Canopy photosynthesis of six major arable crops is enhanced under diffuse light due to canopy architecture

Running Title: Canopy photosynthesis enhancement

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Abstract

Diffuse radiation generally increases photosynthetic rates if total radiation is kept constant. Different hypotheses have been proposed to explain this enhancement of photosynthesis, but conclusive results over a wide range of diffuse conditions or about the effect of canopy architecture are lacking. Here, we show the response of canopy photosynthesis to different fractions of diffuse light conditions for five major arable crops (pea, potato, wheat, barley, rapeseed) and cover crops characterized by different canopy architecture. We used 13 years of flux and microclimate measurements over a field with a typical four-year crop rotation scheme in Switzerland. We investigated the effect of diffuse light on photosynthesis over a gradient of diffuse light fractions ranging from 100% diffuse (overcast sky) to 11% diffuse light (clear-sky conditions).

Gross primary productivity increased with diffuse fraction and thus was greater under diffuse than direct light conditions if the absolute photon flux density per unit surface area was kept constant. Mean leaf tilt angle (MTA) and canopy height were found to be the best predictors of the diffuse *vs.* direct radiation effect on photosynthesis. Climatic factors, such as the drought index and growing degree days (GDD), had a significant influence on initial quantum yield under direct but not diffuse light conditions, which depended primarily on MTA. The maximum photosynthetic rate at 2000 $\mu mol\, m^{-2}\, s^{-1}$ PAR under direct conditions strongly depended on GDD, MTA, leaf area index (LAI), and the interaction between MTA and LAI, while under diffuse conditions this parameter depended mostly on MTA and only to a minor extent on canopy height and their interaction. The strongest photosynthesis enhancement under diffuse light was found for wheat, barley and rapeseed, whereas the lowest was for pea. Thus, we suggest that measuring canopy architecture and diffuse radiation will greatly improve gross primary productivity estimates of global cropping systems.

Introduction

Diffuse radiation plays an important role for ecosystem productivity due to increased light use compared to direct radiation (Gu et al., 2003; Kanniah, Beringer, North, & Hutley, 2012, Cheng et al., 2015, Earles, Théroux-Rancourt, Gilbert, McElrone, & Brodersen, 2017). To feed an ever growing population, the potential of increasing photosynthesis rates should be considered (e.g., Ikawa et al. 2018, Murchie, Yang, Hubbart, Horton, & Peng, 2002, Mann, 1999). For example, an increase in diffuse radiation due to climate change is leading to increased photosynthesis (Rap et al. 2018): the climate-change associated greening of terrestrial vegetation is expected to increase biogenic aerosols, which in turn increase diffuse radiation and thus provide a positive feedback of vegetation to climate change. Understanding the magnitude of the diffuse radiation effect on crop productivity is therefore key to making predictions about climate-change associated yield increases. Diffuse and direct radiation have different spectral composition causing different effects on plant photosynthesis depending on plant species (Kume, 2017).

At the ecosystem scale, Mercado et al. (2009) estimated an increase in GPP on the order of 25% between 1960–1999 due to increased diffuse light conditions associated with global dimming (Wild, Amman, & Roesch, 2012). This resulted in an increase in canopy photosynthesis when the radiation of a canopy shifted from direct to diffuse, although the total amount of photosynthetically active radiation (PAR) reaching the top of the canopy is usually lower under diffuse conditions than under clear-sky conditions (Urban et al., 2011). Healey, Ricker, Hammer, and Bange (1998) found in a field study that increasing diffuse radiation (PAR_{dif}) using solarweave shadecloth increased yields of forage grasses by up to 50% although the total incident radiation was reduced by 25%. This effect is so strong (and seemingly economically relevant) that a fair number of studies have investigated artificially increasing the diffuse fraction for agricultural fields, greenhouses and orchards (Stanhill and Cohan, 2001; Raveh et al., 2003; Chen et al., 2014; Li et al., 2014). Besides artificial

increases in the diffuse fraction, the enhancement of photosynthesis under ambient diffuse light conditions has also been studied at the stand level in forests (Gu, Fuentes, Shugart, Staebler, & Black, 1999; Gu et al., 2003; Cheng et al., 2015; Rocha, Su, Vogel, Schmid, & Curtis, 2004; Jenkins et al., 2007; Knohl and Baldocchi, 2008; Urban et al., 2011; Strada, Unger, & Yue, 2015), grasslands (Turner et al., 2003; Wohlfahrt et al., 2008), subarctic shrubland (Williams, Rastetter, Van der Pol, & Shaver, 2014), orchards (Raveh et al., 2003) as well as for greenhouse crops at the leaf or stand level (Chen et al., 2014; Li et al., 2014). In the case of field crops (Cheng et al., 2015; Strada et al., 2015; Williams, Riley, Kueppers, Biraud, & Torn, 2016), mainly wheat, soybean, and maize were investigated. Only a limited number of studies investigated the effect of canopy architecture (mostly leaf area index, LAI, and mean tilt angle, MTA; Knohl and Baldocchi, 2008; Wohlfahrt et al., 2008; Timlin, Fleisher, Kemanian, & Reddy, 2014; Park et al., 2018). In a comparison study, Cheng et al. (2015) found the effect to be stronger for maize and soybean cropping systems as compared to forests, and related their photosynthesis enhancement to differences in stand architecture. Two studies reported photosynthesis enhancement only being effective above a LAI of 2 m^2 m^{-2} (Goudriaan, 1977: modelling study; Wohlfahrt et al., 2008: grassland). However, for many crop species, no information on photosynthesis enhancement and its drivers is available at all. Furthermore, almost all studies separated their data into two or only a few discrete categories of diffuseness by defining clear *vs.* diffuse days, and did not investigate photosynthesis enhancement over the full range of measured fraction of diffuse radiation (DF). Thus, our knowledge on the effect of diffuse light on canopy photosynthesis is still rather limited. This not only restricts our ability to predict crop productivity under changing environmental conditions, e.g. cloud cover or atmospheric pollution, that affects diffuse light interception (see also Rap et al. 2018), but also restricts evidence-based selection of major crop species for food security under future conditions.

