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Vertical patterns of photosynthesis and related leaf traits in two contrasting agricultural crops

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top/bottom-leaf model; leaf area index; canopy nitrogen.

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Abstract

13 To include within-canopy leaf acclimation responses to light and other resource gradients in photosynthesis modelling, it is imperative to understand the variation of leaf structural, 14 biochemical and physiological traits from canopy top to bottom. In this study, leaf 15 16 photosynthetic traits for top and bottom canopy leaves, canopy structure and light profiles, were measured over one growing season for two contrasting crop types, winter barley 17 (Hordeum vulgare L.) and rape seed (Brassica napus L.). With the exception of quantum yield, 18 other traits such as maximum photosynthetic capacity (Amax), dark respiration, leaf nitrogen 19 and chlorophyll contents, and leaf mass per area, showed consistently higher (p < 0.05) values 20 for top leaves throughout the growing season and for both crop types. Even though Amax is 21 22 higher for top leaves, the bottom half of the canopy intercepts more light and thus contributes the most to total canopy photosynthesis up until senescence sets in. Incorporating this 23 knowledge into a simple top/bottom-leaf upscaling scheme, separating top and bottom leaves, 24 25 resulted in a better match between estimated and measured total canopy photosynthesis, compared to a one-leaf upscaling scheme. Moreover, aggregating to daily and weekly temporal 26 27 resolutions progressively increased the linearity of the leaf photosynthetic responses to light 28 for top leaves.

Keywords: photosynthesis; leaf trait; photosynthesis trait; upscaling; one-leaf model;

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1. Introduction

32 Leaves within a canopy have access to analogous below-ground nutrients and water resources, 33 while light conditions they experience vary greatly depending on their position within the canopy, particularly as a function of height. Among the factors affecting plant functioning, 34 35 light is perhaps the most spatially (i.e., vertical gradient) and temporally heterogeneous, 36 although closed canopies are typically characterized by a drop in light availability from canopy top to bottom (Pearcy 1999). Within-canopy light gradients, which define the past and current 37 light exposure of a given leaf, trigger acclimation responses through variations in leaf structural, 38 39 biochemical and physiological traits (Niinemets et al. 2015). The type of acclimation response is often optimized for the particular species. In slow leaf turnover species, mostly populating 40 the northern forest ecosystems, the light regime at a specific height within the canopy is 41 relatively constant after canopy closure and a passive photosynthesis acclimation response 42 occurs mostly by changes of leaf structural traits to light (Niinemets et al. 2015; Coble et al. 43 44 2016). In contrast, fast leaf turnover species such as grasses and agricultural crops, are characterized by highly dynamic light environments within their canopies (Husse et al. 2016). 45 46 In agricultural crops, every new leaf is born as a sun leaf and as leaves age they occupy successively more poorly lit positions within the plant canopy. The short phenological cycles, 47

and shade acclimation times, in crop species make it unprofitable for the plants to invest in
 slow structural changes (Wright *et al.* 2004; Niinemets *et al.* 2015) and active changes of
 photosynthesis by nitrogen (N) reallocation are rather predominant within the canopy.

Under low light conditions plants need to invest in proteins for building light capturing 51 structures, e.g. chlorophyll a and b, while sunlit leaves invest less in light capturing and more 52 in proteins involved in the assimilation of intercellular CO₂, e.g. in RuBisCO (Evans and 53 Poorter 2001). As both, the RuBisCO and the electron transport limited rate of carboxylation, 54 are expensive in terms of N, there is potentially a trade-off in the investment in structures that 55 increase the capacity for light capture and carbon (C) assimilation (Chen et al. 1993; Niinemets 56 1998). Accordingly, the allocation of resources in light or C capturing structures will point to 57 potential environmental constraints on photosynthesis at a specific leaf position. Commonly, 58 59 N concentrations have repeatedly been shown to increase from bottom to top of canopy, where 60 ample light is available for higher photosynthetic C fixation (De Pury and Farquhar 1997; Evans and Poorter 2001; Kattge et al. 2009; Coble and Cavaleri 2015). At the canopy level 61 however, light availability and interception by leaves, and thus total canopy photosynthesis, 62 ultimately depend on canopy architecture. Canopy architecture, mainly defined by leaf 63 arrangement in space, known as foliage clumping index (Gonsamo and Pellikka 2009), leaf 64 angle and area, can widely vary across crop species, resulting in different light interception for 65 photosynthesis (Falster and Westoby 2003). Therefore, in order to include within-canopy leaf 66 acclimation responses to light and other resource gradients in crop photosynthesis modelling. 67 it is imperative to understand the variation of leaf structural, biochemical and physiological 68 69 traits from canopy top to bottom (De Pury and Farquhar 1997).

Crop photosynthesis is a key driver in many crop models. Photosynthesis models for 70 agricultural crops have evolved from simple statistical modeling of the photosynthetic light 71 response (Blackman 1905) and its upscaling to canopy level (Monsi and Saeki 1953), to linking 72 73 crop growth simulation models with light response functions (e.g., (De Wit 1978)). At the crop canopy scale, radiation use efficiency (RUE), representing crop growth stage in many crop 74 models (Parent et al. 2015), has been successfully used to simulate the total photosynthesis of 75 a given canopy avoiding the need for photosynthesis upscaling (Monteith JL and Moss 1977; 76 Sinclair and Muchow 1999). The RUE concept first introduced by Monteith (1972) states that 77 78 net C gain is a function of the amount of absorbed photosynthetically active radiation (APAR) and the RUE with which vegetation converts the APAR into biomass. The simple empirical 79 linear relationship based on RUE however lacks proper representation of structural, 80 biochemical and physiological processes required to capture canopy photosynthesis responses 81 82 to vertical resource gradients and environmental cues.

On the other hand, mechanistic models of photosynthesis, based on key biochemical 83 processes of photosynthesis, have been developed at the leaf level (Farquhar et al. 1980; von 84 Caemmerer and Farquhar 1981; Farquhar and von Caemmerer 1982; von Caemmerer 2000) 85 and up-scaled to the canopy level following various schemes (Norman and Jarvis 1974; 86 Norman and Welles 1983; Sellers et al. 1992; Leuning 1995; De Pury and Farquhar 1997). The 87 two most commonly used upscaling schemes are, the big-leaf approach, which treats a canopy 88 89 as a big-leaf (Sellers et al. 1992; Sands 1995), and the sun/shade leaf approach, which partitions a canopy into sunlit and shaded leaf types (Sinclair et al. 1976; De Pury and Farquhar 1997). 90 The latter approach can use either single or multiple layers with canopy leaf area index (LAI) 91 in each layer(s) partitioned into sunlit and shade leaf fractions; typically the fraction of sunlit 92 93 leaves decreases going from top to bottom canopy layers (De Pury and Farquhar 1997). Most mechanistic models use a variety of big-leaf or sun/shade leaf schemes, which in some cases 94 have the framework to incorporate vertical gradients of canopy structural (Hammer and Wright, 95 1994) and leaf biochemical traits throughout the crop life cycle, the latter especially via 96 relationship with the canopy leaf nitrogen profile (de Pury and Farquhar, 1997). Additionally 97

to these consolidated state-of-the-art approaches, in more recent years new schemes that
connect biochemical processes with crop growth and development dynamics are getting
traction (e.g., (Yin and van Laar 2005; Parent *et al.* 2015; Wu *et al.* 2016)).

