009 (full dots and solid line) and 2010 (empty dots and dotted line) **(a)**, leaf chlorophyll concentration (ChI, $\mu g g^{-1}$) in 2010 **(b)**, midday IPAR (IPAR_m, $\mu mol m^{-2} s^{-1}$) in 2009 (full dots) and 2010 (empty dots) **(c)** and midday green IPAR ((IPAR_g)_m), $\mu mol m^{-2} s^{-1}$) in 2009 (full dots) and 2010 (empty dots) **(d)**. For LAI and ChI, each point indicates the average value (± standard deviation, *n* = 12).





Fig. 3. Seasonal temporal profiles of measured vegetation indexes in 2009 (full dots) and 2010 (empty dots): **(a)** NDVI, **(b)** MTCI, **(c)** EVI, **(d)** PRI₆₄₅, **(e)** PRI₅₅₅, **(f)** PRI₅₅₁ and **(g)** PRI₆₆₇. Each point indicates the average value between 11:00 and 13:00 (local solar time).





Fig. 4. Seasonal variation of midday gross primary productivity (GPP_m, μ mol CO₂ m⁻² s⁻¹) (a) and midday green LUE ((LUE_g)_m), μ mol CO₂ μ mol⁻¹ photon) (b) in 2009 (full dots) and 2010 (empty dots).





Fig. 5. Temporal changes of monthly grassland reflectance spectra collected at midday during 2009. Grey and shaded areas represent the position and bandwith of the MODIS spectral bands used to compute PRI.





Fig. 6. Time courses of daily GPP ($gCm^{-2}d^{-1}$) estimated from EC measurements (EC-GPP) (full circles), GPP modelled (open circles) with models fed with measured daily inputs (RS-GPP_d) and GPP modelled (full triangles) with models fed with resampled daily inputs (RS-GPP_{res}) in 2009 (left panels) and 2010 (right panels). The best performing formulation of each class of models is shown: model 1 parameterized with MTCI (**a** and **b**), model 2 parameterized with MTCI and In(PAR) (**c** and **d**), model 3 parameterized with MTCI and In(PAR) (**e** and **f**), model 4 parameterized with MTCI, PRI₅₅₅ and In(PAR) (**g** and **h**), and MOD17 parameterized with MTCI and In(PAR) (**i** and **j**).





Fig. 7. Cumulated daily GPP (g C m⁻²) estimated from EC measurements, modelled with daily measured and resampled inputs in 2009 (left bars) and 2010 (right bars).

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