In this study, we used 13 years of eddy-covariance derived gross primary productivity (GPP), PAR and PAR$_{dif}$ measurements, along with additional meteorological and physiological data at the Oensingen Swiss FluxNet cropland site (CH-Oe2) on the Swiss Plateau. The four-year crop rotation system was typical for Swiss wheat growing areas and included five major C$_3$ crop species (pea, potato, wheat, barley, rapeseed) as well as C$_3$ cover crops (*Phacelia* only, or a mixture of *Phacelia*, Alexandrine clover, and summer oat). We aimed to:

(1) determine the effect of diffuse light on crop photosynthesis among six different crop and cover species at stand level considering the full range of diffuse PAR as a fraction of total PAR; and

(1) identify the role of canopy architecture on such a photosynthesis enhancement.

We hypothesize that differences among crop and cover species in their relative response of GPP to fraction of diffuse light are primarily due to canopy architecture, and thus canopy height, leaf area index and/or mean leaf tilt angle should explain such differences.

Material and Methods

Site and measurements set-up

The Oensingen Swiss FluxNet cropland site (CH-Oe2) is located on the Swiss Plateau in the Canton of Solothurn (47°17′11.1″N, 7°44′01.5″E, 452 m a.s.l.). In this study, we used eddy-covariance and meteorological measurements from CH-Oe2 conducted between 2004 and 2016. Carbon dioxide (CO$_2$) fluxes were measured continuously with the eddy-covariance method over this study period with an open-path gas analyser (Licor 7500, Licor, Lincoln, NE, USA) and a three-dimensional sonic anemometer (Gill R3-50, Solent, UK), and 30-min averaged fluxes were computed. In spring 2004, PAR and PAR$_{dif}$ measurements were added to the typical meteorological and soil measurement set-up at the flux site, including air temperature (T_A) and relative humidity (RH). A BF3 (2004–2014) sunshine sensor, which was replaced with the improved BF5 sensor in 2014 (both from Delta-T Devices, Cambridge,

UK), was used to measure PAR and PAR_{dif} (see Section 1 in Supplementary Information for details how the BF3 readings were corrected to be comparable with the BF5 readings). The BF3 and BF5 sensors use seven cosine-corrected photodiodes, which are arranged under a patterned hemispherical dome in a way that ensures at least one out of seven sensors is directly exposed to the sunlight at all times, whilst one of the sensors is in the shade under sunny conditions. The photodiode with the highest reading is then assumed to measure PAR, and the one with the lowest reading is assumed to measure PAR_{dif}.

A detailed description of the field site, measurements and processing of the eddy-covariance data can be found in Emmel et al. (2018). Eddy-covariance derived gross primary productivity (GPP) was modelled from net ecosystem exchange (NEE) measurements with the *REddyProc* package in the statistics software *R* (R Core Team 2019) using the night-time partitioning method after Reichstein et al. (2005).

In addition to the above long-term measurements, vertical profiles of PAR interception were measured at CH-Oe2 and neighbouring fields for several weeks in 2014 and 2015 during the growing season to determine the typical vertical distribution of PAR for different crop species (pea, wheat, barley, rapeseed). Above-ground measurement heights were 0.05, 0.25, 0.45, 0.65, and 0.85 m for pea, 0.05, 0.30, 0.55, 0.80, 1.05 m for wheat and barley, and 0.05, 0.35, 0.65, 0.95, and 1.25 m for rapeseed. PAR was measured with five quantum sensors of model PQS1 (Kipp & Zonen, Delft, The Netherlands; K&Z) in the wheat and the pea fields, and of model SQ-110 (Apogee, Logan, UT, USA) in the barley and the rapeseed fields. All sensors were calibrated against a reference instrument (PAR Lite, K&Z) in an inter-comparison experiment. To validate field horizontal homogeneity and representativeness of measurements by the stationary profile systems, two additional mobile PAR profile systems were installed at other locations in the fields for shorter periods during the growing season. The within-field inter-comparison provided enough confidence for the use of any one system (Figs S4–S6). Absorbed PAR (APAR) was then estimated for the five layers between the

measurement heights by calculating the difference in PAR between the highest and the lowest measurement height. The lower boundary of the lowest layer was the ground, and PAR was assumed zero just below the ground. Average PAR and APAR profiles normalized by PAR measured at the highest measurement level, which was mostly located above the canopy, were calculated for different ranges of DF (= PAR_{dif}/PAR) and called PAR_{rel} and fAPAR, respectively.

LAI of the canopy and MTA of the leaves were measured at several phenological stages over the growing seasons with a hand-held plant canopy analyser (LAI2000, LI-COR Inc., Lincoln, NE, USA). Measurements were made with a 270° view cap on the sensor to minimize problems with direct sunlight (Licor, 1992). The MTA was calculated by the LAI2000 instrument based on optical measurements of light absorption by the canopy relative to corresponding above-canopy readings. Up to five elevation angles of optical measurements (0–13°, 16–28°, 32–43°, 47–58° and 61–74° from nadir) were available for the calculations. Horizontal leaves result in an MTA of 0°, whereas vertical leaves result in an MTA of 90°. Typically, MTA is expected to range between 30° and 60° (Licor, 1992). The instrument averaged readings over a transect, which generally consisted of around ten measurement locations. On the majority of days, average canopy height h_c was measured with a measurement stick at several locations in the field, and the average h_c for a specific day was determined. We ensured that we had measurements available at the time when the plants reached their maximum LAI and h_c.

Best fit function for the light response of GPP

In order to determine the best fit function for the relationships between GPP, above-canopy PAR and DF, we fitted different light response curves to the available half-hourly GPP data. Two common light response curves, rectangular (Ruimy, Jarvis, Baldocchi, & Saugier, 1995; Gu et al., 2002; Rocha et al., 2004; Dengel and Grace, 2010; Cheng et al., 2015) and non-

rectangular (Gilmanov et al. 2003; Knohl and Baldocchi, 2008; Urban et al., 2011; Li et al., 2014) hyperbolic functions, were used as the basis to calculate GPP in combination with two different concepts to account for the effect of diffuse radiation: either (1) a statistical approach with an additive or a multiplicative term of DF to represent the potential photosynthesis enhancement; or (2) using a more biophysical approach in which model parameters were explicitly expressed for diffuse and direct PAR components (for more details see Section 3 in Supplementary Information). Thus, 18 equations were tested (i.e., equations S1 to S18 in the Supplementary Information). Flux data (30-minute averages) were selected for light response curve fitting with all equations if they met the following two criteria in combination: (1) the daily average GPP on which a record was measured had to exceed 3 µmol CO_2 m^{-2} s^{-1}; and (2) these records were only retained if an average air temperature $T_A > 5$ °C was observed during the same 30-minute interval.