Although key to guide modelling efforts, there is to our knowledge a shortage of experimental 101 studies quantifying changes of multiple leaf traits in field crops in function of leaf position and 102 at different times during the season. Most previous studies focused on nitrogen reallocation 103 within the crop canopy (Pons and Pearcy 1994; Vos and van der Putten 2001), with a few meta-104 analysis studies tackling multiple species and traits worldwide (e.g., see Niinemets et al. 2015). 105 In this study, we report on experimental observations of leaf photosynthetic traits for two crop 106 107 types, winter barley (Hordeum vulgare L.) and rape seed (Brassica napus L.), with contrasting canopy architecture, at two positions, canopy top and bottom, and over the growing season. 108 We hypothesize that leaf position in these crop types influences photosynthesis and related leaf 109 110 traits and that bottom leaves provide an important contribution to total canopy photosynthesis, often overlooked in approaches estimating total photosynthesis based on top leaves only. Our 111 objectives thus are: (1) to understand how leaf position within the canopy, linked with the light 112 regime experienced by a leaf, influences photosynthesis and underlying traits in barley and 113 rape seed cropping-systems over the season; and (2) to assess whether differentiating top and 114 bottom leaves, and thus partitioning the canopy to specifically account for the contribution of 115 the bottom part throughout the season, improves the estimation of total canopy photosynthesis. 116 To tackle the second objective, we apply simple upscaling schemes. It should be noted that the 117 aim of this study is not to develop a new upscaling scheme requiring additional field 118 119 measurements. We farther compare our simple upscaling schemes with an approach typically used with satellite based remote sensing observations and employing the RUE concept. To this 120 regard we are particularly interested to evaluate whether nonlinear processes such as leaf 121 photosynthesis response to light can effectively be linearized if integrated over longer time 122 123 scales.

124

2. Methods

125 **2.1 Study site and sampling scheme**

126 The study was conducted at the arable field site near the town of Oensingen (47°17'11.1" N, 127 7°44'01.5" E, 452 m a.s.l.) on the Central Swiss Plateau, one of the most productive agricultural 128 regions of Switzerland. The cropland is managed under the regulations of the Proof of 129 Ecological Performance (PEP), with a crop rotation mainly focusing on winter wheat, 130 alternating with winter barley, rape seed, peas, potatoes and intermediate cover crops (Emmel 131 *et al.* 2017). The climate is temperate continental, with annual rainfall of 1100 mm and an 132 average annual temperature of 9°C.

A field campaign took place during the 2015 growing season on the main field (CH-Oe2) 133 134 planted with winter barley (Hordeum vulgare L.), and on the adjacent field where rape seed was grown (Brassica napus L.). Sowing occurred at the beginning (06/09/2014) and at the end 135 (29/09/2014) of September of the previous year for rape seed and barley, respectively; harvest 136 took place beginning of July (04/07/2015) for barley and mid of July (17/07/2015) for rape 137 138 seed. Measurements started in mid of April when canopies reached a height of 25 cm, which allowed partitioning into a top and a bottom canopy layer, and continued at weekly intervals 139 until the lower canopy started senescing in the beginning of June. 140

The spatial sampling in both fields included one transect for leaf-level measurements and one parallel transect for leaf area index (LAI) measurements (Fig. 1). Leaf-level measurements were taken at five locations along the transect, each 5 m apart, and at two canopy heights. The definition of a top and a bottom canopy was based on its partitioning into two layers of equal vertical extent. At each location along the transect one attached healthy, green, fully expanded leaf was measured at each height. Measurements included i) optical leaf properties using an 147 ASD field spectrometer (ASD Inc. Boulder, CO, USA); ii) photosynthesis light response curves using a LI-6400 portable gas exchange system (LI-COR, Lincoln, NB, USA); and iii) 148 leaf chlorophyll (Chl) content using the chlorophyll content meter (CCM-300, Opti-Sciences 149 Inc., Hudson, NH, USA). The same leaves were sampled and brought back to the laboratory 150 151 for i) LAI determination using scans and subsequent image analysis with the ImageJ-based software Fiji (ImageJ Version 2.0.0,); ii) dry weight determination following drying leaves in 152 55°C: 153 oven for 48 hours at and iii) measurement of С and an 154 N elemental content. The measurement of the elemental carbon (% C) and elemental nitrogen (% N) content was performed using a Flash EA 1112 Series elemental analyzer (Thermo Italy, 155 former CE Instruments, Rhodano, Italy) coupled to a Finnigan MAT Delta^{plus}XP isotope ratio 156 mass spectrometer (Finnigan MAT, Bremen, Germany) as described by Brooks et al. (2003) 157 and . LAI measurements were taken at ten locations along the second transect, each 5 m apart, 158 159 and at five equally spaced heights within the canopy (5, 30, 55, 80 and 105 cm above ground for barley, and 5, 35, 65, 95, 125 cm for rape seed) using a LAI-2000 Plant Canopy Analyzer 160 (LI-COR) under mostly overcast conditions. A 90° view cap was used for the LAI-2000 161 162 measurements. Top measurements were repeated at every point along the transect, or every second, depending on the stability of the illumination conditions. 163

In addition to measurements performed at regular intervals during the 2015 field campaign, 164 the Oensingen research site (CH-Oe2) features a closed-path eddy covariance (EC) system for 165 continuous gas exchange and climatological measurements since December 2003. The EC 166 system consists of an R3-50 three-dimensional ultrasonic anemometer (Gill Instruments Ltd., 167 Lymington, Hampshire, UK) and a LI-7500 open-path infrared gas analyser (LI-COR), both 168 delivering data at 20 Hz. Since 2014, a Unispec-DC dual channel spectro-radiometer (PP-169 Systems, Amesbury, MA, USA) measuring incoming light and light reflected by the underlying 170 vegetation in 256 contiguous bands (350-1200 nm) is operational at the site. 171

172 Fig 1. Here

173 **2.2 Photosynthetically active radiation measurements**

174 At the beginning of the 2015 growing season two stationary profile systems measuring photosynthetically active radiation (PAR) located at five different heights were installed at a 175 representative location within the barley and the rape seed fields. Each system consisted of five 176 SQ-110 quantum sensors (Apogee Instruments Inc., Logan, Utah, USA) and a CR10X data 177 logger (Campbell Scientific Inc., Logan, UT, USA). Measurement heights above ground 178 corresponded to those at which LAI measurements were taken (barley: 5, 30, 55, 80, 105 cm; 179 rape seed: 5, 35, 65, 95, 125 cm). The upwards facing sensors were installed on the south side 180 of the boom and slightly offsetted to avoid self-shading. Measurements were made every 181 second and recorded as 1-minute averages with standard deviations. The PAR sensors were 182 calibrated using a reference PAR lite photosynthetic active radiometer (Kipp & Zonen, Delft, 183 184 The Netherlands).