Days that were included in the analysis are shown in Figs S14 to S16. The above criteria were chosen to ascertain that only days with appropriate conditions for plant growth were included in the analysis, leaving out cold periods or days at the end of senescence. The T_A and GPP thresholds were chosen by plotting GPP *vs.* T_A and determining visually above which threshold GPP was dependent on T_A (not shown). The T_A threshold is also corresponding to the threshold typically used for growing degree days (GDD; Gordon and Bootsma, 1993; Körner, 2006).

The best fit function was chosen by comparing the percentage of significant coefficients (at $p < 0.00001$). If several functions had the same fraction of significant coefficients, the function with the lowest AIC (Akaike's information criterion) value was chosen (Gbur et al. 2012, Akaike 1974).

Two kinds of fitting were conducted: (1) the seasonal fit and (2) the species fit. In the seasonal fit, the models were fit to the observations in each of the 16 crop seasons, whereas, in the species fit, the models were fit to the observations that were pooled together by the

crop species and cover crop. We did the two kinds of fitting because a given crop might show a different response in different years detectable in the seasonal fit, but overall a more general finding is expected, if inter-annual variation within the species of interest is low, and thus pooling available data lead to more robust light response parameter estimates.

Determinants of the variability of the light response parameters

We employed a linear mixed model (LMM) in *R* (*lmer* function of the *lme4* package) in order to find the best predictors for photosynthesis enhancement due to DF. For each seasonal light response parameters of the best fit function we started an LMM with the following fixed effects: seasonal maximum LAI (in m^2 m^{-2}), seasonal maximum h_c (in m), seasonal maximum mean leaf tilt angle (MTA, in °), and the first-order interactions among the three. Furthermore, seasonal growing degree days (GDD, calculated using method 2 in McMaster and Wilhelm, 1997, for a base temperature T_{base} = 5 °C and an upper threshold temperature T_{UT} = 35 °C), and the seasonal Thornthwaite drought index (DI, Thornthwaite, 1948; Vicente-Serrano, Beguería, & López-Moreno, 2010) were included in the model to test whether variations in weather conditions among seasons had an influence on the photosynthesis enhancement due to DF. As the random effect we used year of observation. Then, step by step, all fixed effect variables without a significant contribution ($p \geq 0.05$) were eliminated using the *step* function in *R*. We applied a type III linear mixed model using the *lmer* function from the *lmerTest* (tests in linear mixed effects models) package in *R* and determined the relative contributions of each variable to total variance by partitioning the explained variance (determined by the marginal coefficient of determination of the linear mixed model) according to the sum of squares (SSQ) of each variable retained in the model, excluding the random effect (year of observation). The marginal coefficient of determination, that is the one not including the random effect, was calculated with the *r.squaredGLMM* function of the *MuMIn* (multi-model inference) package in *R*.

Results

Light response with diffuse light fraction

From all 18 light response models we determined the model that best described GPP response to PAR and DF at the stand level. In both seasonal and crop species fits, Eq. (1), shown in the Supplementary Information as Eq. (S15), most often gave the best fit: 11 out of 16 seasons and 3 out of 6 species (see Tables S1 and S2). Eq. (1) was the best choice for all winter wheat, winter barley and rapeseed seasons. The performance of Eq. (1) was also comparable to other models when applied to pea, potato and cover crops (see details at the end of Section 3 in Supplementary Information). None of the other equations resulted in the best fit for more than one crop season or crop species. Therefore, we used the rectangular hyperbolic light response according to Eq. (1) for all subsequent evaluations in this study,

$$GPP = \frac{\alpha_{dir} \cdot PAR_{dir} \cdot A_{max,dir} + \alpha_{dif} \cdot PAR_{dif} \cdot A_{max,dif}}{\alpha_{dir} \cdot PAR_{dir} + (1 - DF) \cdot A_{max,dir} + \alpha_{dif} \cdot PAR_{dif} + DF \cdot A_{max,dif}} \quad , \tag{1}$$

with separate light response parameters α_{dir} and $A_{max,dir}$ for direct radiation (PAR_{dir}), and α_{dif} and $A_{max,dif}$ for diffuse radiation (PAR_{dif}). DF is the diffuse fraction (DF = PAR_{dif}/PAR). PAR_{dir} was derived from PAR and PAR_{dif} measurements as $PAR_{dir} = PAR - PAR_{dif}$.

Fig. 1 shows examples of the best light response model (Eq. 1) out of the 18 models for one wheat season and one pea season (all fits and residual analysis are shown in Figs S7–S12). Eq. (1) uses separate light response parameters for the direct and diffuse light components in such a way that under absence of an effect of diffuse *vs.* direct light on photosynthesis $\alpha_{dir} = \alpha_{dif}$ and $A_{max,dir} = A_{max,dif}$, and Eq. (1) would converge to the well-known light response model (Ruimy et al. 1995),

$$GPP = \frac{\alpha \cdot PAR \cdot A_{max}}{\alpha \cdot PAR + A_{max}} \quad . \tag{2}$$

$A_{max,dir}$ and $A_{max,dif}$ can easily reach values that are outside the observed assimilation maxima in cases where the light response is not strongly curvilinear. Hence, for interpretation we use the

derived parameters $A_{2000,dir}$ and $A_{2000,dif}$, which are the modeled assimilation rates at incident PAR of 2000 µmol m^{-2} s^{-1}. To convert from the light response parameters in Eq. (1) to these derived parameters, a simple algebraic conversion is possible,

$$A_{2000,dir} = \frac{\alpha_{dir} \cdot 2000 \cdot A_{max,dir}}{\alpha_{dir} \cdot 2000 + A_{max,dir}} \quad \text{and} \quad A_{2000,dif} = \frac{\alpha_{dif} \cdot 2000 \cdot A_{max,dif}}{\alpha_{dif} \cdot 2000 + A_{max,dif}} \quad . \tag{3}$$
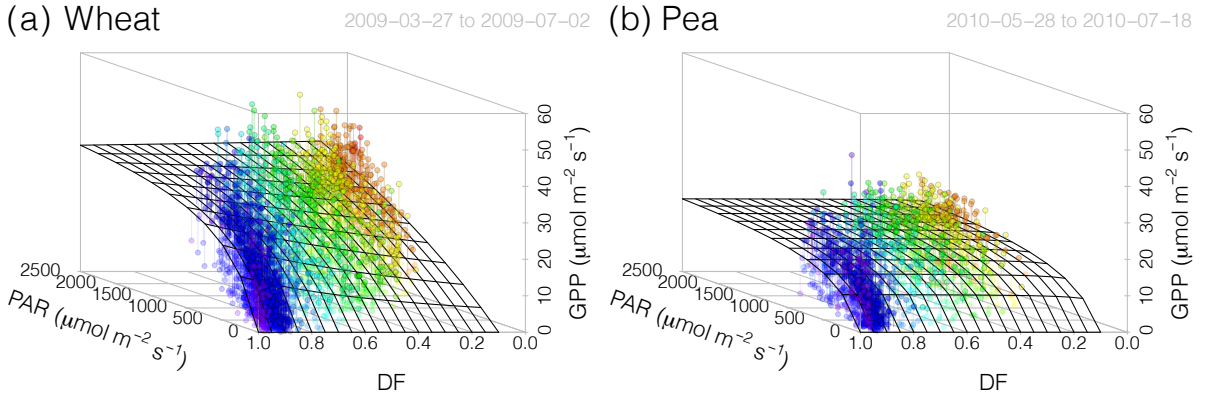

FIGURE 1: *Example light response fits (Eq. 1) for wheat in 2009 (a) and pea in 2010 (b) as a function of diffuse light fraction (DF). The symbol colors indicate the grouping by DF.*

The light response parameters α (the initial slope of the light response curve, also called initial quantum yield) ranged from 0.000 to 0.038 µmol CO_2 (µmol photons)$^{-1}$ (from now on expressed as dimensionless number) for the PAR_{dir} component, and 0.055 to 0.095 for the PAR_{dif} component. $A_{max,dir}$ and $A_{max,dif}$ (the maximum assimilation rates based on Eq. 1) for PAR_{dir} ranged from 1 to 470 µmol m^{-2} s^{-1}, and from 16 to 90 µmol m^{-2} s^{-1} for PAR_{dif} for the 16 different crop and cover seasons (Table S1). This corresponds with $A_{2000,dir}$ and $A_{2000,dif}$ ranging from 0.0 to 30.5 µmol m^{-2} s^{-1}, and from 14.2 to 57.2 µmol m^{-2} s^{-1}, respectively. In the fits for the six crop and cover species (crop species fitting), α_{dif} (α_{dir}) and $A_{2000,dif}$ ($A_{2000,dir}$), ranged from 0.056 to 0.087 (from 0.000 to 0.018) and from 17.3 to 21.5 (from 0.0 to 28.9) µmol m^{-2} s^{-1}. Because light response curves under direct light tend to show much less curvilinear behavior than under diffuse light, the assimilation rate A estimated at 2000 µmol m^{-2} s^{-1} PAR is shown in Fig. 2 in place of $A_{max,dir}$ and $A_{max,dif}$ (panels

c, d, g, h,k,l). Irrespective of species, the initial quantum yield observed with diffuse radiation is roughly 4 times that of direct radiation ($\alpha_{dif}/\alpha_{dir} \approx 4$ in Fig. 3), although variability is substantial among seasons.
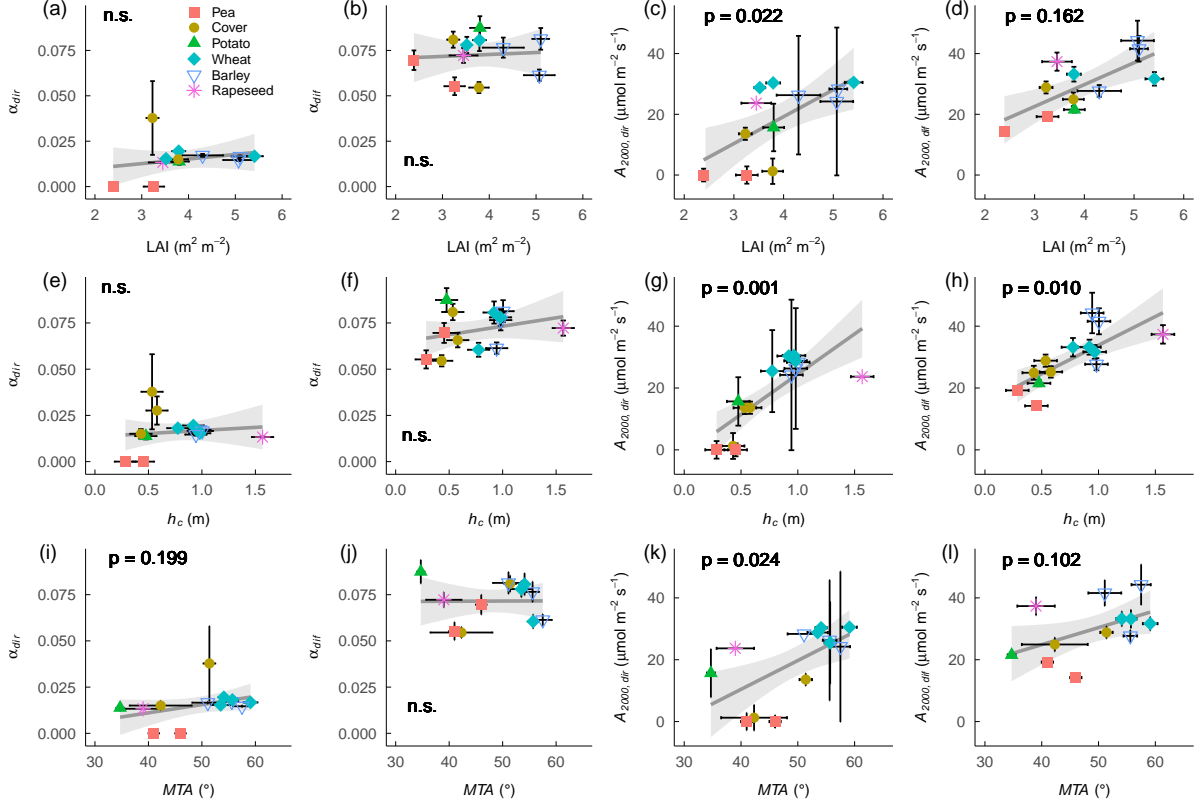