185 To verify field horizontal homogeneity and representativeness of measurements by the 186 stationary profile systems, two additional mobile PAR profile systems were installed at other 187 locations in the fields for shorter periods during the growing season. The within-field 188 intercomparison provided enough confidence for the use of one system (data not shown).

189 Continuous light penetration profiles for both crop fields were obtained by iteratively fitting 190 a logistic function of height to the minute resolution data acquired by the stationary PAR profile 191 systems. In a second step, continuous light penetration profiles were spatially integrated (i.e., 192 vertically) for each of the two canopy layers, i.e., top and bottom canopy, using daily canopy 193 height measurements that allowed to estimate the PAR absorbed by each layer at hourly, daily 194 and weekly resolutions.

195 **2.3 Leaf-level photosynthesis measurements**

196 Net photosynthesis light response curves (LRCs) were measured on selected leaves using the LI-6400 portable gas exchange system and the standard leaf chamber with the 6400-02B 197 198 red/blue LED source. Leaves were placed into the LI-6400 leaf chamber at environmental conditions controlled for temperature, set to optimal 20° C, and CO₂, set to ambient 400 µmol 199 mol⁻¹. Flow rate was set to 500 μ mol s⁻¹. Humidity was monitored throughout the 200 measurements and regulated through manual scrubbing to keep it around 65%. LRCs were 201 measured going from light to dark, i.e., leaves were equilibrated to high PAR (2000 µmol m⁻² 202 s^{-1}), followed by a stepwise decrease of PAR down to zero (1800, 1500, 1000, 800, 600, 400, 203 200, 100, 50, 0 μ mol m⁻² s⁻¹). The leaf was given enough time to equilibrate at each light level 204 205 following pre-set stability criteria. The field campaign started several weeks after the beginning 206 of the growing season when leaves had already acclimated to high light levels. Thus going 207 from high to low light levels was not expected to result in saturation of the photosynthetic 208 pathway, which earlier in the season could instead lead to non-photochemical quenching. 209 Moreover, tests on field-grown plants in a previous study (Singsaas et al. 2001) found that 210 starting LRC at low light could lead to limitation of photosynthesis at high light due to 211 insufficient stomatal opening.

The photosynthesis rate as a function of absorbed light was described using the Mitscherlich
 response model (Mitscherlich 1928) as:

214 An =
$$(Amax + Rd) \left(1 - \exp\left(\frac{-\phi APAR}{Amax + Rd}\right)\right) - Rd$$
 (1)

215 In Eq. 1, An is net photosynthesis and APAR is the incident light corrected for the absorption 216 capacity of the specific leaf. APAR is the closest estimate of light between 400 - 700 nm truly 217 absorbed by the leaf. It is often approximated as equivalent to the incident light but in reality amounts to ca. 80% of it and varies in function of biochemical and structural leaf traits. Leaf 218 219 APAR was estimated by measuring optical leaf properties, i.e., leaf reflectance and 220 transmittance spectra, using the ASD Field Spectrometer and a leaf clip with an built-in halogen 221 light source. Ten spectra were averaged per measurement and the leaf absorbance spectrum was calculated from the reflectance and transmittance spectra. Values of incident light by the 222 223 embedded LI-6400 Red/Blue LED source were subsequently corrected by the derived leaf 224 spectral absorption coefficients. Physiological leaf traits were parametrized in the Mitscherlich 225 model (Eq. 1) as ϕ , the slope of the linear part of the light response curve, also called apparent 226 quantum yield; Amax, the asymptote representing photosynthesis at light saturation, also called 227 maximum photosynthetic capacity, and Rd, the dark respiration rate. The Mitscherlich model 228 was chosen because its variables have a physiological meaning. Curve fitting was done using 229 a nonlinear least squares procedure, and variables (ϕ , Amax, Rd) were extracted for each curve. 230 The sample size for each date and at each of the two canopy heights was of five leaves, corresponding to the five locations along the transect. Variables were estimated for each leaf 231 232 and, only in a second step, averaged to obtain representative field level estimates for top and 233 bottom canopy leaves, as well as over time since no clear seasonal trend was identified for the 234 investigated time window.

235 **2.4 Estimations of canopy photosynthesis from leaf-level measurements**

236 2.4.1 Leaf-to-canopy photosynthesis upscaling schemes

Four different leaf-to-canopy photosynthesis upscaling schemes were evaluated (Table 1). Each scheme is distinct in the way it deals with two aspects: 1) the relationship between photosynthesis response and light; and 2) the variation of leaf traits within a canopy.

For the first aspect, we evaluated upscaling approaches based on linear and nonlinear photosynthesis responses to light. While nonlinear approaches draw their rationale from the relationship between photosynthesis and absorbed light at the leaf scale, known to be strongly
nonlinear, linear approaches are based on the RUE concept introduced by Monteith (1972). In
the present study, the RUE term is defined as the C uptake (defined as gross primary production,
GPP) divided by the irradiance (defined as absorbed PAR) (Gitelson and Gamon 2015).

For the second aspect, we compared upscaling schemes partitioning the canopy into a top and a bottom layer, referred to as top/bottom-leaf models, with those that consider the canopy as a single entity, referred to as one-leaf models. In all cases, gross leaf-level photosynthesis was obtained as the sum of net photosynthesis (A_n) and dark respiration (Rd).

Table 1. here

251 **2.4.2 Leaf Area Index for leaf-to-canopy photosynthesis upscaling**

The LAI-2000 plant canopy analyzer was used in this study for the derivation of discrete LAI and mean leaf tilt angle (MTA) values. Measurements above and below a canopy layer were used to determine the canopy gap fraction, from which the LAI and MTA are computed (Lang 1986; Gonsamo *et al.* 2018).

Continuous LAI time series for top and bottom canopy layers, used for the upscaling of leaf 256 photosynthesis to canopy level, were derived by combining temporally discrete LAI 257 measurements performed at five heights within the canopy with the continuous light 258 penetration estimates from PAR profiles (see section 2.2). A four-step procedure was adopted 259 260 as follows: (i) height-specific relative PAR time series were obtained by dividing daily average PAR values at the specific height by the incoming daily average PAR at top of the canopy, to 261 which a double logistic function of time was fitted; (ii) the light extinction coefficient for each 262 cumulative layer was derived by an iterative search for the denominator that minimized the 263 difference between the fitted daily relative PAR time series and the corresponding discrete LAI 264 measurements (this resulted in the continuous cumulative LAI time series for the four layers 265 266 0-100 cm, 25-100 cm, 50-100 cm, 75-100 cm); (iii) continuous vertical profiles of cumulative LAI for each single day were obtained by fitting a logistic function of canopy depths to the 267 cumulative LAI values; (iv) top and bottom canopy LAI time series were estimated by 268 269 integrating continuous vertical profiles of cumulative LAI within the extents corresponding to the top and to the bottom canopy layers. Measurements of canopy height were used to 270 determine the extents of top and bottom canopy in time. 271

272 **2.5** Approaches to estimate gross photosynthesis productivity

273 **2.5.1 Eddy covariance (EC) technique**

GPP from EC was calculated based on a hyperbolic light response curve fit to daytime net 274 275 ecosystem CO₂ exchange (NEE) measured at the flux tower site (i.e., CH-Oe2), modified to account for the temperature sensitivity of respiration and the vapor pressure deficit (VPD) 276 limitation of photosynthesis (Lasslop et al. 2010). The partitioning was done with the R 277 package, REddyProc, by MPI Jena. When observations were not available, gap-filled data were 278 279 generated using the Marginal Distribution Sampling (MDS) method, i.e., a moving look-up table technique that uses similar meteorological conditions (of a fixed margin) sampled in the 280 temporal vicinity of the gap to be filled (Moffat et al. 2007). 281

282 2.5.2 Remote sensing

GPP from spectral measurements was estimated using an approach in line with those
commonly adopted by Production Efficiency Models (PEMs) in satellite-based studies.
Specifically, we followed the MODIS GPP (MOD17) model (Running *et al.* 2004):

286
$$GPP = \varepsilon_{max} \times TMIN_s \times VPD_s \times PAR \times FPAR$$

(2)

287 where ε_{max} (gC MJ⁻¹) is the maximum RUE when the environment is not limiting for plant CO₂ 288 uptake. TMIN_s and VPD_s are the attenuation scalars for the daily minimum temperature (TMIN) 289 and daily VPD. These scalars vary linearly between 0 and 1 as a consequence of suboptimal 290 temperature and water availability. For example, high VPD is known to induce stomata closure 291 while low temperatures are known to inhibit the photosynthesis process in many species. The 292 values of the scalars were computed with the following simple linear ramp functions:

293
$$TMIN_{s} = \frac{TMIN - TMIN_{min}}{TMIN_{max} - TMIN_{min}}$$
(3)
294
$$VPD_{s} = \frac{VPD_{max} - VPD}{VPD_{max} - VPD_{min}}$$
(4)

where TMIN_{max} and TMIN_{min} are daily minimum temperatures at $\varepsilon = \varepsilon_{max}$ and $\varepsilon = 0$, 295 respectively; and VPD_{max} and VPD_{min} are daylight vapor pressure deficits at $\varepsilon = 0$ and $\varepsilon = \varepsilon_{max}$, 296 respectively. The MOD17 type of model employs specific parameters available from the 297 Biome-Properties-Look-Up-Table (BPLUT) for each biome category. For cropland in MOD17 298 299 Collection 5.1, the ε_{max} , TMIN_{min}, TMIN_{max}, VPD_{min}, and VPD_{max} are defaulted as 1.044 gC MJ⁻¹, -8.00°C, 12.02°C, 650 Pa, and 4300 Pa, respectively (Zhao and Running 2010). PAR is 300 301 given by the photosynthetically active radiation incident on the canopy for which above canopy PAR profile measurements are used. FPAR (dimensionless) is the fraction of incident PAR 302 303 absorbed by the canopy, which we approximate with the normalized difference vegetation index (NDVI) derived from reflectance spectra obtained from UniSpec-DC measurements 304 (Gitelson et al. 2014). 305

3. Results

307 3.1 Leaf photosynthesis traits as a function of leaf position

306

We assessed top and bottom canopy differences in eight key leaf structural (leaf mass per unit 308 area, LMA; leaf area per leaf, LA; leaf mean tilt angle, MTA), chemical (N, C and chlorophyll, 309 Chl, contents) and physiological (quantum yield, ϕ ; maximum photosynthetic capacity, Amax; 310 dark respiration, Rd) traits that play an important role in photosynthesis dynamics. For both 311 crops, barley and rape seed, traits differed between top and bottom leaves, with top leaves 312 313 showing consistently higher values, with the only exception of ϕ and LA, which were higher for bottom leaves (Fig. 2). These leaf position dependent patterns remained mostly stable 314 throughout the measurement campaign of ca. 1.5 months, between mid of April and beginning 315 of June 2015, leading up to ripening and senescence of the crops. A two-sample t-test 316 examining the significance of differences between top and bottom canopy leaves, resulted in 317 the null hypothesis of equal means of top and bottom leaves being rejected for all of the 318 variables with a two-tailed 95% confidence level (Table S1). Amax showed the most 319 320 significant difference among the physiological traits (p = 0.0009 for barley; p = 0.001 for rape seed), while leaf N content showed the most significant differences among the chemical traits 321 322 (p < 0.00001 for barley; p = 0.006 for rape seed). Evidence of statistically significant differences between rape seed top and bottom leaves was not found for leaf Chl content, LMA 323 and MTA. Lack of significance was also found for barley LA, albeit bottom leaves showing 324 325 consistently higher values except at the start of the seasons.

Seasonal variations in leaf traits within the measurement period were observed but did not show a clear seasonal trend. Rape seed leaf traits for which a seasonal trend was most pronounced were Rd, dropping from 2.3 to 0.7 μ mol (bottom) and from 4 to 0.9 μ mol (top), and N content, dropping from 2.6 to 1.5 g (bottom) and from 4.3 to 1.6 g (top), within one month from end of April to end of May. Mostly however, seasonal differences were smaller than differences found between top and bottom leaves (Fig. 2). Therefore, seasonal mean

- 332 values of Amax, ϕ and Rd, were used in this study for leaf-to-canopy photosynthesis upscaling 333 schemes.
- Fig 2. Here

335 3.2 Top and bottom leaves contributions to total canopy photosynthesis

In the measurement period, the amount of light absorbed by the bottom half of the barley 336 canopy always exceeded that absorbed by the top half. The relative fraction of light absorbed 337 by the top canopy increased through the season in response to increasing LAI in the 338 corresponding top layer (inset Fig 3). On April 29, the bottom canopy absorbed 80% of total 339 daily PAR, with a LAI value of 3.6 against a LAI of 0.5 for the top layer. More than a month 340 later on June 5, the bottom canopy absorbed only 54% of the PAR with a LAI value of 1.8 341 against a LAI of 2.0 for the top layer (Fig. 3, top panels). Contributions of top and bottom 342 layers to total barley canopy photosynthesis followed a similar trend, with a steady decrease in 343 344 bottom canopy contribution to total canopy photosynthesis: 89% on April 29, 82% on May 8, 345 51% on May 22 and only 36% on June 5. Diurnal courses of GPP up-scaled from exact-day leaf-level measurements using the top/bottom-leaf scheme compare remarkably well with 346 measured GPP, with the exception of the time interval around noon on June 5th when up-scaled 347 348 estimates seem to underestimate GPP (Fig. 3). For the same day a better match was found with 349 EC estimated GPP, when using seasonal mean values of Amax, ϕ and Rd, with the top/bottom-350 leaf upscaling scheme (see Fig. 4). We thus hypothesize that this is due to the specific Amax parameter measured on June 5th that was either underestimated or measured for leaves not 351 representative of overall field conditions. Worth noting is also the mid-day depression in up-352 scaled total canopy GPP on June 5th (Fig. 3) and some other dates (Fig. 4). This underestimation 353 could be related to lower noon time PAR absorbed by the top canopy layer (top panel in Fig. 354 355 3), which is caused by mostly vertical leaf angles of barley which aligns with noon time solar rays, resulting in lower radiation interception area. An alternative explanation for this recurrent 356 feature is that some of the bottom leaves have top-canopy traits because they have access to 357 358 sunflecks.