FIGURE 2: *Dependence of the light response parameters α (a, b, e, f, i, j)*, and *A at 2000 $\mu mol\ m^{-2}\ s^{-1}$ PAR (c, d, g, h, k, l) for direct (index dir) and diffuse (index dif) light components on canopy architecture (LAI in top row, h_c in middle row, and MTA in bottom row) for different crop and cover species. Each symbol represents one crop season. The gray shaded area is the 90% confidence interval of the linear fit (bold gray line). Vertical error bars are standard errors of the light response parameters, and horizontal error bars are standard errors of the measurements of LAI, h_c and MTA, respectively. P values of the regression fits > 0.2 are shown with "n.s.".*
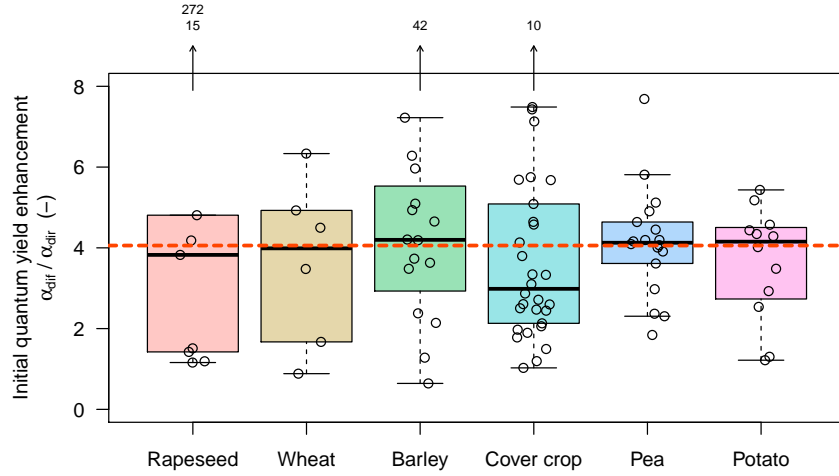
FIGURE 3: *Enhancement of initial quantum yield by diffuse vs. direct PAR derived from the ratio of the two light response parameters $\alpha_{dif}/\alpha_{dir}$. High positive outliers are related to cases when GPP almost exclusively responded to diffuse light and hence $\alpha_{dir} \approx 0$. Horizontal line shows the median of the crop-specific medians (4.1). Differences among crops are not significant ($F_{5,85} = 1.86$, p = 0.11).*

We found a strong linear relationship of the asymptotic assimilation maxima under direct ($A_{max,dir}$, p = 0.008) and diffuse light ($A_{max,dif}$, p = 0.024) as a function of h_c (Fig. 2, where A_{2000} instead of A_{max} is shown for better comparability between direct and diffuse light, hence p = 0.001 and p = 0.010 for the regression with A_{2000}) whereas α_{dir} and α_{dif} varied strongly around a value that did not significantly depend either on LAI or h_c (Fig. 2a,b,e,f), whereas MTA had a weak influence on α_{dir} but not on α_{dif} (Fig. 2i,j). The dependence of $A_{2000,dir}$ and $A_{2000,dif}$ on LAI and MTA was qualitatively similar to the relationship with h_c, but with weaker statistical significance than with h_c (*Fig. 2c,d,g,h,k,l*). In summary, Fig. 2 indicates that there was a highly significant difference between initial quantum yields under direct (α_{dir}) *vs*. diffuse (α_{dif}) radiation ($t = -14.7$, p < 0.0001), and both $A_{2000,dir}$ (and thus $A_{max,dir}$) and $A_{2000,dif}$ ($A_{max,dif}$) increased substantially with increasing LAI, canopy height, and MTA.

Pea, potato and cover crop photosynthesis showed a more pronounced response to increases in DF when DF was low (Fig. 4a–c), but much less so at DF > 0.5 in contrast to

wheat, barley and rapeseed, which showed the opposite pattern: smaller response at low DF with an increasing effect as DF increased (Fig. 4d–f). We chose DF = 0.10 as the reference in Fig. 4 because DF < 0.10 are rather uncommon at this site. Moreover, pea with its short stature almost exclusively responded to diffuse radiation in a way that no unconstrained estimate for α_{dir} could be obtained (the value of 0.0 shown in Tables S1–S3 is the lower constraint imposed on the nonlinear fitting procedure).
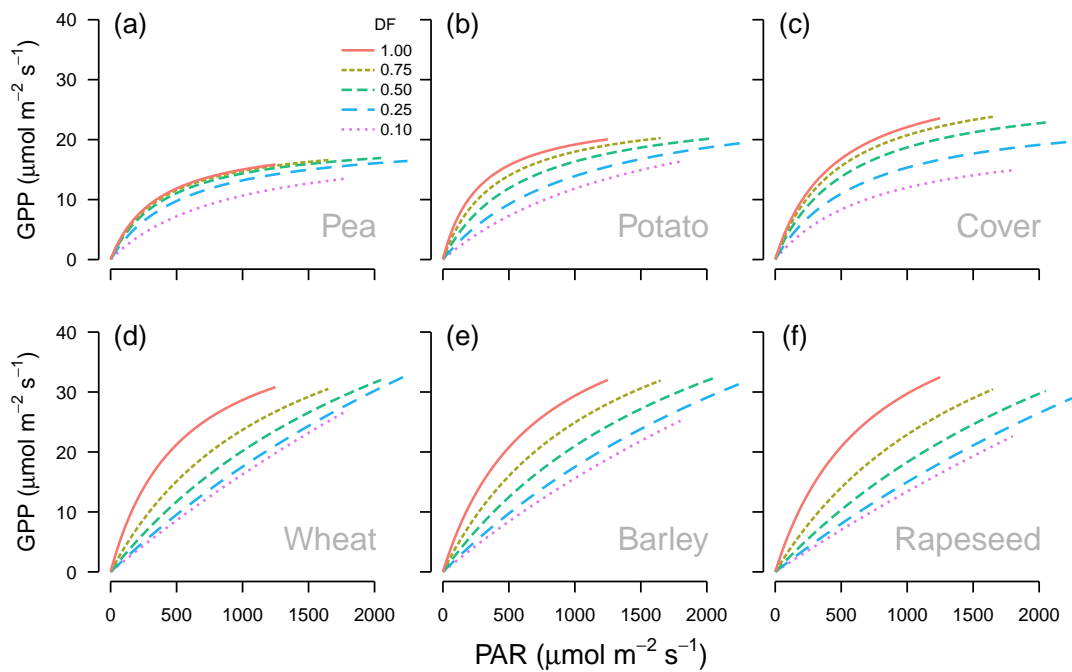