- 359 Fig 3. Here
- Fig 4. Here

361 **3.3 Linearity of photosynthesis response to light**

Adjusted r-square was used to assess the linearity of the photosynthesis response to light for leaves at the top and at the bottom of the barley and rape seed canopies. For both crop types, integrating from hourly to daily temporal resolutions increased the linearity of top leaves' photosynthesis response, with changes in APAR explaining over 93% and over 91% of the variation for barley and rape seed leaves, respectively (Fig 5). At weekly temporal resolution, the effect of light saturation on bottom leaves was most evident, resulting in the lowest adjusted r-square (barley: 0.33; rape seed: 0.24) (Fig. 5).

369 Fig 5. Here

370 **3.4 Leaf-to-canopy photosynthesis upscaling schemes**

Four different leaf-to-canopy photosynthesis upscaling schemes were evaluated in this study.

Table 2 presents the complete set of coefficients to derive leaf-level photosynthesis rate for barley and rape seed leaves starting from measurements or estimates of PAR absorbed by green

- 374 fully expanded leaves.
- Table 2. Here

- For barley, photosynthesis upscaling schemes were evaluated against total GPP derived from EC flux measurements at daily and weekly temporal resolutions. If we consider overall performance, including the explained variance by adjusted r² and total errors by RMSE and bias, top/bottom-leaf schemes performed better than one-leaf schemes for both LRC and RUE
- models (Fig. 6). Between the two, LRC overall performed better than RUE models, in that
 LRC resulted in lower bias and RMSE magnitudes than RUE at each temporal resolution whilst
- both explained the observed variance significantly (p<0.001) at daily time scales (Fig. 6). The
- 383 comparison is limited to daily and weekly temporal resolutions since RUE type models are not
- intended for hourly simulations.
- Fig 6. Here

386 **3.5 Comparison with MODIS satellite GPP approach**

387 RUE models are at the base of photosynthesis models relying on remote sensing datasets. Among the most commonly used satellite-based GPP products is the moderate-resolution 388 imaging spectroradiometer (MODIS) GPP product (MOD17) (Running et al. 2004). In the 389 current study, we have applied a ground-based version of the MOD17 algorithm in which 390 FPAR is approximated with the NDVI derived from reflectance spectra measured with a 391 392 UniSpec-DC. The MODIS-GPP ground (MOD17_{gr}) and the two best performing leaf-tocanopy upscaling schemes, i.e., LRCtb and LRC1L, are compared over time and against EC GPP 393 394 at daily time scales in Fig. 7. GPP was largely underestimated by the MOD17gr model, whereas GPP estimates obtained with the LRC_{tb} upscaling scheme best matched the EC GPP estimates, 395 but were prone to a slight overestimation throughout the measurement period. 396

397 Fig 7.

398

4. Discussion

4.1 Photosynthesis trait variation as function of leaf position and crop type

The first objective of this study was to understand how leaf position within the canopy, linked with the light regime experienced by a leaf, influences leaf photosynthesis and underlying traits. We found top and bottom leaves differed in terms of photosynthesis and underlying biochemical, structural and physiological leaf traits in both, winter barley and rape seed crop types. Differences along crop growth stage were not consistent throughout the measuring period and a clear seasonal trend could not be identified (Fig. 2).

Top canopy leaves evidenced significantly higher Amax and Rd than bottom canopy leaves, 406 a typical adaptation to high light environments. Whereas bottom canopy leaves were found 407 408 having higher quantum yield (ϕ) and thus deal more efficiently with low diffuse light conditions they are adapted to. While the theoretical maximum quantum yield (ϕ_{max}) was 409 reported to be 0.125 in the absence of photorespiration, with 8 moles of photons required to 410 411 reduce 1 mole of CO₂ (Long *et al.* 1993), photosynthesis studies report measured values to be 30-50% lower than the theoretical maximum (Singsaas et al. 2001). This is in agreement with 412 our findings; an exception is given by rape seed bottom leaves for which higher values (0.103 413 ± 0.027) were measured in the field. Considerable variation in measured ϕ values is however 414 415 still found in the literature and is mostly ascribed to plants experiencing different levels of environmental stress (Björkman 1981; Singsaas et al. 2001) and/or as a consequence of leaves 416 acclimation to different spectral composition of the light environment (Hogewoning et al. 417 418 2012).

419 Interestingly, while top and bottom leaf values of Amax and ϕ differed considerably 420 between barley and rape seed, the rate of down-regulation in response to canopy position 421 (proportional decrease in Amax or increase in ϕ relative to the value of the top position) was 422 similar between crop types. Amax of top leaves was 1.8 times higher and ϕ was 1.2 times lower 423 than for bottom leaves for both, rape seed and barley leaves. This suggests that despite differences in crops canopy architectures resulting in different light availabilities and 424 interception within canopies, simple down-regulation functions accounting for leaf position 425 might be applicable, although further testing would be required. A study looking at gradients 426 of maximum photosynthetic capacity and respiration rates for saplings of six temperate tree 427 species, found that the rate of down-regulation in response to shade was not significantly 428 species- or taxon-specific, nor was it different between sun-grown plants and shade-grown 429 plants (Chen et al. 2014). The authors (Chen et al. 2014) attributed most of the down-regulation 430 of per unit area Rd and Amax to reductions in LMA, i.e., leaves getting thinner as light 431 432 decreases, while per unit mass Amax and Rd remained nearly constant. Contrary to this finding by Chen and co-authors (2014), our data shows that Amax and Rd per unit mass remains higher 433 (p<0.05) for top over bottom leaves for both crop types (not presented here for brevity). As 434 435 already discussed in the introduction, fast-return species such as crops follow completely different patterns of growths and development. In our study, LMA seems to have a less 436 important role as compared to N in driving the down-regulation of photosynthesis with 437 438 increasing canopy depth. Although, in average over the season LMA is higher for top leaves as compared to bottom leaves, this difference was not significant for rape seed (Fig. 2). 439 Typically top leaves, experiencing a higher degree of direct collimated light, are thicker 440 because their anatomy is characterized by the presence of columnar palisade cells which 441 facilitate the penetration of the direct collimated light component and the more equal 442 distribution of light to chloroplasts deeper within the leaf (Vogelmann and Martin 1993). 443 However, in crops top leaves are in an earlier developmental stage and have not accumulated 444 445 dry matter by the time they occupy the top most sunlit position in the canopy.

On the other hand, nitrogen reallocation is a faster mechanism adopted by crop species to 446 maximize whole-plant canopy photosynthesis at a given resource availability. Nitrogen 447 448 concentrations have been shown to increase from bottom to top of the canopy, where ample light is available for higher photosynthetic C fixation (Pons and Pearcy 1994; Vos and van der 449 Putten 2001; Niinemets et al. 2015; Niinemets 2016). To understand potential environmental 450 constraints on photosynthesis at a specific leaf position we looked at the ratio between the 451 chlorophyll concentration and the total amount of nitrogen in the leaves (chlorophyll per 452 nitrogen, Chl/N). The higher Chl/N ratio for bottom leaves for both crop species pointed to 453 leaves limited by light capture (high Chl/N) rather than CO₂ assimilation (low Chl/N) in the 454 bottom half of the canopy. This despite top leaves being still characterized by higher Chl levels 455 456 overall.

These leaf-level traits variations however provide only a partial picture and need to be
 combined with canopy structure and crop growth and development information to gain a better
 understanding of total canopy photosynthesis dynamics.

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461 **4.2 Implications of leaf position for canopy photosynthesis modelling**

The second objective of this study was assessing whether differentiating between top and 462 bottom leaves improves the estimation of total canopy photosynthesis. It should be noted that 463 464 the top/bottom-leaf dichotomy adopted here distinguishes top from bottom leaves and is thus different from the sunlit vs. shaded leaf dichotomy adopted in sun/shade scheme and amply 465 discussed by De Pury and Farquhar (1997). Although the top and bottom halves of the canopy 466 are typically associated with high and low light conditions, respectively, this does not necessary 467 translate into the same partitioning of absorbed PAR. We found that, despite leaf-level 468 maximum photosynthetic capacity (Amax, Fig. 2) being higher for top leaves, the bottom half 469 470 of the canopy absorbs more light and is thus the major contributor to total canopy photosynthesis for most of the season, until the onset of senescence in the lower canopy (Fig. 471

472 3-4). Under diffuse light conditions typical of overcast days, the contribution of the bottom canopy is higher than that of the top canopy even at the leaf-level, with bottom leaves having 473 higher or comparable net photosynthesis as compared to top leaves (see Fig S1). The following 474 are possible explanations of why the bottom canopy is the major contributor to total canopy 475 photosynthesis. Firstly, before the senescence of the bottom half of the canopy sets-in in late 476 May, the bottom layer is characterized by higher LAI (Fig. 3), due to more leaves with higher 477 leaf area per leaf (LA, Fig. 2). Higher LA and quantum yield (ϕ) are the two mechanisms which 478 bottom leaves have adopted to cope with low diffuse light conditions. Secondly, bottom leaves 479 were found having lower mean tilt angles (MTA, Fig. 2), typical of leaves perpendicular to the 480 481 sun's rays. Leaf angle defines the amount of intercepted irradiance. At the top of the canopy, leaves might adopt angles parallel to the sun's rays and absorb mostly diffuse and scattered 482 irradiance to avoid photodamage during the time of day when the sun is highest above the 483 484 horizon.

485 It should be farther noted that especially during the reproductive and senescence stages not all PAR absorbed by the canopy is used for photosynthesis. This is primarily due to seasonal 486 changes in pigment composition, i.e., chlorophyll vs. carotenoid content, relative levels of 487 xanthophyll cycle pigments (Gitelson et al. 2014; Gitelson et al. 2015) and the related excess 488 energy dissipation mechanisms. As evidenced by the drop in Chl content of the bottom half of 489 the barley canopy (Fig. 2), not all APAR might be used for photosynthesis, potentially leading 490 to a slight overestimation of bottom canopy photosynthesis for our very last days of 491 measurements. However, since our measuring period predominantly overlaps with the crop's 492 vegetative stage, potential overestimations can be considered negligible. 493

494 We found that the top/bottom-leaf upscaling schemes, separating between top and bottom leaves types, outperformed the one-leaf upscaling scheme when compared with measured GPP. 495 This was particularly evident at high temporal resolutions (from minutes to hours), and less so 496 497 for resolutions spanning days to weeks (Fig. 6). Nevertheless, for all models, one-leaf schemes exhibited higher errors as compared to their top/bottom-leaf counterparts. Both our one-leaf 498 and top/bottom-leaf upscaling schemes were parameterized directly from leaf-level 499 measurements (Table 1) and thus truly capture leaves biochemical variation within a canopy, 500 however, they require additional field measurements whose collection might not be feasible 501 for broad scale applications. To the best of our knowledge, there are no other studies which 502 503 separate top and bottom canopy layers based on actual leaf traits so a direct comparison with other studies was not possible. 504

505 **4.3 Linearity of photosynthesis light response only observed for top leaves**

506 Based on the field dataset we also evaluated whether nonlinear processes such as leaf photosynthesis response to light for both, top and bottom leaves, could effectively be linearized 507 if integrated over longer time scales. This is particularly relevant in the context of remote 508 sensing based approaches for GPP estimation, since these commonly combine RUE models 509 510 and remotely sensed data collected at weekly to bi-weekly intervals. At the base of RUE models first introduced by Monteith (1972) is the finding that a nonlinear process such as the leaf 511 photosynthetic response to light can be linearized if longer time intervals are considered. 512 Among the most credited theories explaining this phenomenon is functional convergence, i.e. 513 the interaction with other resource limitations over time (Field 1991; Goetz and Prince 1999; 514 515 Medlyn et al. 2003). This theory predicts that, since leaves are expensive to produce and maintain, when plants are nutrient-limited, experiencing drought, or exposed to other adverse 516 conditions, they reduce their leaf area to use resources efficiently, although full optimization 517 might never be truly achieved (Niinemets 2007). 518

519 In this study, a linearization of the leaf photosynthesis response to light was observed mainly 520 for top leaves, integrated to daily and to weekly resolutions. Bottom leaves on the other hand showed linear responses at daily resolutions, while weekly photosynthetic responses remained
nearly constant with changing weekly APAR levels (Fig. 5). This reinforces the use of linear
RUE models in concomitance with remotely sensed observations which mainly capture signal
from the upper canopy, however at the same time questions their representativeness of total
canopy photosynthesis.

At the canopy level, linear RUE models used to upscale leaf-level photosynthesis 526 overestimated GPP for daily and weekly resolutions (Fig. 6). Findings by previous studies 527 suggest that linear models are applicable on time-scales of two weeks and more (Medlyn 1998), 528 however evidence of whether this applies also to the lower half of the canopy is currently 529 missing. On the other hand, the MODIS-GPP ground (MOD17_{gr}) linear model employing a 530 fixed maximum RUE (ε_{max}) term prescribed in the current biome property look-up table 531 (BPLUT), resulted in an underestimation of GPP. There are two possible reasons at the base of 532 533 this underestimation. The first one is the use of NDVI as a proxy of fAPAR in crops. Although there is ample empirical evidence that fAPAR is related to top of the canopy spectral vegetation 534 indices (VIs), linear relationships are mainly found during the reproductive stages of crops 535 536 (Gitelson et al. 2014). During the crop's vegetative stage, characterized by moderate-to-high green LAI, in situ measured NDVI has been shown to saturate and underestimate fAPAR in 537 C3 and C4 crops (Asrar 1984; Gallo et al. 1985; Viña 2005). Furthermore, spectral VIs are not 538 able to capture vertical heterogeneity of chlorophyll content and green LAI within the canopy, 539 which is instead accounted for in our top/bottom-leaf upscaling approach, separating top and 540 bottom leaves (Fig. 7). This is a common problem of spectral remote sensing proxies used for 541 the estimation of canopy biochemical, physiological and structural canopy traits (Gitelson et 542 543 al. 2014). The second reason for the underestimation by the $MOD17_{gr}$, is seen in the too low ε_{max} term for crops used by the MODIS GPP/NPP algorithm (Chen *et al.* 2011; Bandaru *et al.* 544 545 2013; Xin et al. 2015). Gitelson et al. (2015) found ε_{max} to be 50% higher in C3 soybean and 546 250% higher in C4 maize than the value used in the MODIS model. At present, in an effort to generalize model parameterization, the MODIS Land Science Team does not differentiate ε_{max} 547 between geographical regions, crop types or spatial scales. 548