FIGURE 4: *Light response curves at ecosystem level (GPP, gross primary productivity and PAR, photosynthetically active radiation) for (a) pea (based on 2 seasons of data), (b) potato (1 season), (c) cover crop (3 seasons), (d) wheat (5 seasons), (e) barley (3 seasons) and (f) rapeseed (2 seasons) at 5 different diffuse fractions (DF) based on Eq. (1) using the light response parameters of crop species in Table S3.*
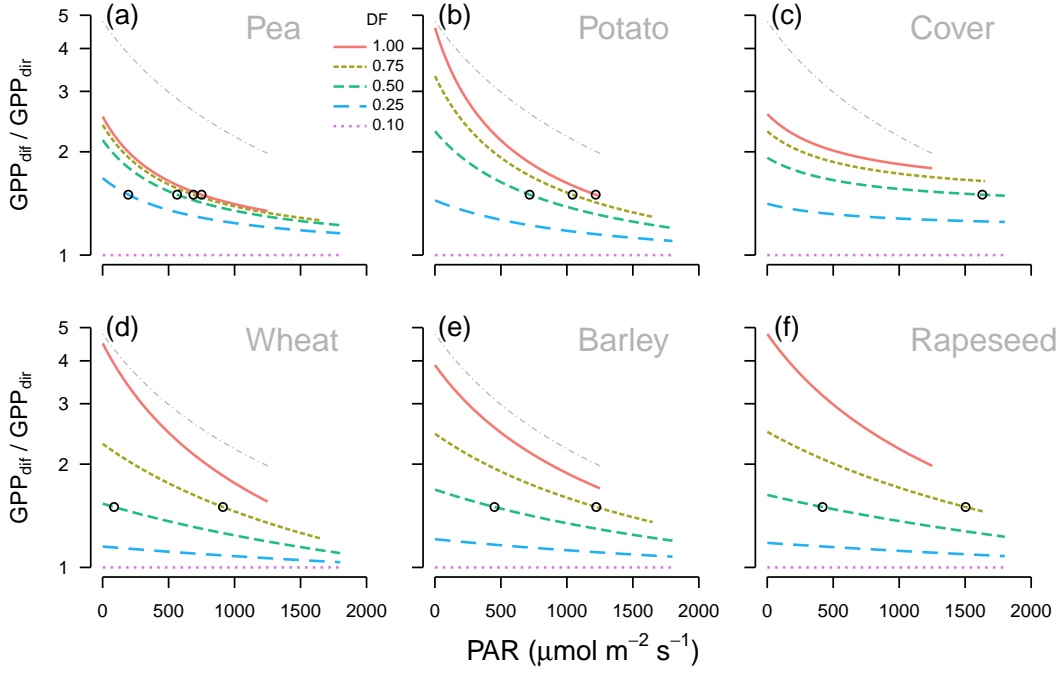
FIGURE 5: *GPP enhancement (GPP$_{dif}$ / GPP$_{dir}$) at the same diffuse fraction (DF) levels as in Fig. 4. GPP$_{dir}$ is defined here as GPP at DF = 0.1. The circles show the position on each curve above which a >50% enhancement is expected as mentioned by Healey et al., 1998 based on a shading experiment that reduced PAR by 25%. Note the logarithmic y-axis. The gray broken lines in panels (a)–(e) show rapeseed at DF = 1 for reference.*

If the enhancement of assimilation due to DF is expressed relative to the conditions at DF = 0.10 as in Fig. 5, rapeseed emerges as the crop with the highest relative response. At lowest PAR (< 200 µmol m^{-2} s^{-1}), which represents dusk and dawn, also potato and wheat show a similarly large effect of GPP enhancement. An effect on the order of +50% or more, as reported by Healey et al. (1998), thus appears to be also realistic for the crops used in this study, although it should be recalled that the Healey et al. (1998) experiment was not done with constant PAR, but reduced PAR by 25% via shade cloth.

None of the variables used in our study to explain the variability of light response parameters are independent of each other, as was clearly seen in the qualitatively similar responses to LAI, h_c, and MTA in Fig. 2. Thus, with a linear mixed model (LMM), we

tried to find out, which of the three canopy architecture parameters is most important for the four light response parameters. Table 1 summarizes the main findings, whereas the full statistical output is presented in Tables S4–S11. Overall, only MTA was retained in the LMMs of all four light response parameters, explaining from 13.5% (α_{dir}) to 25.1% (α_{dif}) of the variance in the respective parameter. The gain in explanation by adding LAI and h_c observations was greatest for α_{dir} (LAI added 13.3% and h_c added 16.9% to explained variance, Table 1). In case of $A_{2000,dir}$, LAI explained an additional 17.8%, but was not relevant for α_{dif} and $A_{2000,dif}$. Canopy height h_c was not relevant for $A_{2000,dir}$ and α_{dif}, and the additional 0.9% gained by h_c for explaining $A_{2000,dif}$ are not as relevant as expected from Fig. 2, and clearly indicate that in a multivariate assessment MTA reveals to be much more important than h_c. The reason for this is the strong correlation between crop species and h_c, which are not independent as an assessment via principal component analysis revealed (see Section 7.2 in Supplementary Information).

Climatic factors (GDD and DI) had no influence on the light response parameters under diffuse conditions, and only GDD was very significant (p = 0.003) for $A_{2000,dir}$, where it was the most important predictor, explaining 26.3% of total variance. Both GDD and DI had a weakly significant effect on α_{dir} with 4.4% and 5.1% contribution to the 74.1% of explained variance, respectively.

TABLE 1: *Explained variance in light response parameters explained by LAI (leaf area index), h_c (canopy height), MTA (mean tilt angle of leaves), including first-order interactions among the three, GDD (growing degree days), and DI (drought index) of α (the initial slope of the light response curve), and A_{2000} (the assimilation rate 2000 $\mu mol\ m^{-2}\ s^{-1}$ incident PAR) related to direct (index dir) and diffuse (index dif) incident photosynthetic active radiation (PAR) determined with a linear mixed model based on the seasonal fits. Year of observation was used as the random effect in this analysis. Only variables with $p < 0.05$ were retained in the model. Besides the model coefficient (coeff) its p-value in the final model, and percentage of explained variance (%exp) of each fixed effect is shown.*

| | Direct PAR | | | | | | Diffuse PAR | | | | | |
| | α_{dir} | | | $A_{2000,dir}$ | | | α_{dif} | | | $A_{2000,dif}$ | | |
	coeff	p	%exp	coeff	p	%exp	coeff	p	%exp	coeff	p	%exp
LAI	0.048	0.006	13.3	71.9	0.008	17.8	—	—	—	—	—	—
h_c	0.0043	0.003	16.9	—	—	—	—	—	—	0.830	0.020	0.9
LAI : h_c	$-0.46 \cdot 10^{-3}$	0.011	9.5	—	—	—	—	—	—	—	—	—
MTA	0.0069	0.006	13.5	6.09	0.005	21.8	$1.37 \cdot 10^{-3}$	0.048	25.1	1.76	<0.001	19.0
LAI:MTA	—	—	—	-1.36	0.009	16.9	—	—	—	—	—	—
h_c:MTA	$-67.5 \cdot 10^{-6}$	0.008	11.4	—	—	—	—	—	—	-0.017	0.009	1.2
GDD	$28.6 \cdot 10^{-6}$	0.045	4.4	0.025	0.003	26.3	—	—	—	—	—	—
DI	$-38.8 \cdot 10^{-6}$	0.035	5.1	—	—	—	—	—	—	—	—	—
Total explained [a]		74.1			82.8			25.1			21.1	

[a] total explained variance of the full model, excluding the random effect

Light interception across canopy profiles

To test if the increase in photosynthesis is due to an increased amount of PAR in the lower canopy, we analysed vertical profiles of photosynthetically active radiation compared to PAR above the canopy (PAR$_{rel}$, Fig. 6a–d) and fraction of absorbed photosynthetically active radiation (fAPAR, Fig. 6e–h) during single years in pea (MTA in the range 41–46°), wheat, (MTA 54–60°), barley (MTA 51–58°), and rapeseed (MTA ≈ 39°) canopies. PAR$_{rel}$ in the lower canopy was lower under diffuse than under clear-sky conditions (Fig. 6a–d) for all crop and cover species. Pea intercepted a much smaller fraction of PAR (43–63%) than all other crop species (> 80%). However, the interception in the lowest canopy layer also increased for pea with DF < 0.8 (Fig. 6e).
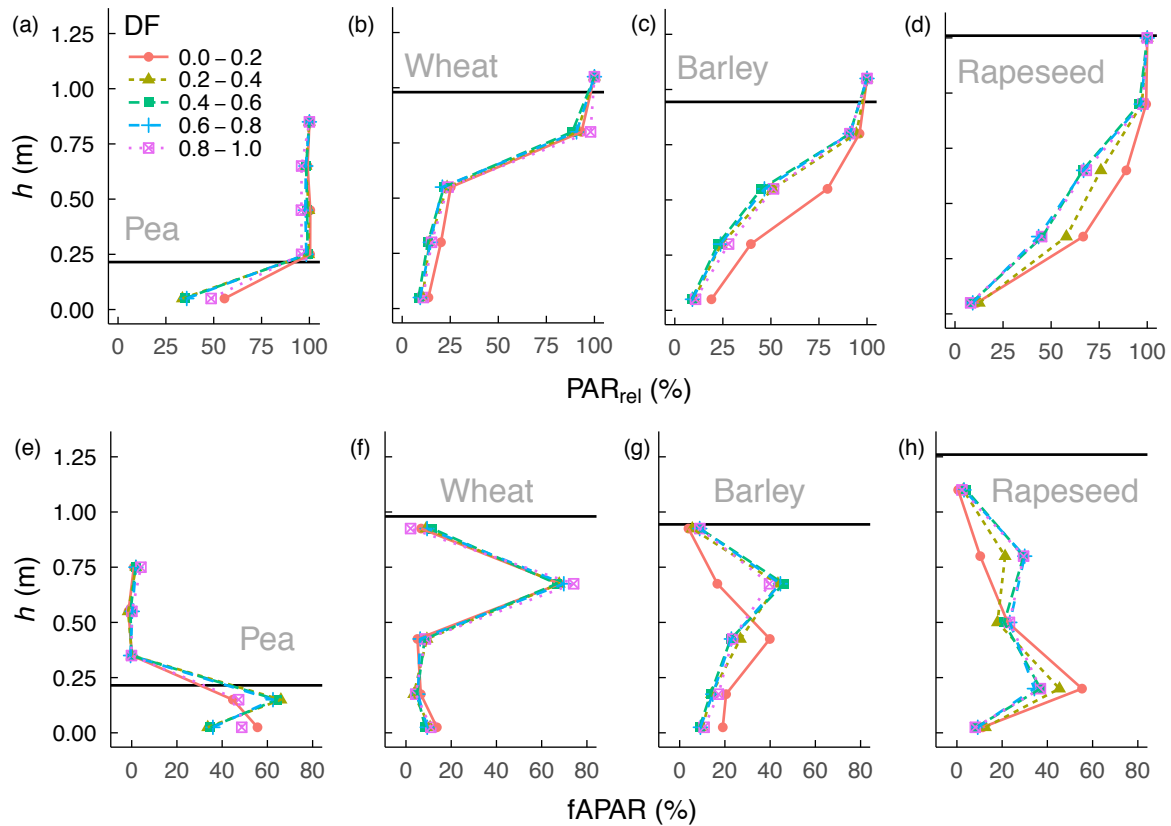
FIGURE 6: Top row: Vertical profiles of relative photosynthetically active radiation (PAR_{rel}) within (a) pea, (b) wheat, (c) barley and (d) rapeseed canopies under different diffuse fraction (DF) ranges. PAR at each height (h) was normalized by PAR at the top measurement height of the profile. Bottom row: Vertical distribution of the fraction of absorbed photosynthetically active radiation (fAPAR) within and above stands of (e) pea, (f) wheat, (g) barley and (h) rapeseed under different diffuse fraction (DF) ranges. Absorbed PAR of each layer was normalized by PAR at the top measurement height of the profile. The heights (h) given on the y-axis represent midpoint heights for canopy layers. The lowest layer was defined as the layer between 5 cm and the ground while all other layers had a thickness of 20, 25, 25, and 30 cm for pea, wheat, barley and rapeseed, respectively. In all panels, the black line shows the maximum measured average canopy height in the same year as the profiles were measured. Profiles are based on one season per crop species.