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5. Conclusions

Results presented in this study contribute to the understanding of biophysical controls on C 551 fluxes in crop ecosystems by investigating the effect of within canopy light regimes on 552 photosynthesis and related traits. Our findings confirm those by previous authors, showing how 553 fast growing species adopt nitrogen and, to a lesser degree, dry matter reallocation strategies 554 to deal with the excess light at the top of their canopies. For both crop types, barley and rape 555 seed, top leaves showed higher photosynthetic capacity, dark respiration, leaf nitrogen, carbon 556 and chlorophyll contents, and leaf mass per area. Whereas bottom leaves showed higher 557 photosynthetic efficiency (i.e., quantum yield) at low light levels. Despite this, the bottom 558 559 canopy layer remained the main contributor to total canopy photosynthesis until the start of senescence, which progresses upwards from the lower canopy. This is mainly explained by 560 greater radiation interception by the bottom half of the canopy, due to the combined effect of 561 higher leaf area per leaf, more horizontal leaf orientation, and higher photosynthetic efficiency 562 563 under low light.

We presented our observations in the context of four leaf-to-canopy photosynthesis upscaling schemes. These schemes address the challenge of integration of photosynthesis over time and within the canopy space. Integration of photosynthetic response over time tends to transforms a nonlinear process, such as the leaf photosynthesis response to light, into a linear relationship whose strength increases with the increase of the temporal integration interval. Although not perfectly valid under all conditions, this simplification allows the use of remote sensing based 570 approaches to parametrize the linear model either using fixed slope coefficients (e.g., MOD17 product; Running et al. 2004) or vegetation indices that scale with light use photosynthetic 571 efficiency (e.g., PRI; Peñuelas et al. 2011). Top leaves showed a more linear response with 572 light than bottom leaves, while the effect of light saturation on bottom leaves resulted in the 573 lowest linearity. This finding is validating RUE models relying on remotely sensed 574 observations, which predominantly capture signal from the upper canopy. However, it should 575 also raise awareness that such approaches might be underrepresenting bottom canopy traits and 576 photosynthesis. This is especially concerning given the importance of bottom canopy 577 contribution to total canopy photosynthesis shown in this study. 578

579 Integration of photosynthesis within the canopy space, was investigated by comparing oneleaf vs. top/bottom-leaf schemes, distinguishing top from bottom leaf types, against EC 580 estimated GPP for barley. Findings showed that top/bottom upscaling schemes, which 581 582 distinctively account for bottom canopy contribution over the season, generally outperformed one-leaf schemes, highlighting the importance of the bottom canopy. The observed within 583 canopy trait variability and the requirement for additional field measurements, remain an 584 585 outstanding challenge in the derivation of broadly applicable leaf-to-canopy photosynthesis upscaling schemes. Future research thus must bridge the gap between greater realism, obtained 586 through field measurements, and the model requirements for simplification. 587

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Fig 1. Study site near Oensingen, Switzerland. At the long-term agricultural measurement station CH-Oe2, greenhouse gas exchange and meteorological variables are continuously measured with the eddy covariance technique. Measurement transects for light response curve (LRC) measurements at two canopy heights as well as leaf area index (LAI) measurements are shown for each field. Location and set-ups of photosynthetically active radiation (PAR) profiles are shown early in a crop seasonal cycle.



Fig 2. Leaf-level traits: quantum yield (ϕ), maximum photosynthetic capacity (Amax), dark respiration (Rd), nitrogen content (N), chlorophyll content (Chl), chlorophyll to nitrogen ratio (Chl/N), leaf mass per area (LMA), leaf area per leaf (LA) and mean tilt angle (MTA), for barley and rape seed crops, measured for top (white) and bottom (black) canopy leaves. Bar plots represent average variables over the course of the entire growing season with error bars of ±1 standard deviation. P-values from a two-tailed test are given as: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$; NS, not significant. Inset plots show temporal variability over the growing season with error bars of ±1 standard deviation representing spatial heterogeneity across the field transect.



Fig 3. Upper panel: Diurnal courses of incoming photosynthetically active radiation (PAR) (dotted black line), absorbed by top canopy layer (solid red line) and absorbed by bottom canopy layer (dashed red line) of barley crop. Insert: seasonal courses of total canopy leaf area index (LAI) (solid black line) and bottom canopy layer LAI (dashed black line) of barley crop; the exact days corresponding to the plotted PAR, APAR and GPP diurnal courses are indicated by a blue vertical line. Lower panel: Diurnal courses of photosynthesis (GPP) estimated through Eddy Covariance measurements (dotted black line) and upscaled from leaf-level photosynthesis measurements for bottom canopy layer (dashed red line) and for total canopy GPP (solid red line) based on the top/bottom-leaf light response curve scheme. The four days for which the diurnal courses are presented correspond to days with leaf-level photosynthesis and LAI measurement; top and bottom canopy layers are defined as the upper and lower half of the total canopy height, respectively.



Fig 4. Diurnal courses of barley gross primary production (GPP) derived from eddy covariance measurements (dotted black) and upscaled from leaf-level photosynthesis measurements for the bottom half of the canopy (dashed red) and the total canopy (solid red) based on the top/bottom-leaf light response curve scheme. The seasonal averages of the light response curve parameters (Amax, ϕ , Rd) were used for all dates. The considered temporal window represents the measurement period from 29 April (plants reached 25 cm of height) until 7 June (plants senescing).



Fig 5. Hourly, daily and weekly relationships between leaf-level gross photosynthesis (A_g) and absorbed photosynthetically active radiation (APAR) at the top (white) and bottom (black) of the barley and rape seed canopies. At daily and weekly temporal resolutions, lines represent the linear regression model for top and bottom leaves, respectively. Statistical significance of the adjusted r-square are denoted by asterisks (* p-value<0.05; ** p-value<0.01; *** p-value<0.001). Daily and weekly APAR values were obtained by summing hourly measurements and then diving by number of hours in a day and number of days in a week, respectively.



Fig 6. Upscaled barley leaf-level photosynthesis (GPP_{up}) plotted against eddy covariance (EC) gross primary production (GPP_{EC}) estimates. Four different leaf-to-canopy photosynthesis upscaling schemes were used: top/bottom-leaf Light Response Curve (LRC_{1L}), one-leaf Light Response Curve (LRC_{1L}), top/bottom-leaf Radiation Use Efficiency (RUE_{tb}), one-leaf Radiation Use Efficiency (RUE_{1L}). Comparisons are presented at daily and weekly temporal resolutions. The adjusted r^2 (Adj r^2), the root mean square error (RMSE) and the bias are reported, statistical significance of r^2 and of bias are denoted by asterisks (* p-value<0.05; ** p-value<0.01).



Fig 7. Barley upscaled gross primary production (GPP_{up}) plotted against eddy covariance (EC) gross primary production (GPP_{EC}) estimates. Three upscaling approaches are compared: the two best performing leaf-to-canopy photosynthesis upscaling schemes (i.e., the top/bottom-leaf light response curve (LRC_{tb}) and the one-leaf light response curve (LRC_{1L})) and a remote sensing approach based on a ground adaptation of MODIS gross primary productivity algorithm (MOD17_{gr}) and proximal sensing daily NDVI time series obtained from UniSpec-DC (PP Systems) measurements. Inset: Daily GPP_{up} and GPP_{EC} during the measurement period.

Table 1. Four different leaf-to-canopy photosynthesis upscaling schemes considered in this study. Absorbed PAR for top, bottom and entire canopies are obtained from PAR profile measurements. Required inputs and datasets used for model calibration are listed.

Scheme	Formulation	Inputs	Data used for model calibration (References)		
top/bottom-leaf light response curve (LRC _{tb})	$A_{total} = A_{top} + A_{bottom}$, where	Amax _{top} , Amax _{bottom}	Physiological variables are derived from top and bottom leaves Li-6400 LRC		
	$A_{top} = (Amax_{top} + Rd_{top}) \left(1 - exp \left(\frac{-\phi_{top} APAR_{top}}{Amax_{top} + Rd_{top}} \right) \right) - Rd_{top}$	$\phi_{ ext{top}}$, $\phi_{ ext{bottom}}$	measurements.		
		Rd _{top} , Rd _{bottom}			
	$A_{bottom} = (Amax_{bottom} + Rd_{bottom}) \left(1 - \exp\left(\frac{-\phi_{bottom}APAR_{bottom}}{Amax_{bottom} + Rd_{bottom}}\right) \right) - Rd_{bottom}$	APAR _{top} , APAR _{bottom}			
one-leaf light	$(\overline{A}, \overline{A}, A$	$\overline{ m Amax}$, $ar{oldsymbol{\phi}}$, $\overline{ m Rd}$	Average physiological variables derived from leaf-level Li-6400 LRC		
response curve (LRC ₁₁)	$A_{\text{total}} = (Amax + Rd) \left(1 - \exp\left(\frac{1}{Amax + Rd}\right)\right) - Rd$	APAR	measurements.		
()					
top/bottom-leaf radiation use efficiency (RUE _{tb})	$A_{total} = A_{top} + A_{bottom}$, where	RUE _{top} , RUE _{bottom}	The Radiation Use Efficiency (RUE) coefficients are obtained as the ratio of		
	$A_{top} = RUE_{top} * APAR_{top}$	APAR _{top} , APAR _{bottom}	photosynthesis (measured at leaf-level and unscaled based on LAI) to absorbed PAR		
	$A_{bottom} = RUE_{bottom} * APAR_{bottom}$		for top and bottom canopy separately.		
one-leaf radiation use efficiency (RUE _{1L})	$A_{total} = \overline{RUE} * APAR$	RUE, APAR	Average Radiation Use Efficiency (RUE) coefficient obtained as the ratio of photosynthesis (measured at leaf-level and upscaled based on LAI) to absorbed PAR by entire canopy.		

LRC is Light Response Curve; PAR is Photosynthetically Active Radiation; APAR is Absorbed Photosynthetically Active Radiation; RUE is Radiation Use Efficiency. Subscripts tb and 1L indicate top/bottom and one-leaf upscaling schemes, respectively. Amax is maximum photosynthetic capacity; Rd is dark respiration; and Φ is quantum yield; overbar denotes averages.

Table 2. Coefficients used for the four photosynthesis upscaling schemes applied for barley and rape seed crop types expressed in units of μ mol m⁻² s⁻¹. The upscaling schemes are given in Table 1.

Madal	Coefficients			
Model	Barley	Rape seed		
LRC _{tb}	$\phi_{top} = 0.058; Amax_{top} = 13.07; Rd_{top} = 1.07$	$\phi_{top} = 0.083; Amax_{top} = 20.75; Rd_{top} = 2.60$		
	$\phi_{bottom} = 0.074; Amax_{bottom}$ = 6.93; $Rd_{bottom} = 0.74$	$\phi_{bottom} = 0.103; Amax_{bottom}$ = 11.08; $Rd_{bottom} = 1.52$		
LRC_{1L}	$\overline{\phi} = 0.066; \overline{Amax} = 10; \overline{Rd} = 0.9$	$\bar{\phi} = 0.093; \ \overline{Amax} = 15.92; \ \overline{Rd} = 2.06$		
RUE _{tb}	$RUE_{top} = 0.022$ $RUE_{hottom} = 0.012$	$RUE_{top} = 0.037$ $RUE_{hottom} = 0.017$		
RUE _{1L}	$\overline{RUE} = 0.017$	$\overline{RUE} = 0.022$		



Fig S1. Frequency distribution of the total PAR absorbed by top (unfilled circles) and bottom (filled circles) canopy during subsequent clear and overcast days for barley (top row) and rape seed (bottom row). Each point represents the natural log of number of minutes per day for which absorbed PAR was within a given class of PAR. The leaf-level net photosynthesis light response curves (A_n) as estimated using Eq. 1 for top (solid line) and bottom (dashed line) leaves are also shown for the same days. The measured photosynthesis light response curve parameters (Amax, ϕ , Rd) for top and bottom leaves were used in combination with the measured APAR at the respective leaf height.

Variables	Crop	Тор	Bottom	t- value	df	p- value
Amay	barley	13.1 (±6.7)	6.9 (±2.6)	3.7	32	***
$[\mu \text{mol } \text{m}^{-2} \text{ s}^{-1}]$	rape seed	20.8 (±5.8)	11.1 (±6.7)	3.7	25	**
	barley	0.058 (±0.032)	0.074 (±0.025)	2.069	32	*
φ	rape seed	0.083 (±0.019)	0.103 (±0.027)	2.17	25	*
	barley	1.1 (±0.5)	0.7 (±0.3)	2.1	30	*
$[\mu \text{mol } \text{m}^{-2} \text{ s}^{-1}]$	rape seed	2.6 (±1.4)	1.5 (±0.7)	2.9	25	**
N	barley	2.0 (±0.2)	1.0 (±0.2)	14.2	41	***
[g m ⁻²]	rape seed	3.3 (±1.0)	2.3 (±0.5)	3.0	25	**
C	barley	23.0 (±2.4)	18.3 (±2.3)	6.2	41	***
[g m ⁻²]	rape seed	32.8 (±9.5)	29.2 (±7.5)	1.1	25	NS
Chl	barley	507.6 (±59.6)	406.2 (±60.4)	5.2	36	***
$[mg m^{-2}]$	rape seed	518.6 (±34.9)	511.3 (±41.6)	0.4	20	NS
T MA	barley	51.9 (±5.8)	42.7 (±5.2)	5.4	41	***
$[g m^{-2}]$	rape seed	77.1 (±22.6)	70.9 (±18.1)	0.8	25	NS

Table S1. Means (\pm standard deviations) of top and bottom barley and rape seed leaf traits. Statistics for top and bottom leaf mean difference: degree of freedom (df), *p*-values and t-values are given from a two-tailed test. *, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$; NS, not significant.