Wheat and barley with more erect leaves than forbs (rapeseed, pea) had the highest MTA with most of the solar radiation being absorbed in the top canopy (Fig. 6f,g), whereas light penetration into the bottom canopy was greatest in pea and rapeseed (Fig. 6e,h). The short-statured pea showed the least complex canopy architecture and thus could only be resolved by one single measurement layer (Fig. 6a). Wheat was the only crop where the PAR profiles at different DF were almost identical (Fig. 6b). For the denser and taller canopies (barley and rapeseed), there was one pronounced peak in fAPAR in the middle to lower canopy under clear-sky conditions (DF < 0.2). This peak shifted to higher layers for barley while the profile became more vertically uniform for rapeseed with increasing DF (Fig. 6g,h).

Variations of diffuse and direct light inside the canopy

At 5 cm above ground level (bottom row in Fig. 7), pea with a short-statured canopy and horizontal leaves showed a distinctly different pattern than wheat, barley, and rapeseed. In the

latter three crops typically less than 40% of the above-canopy PAR radiation was available in the lower canopy. However, in pea up to 100% and 90% of the above-canopy direct and diffuse PAR, respectively, was available near the ground surface, which is a much larger proportion than for the other species. In the top part of all canopies (Fig. 7, top row), a unimodal distribution of in-canopy light levels could be observed, with typically more than 80% of the above-canopy PAR under both conditions with direct-light dominance (DF < 0.5) and diffuse-light dominated conditions (DF ≥ 0.5). PAR_{rel} in the top of the canopy of wheat, barley, and rapeseed was similar under diffuse and direct light conditions (Fig. 7e,i,m). At the bottom of the canopy, all three crops showed comparably low PAR_{rel} under both direct and diffuse conditions (Fig. 7h,l,p). The transition from upper to lower canopy, however, differed strongly among the crops: while both diffuse and direct PAR were strongly intercepted already between the first and second layer in the wheat canopy (Fig. 7e,f), the absorption of diffuse light was more evenly distributed over the entire canopy in barley and rapeseed. Contrastingly, a substantial share of direct PAR could reach the second (barley, Fig. 7j) or even the third layer (rapseed, Fig. 7o), where it was most strongly intercepted, leaving only a small fraction of direct light for the bottom canopy layer (Fig. 7l,p).
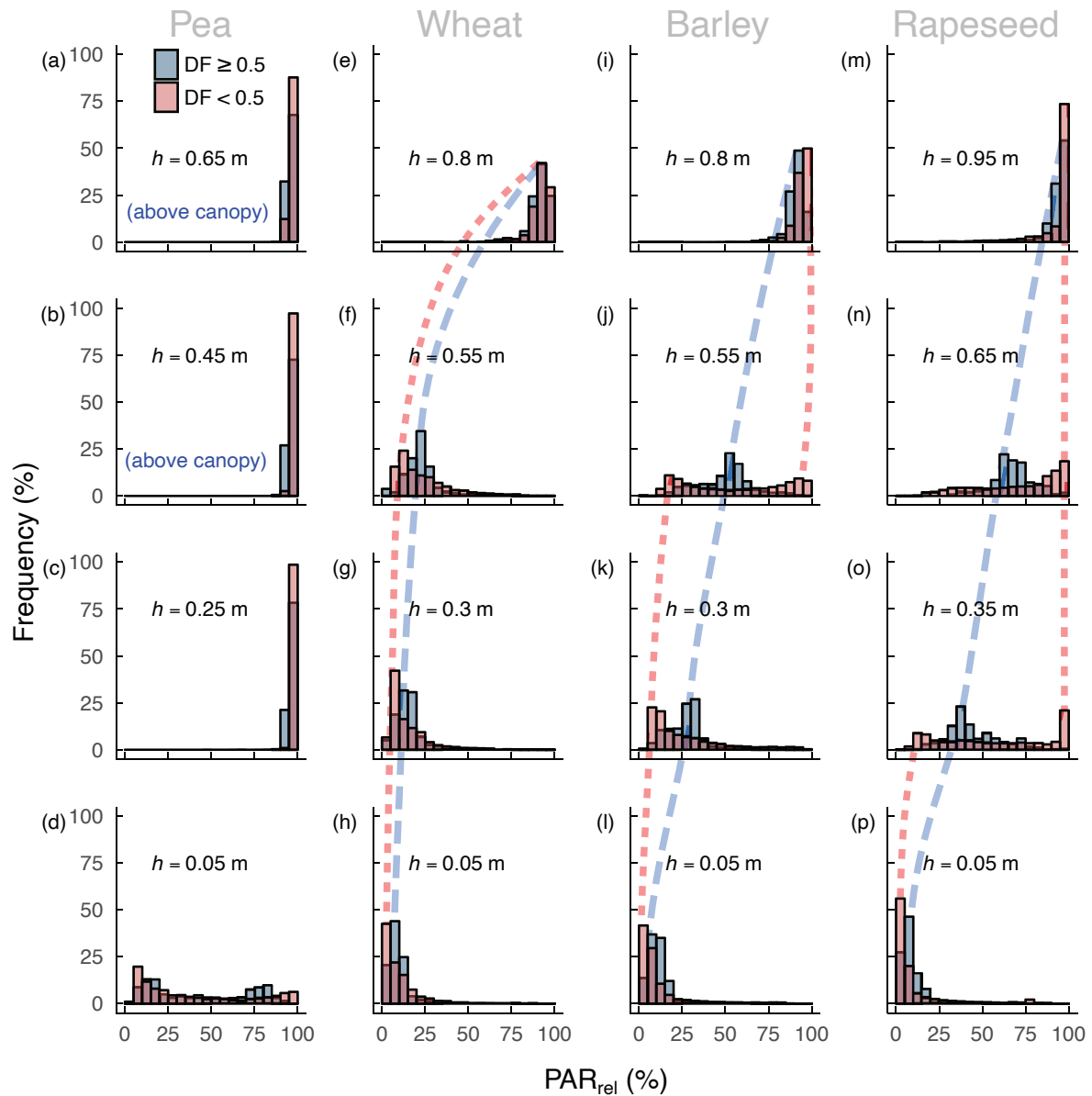
FIGURE 7: *Frequency distribution of relative photosynthetically active radiation (PAR$_{rel}$) at different heights (h) above the ground for (a–d) pea, (e–h) wheat, (i–l) barley and (m–p) rapeseed canopies. Histograms are based on profile measurement of one month during the peak growing period per crop species in 2014 for wheat and 2015 for pea, barley and rapeseed. The red dotted and blue dashed lines follow the distribution peaks for DF < 0.5 and DF ≥ 0.5, respectively. Average canopy heights were 0.215, 0.980, 0.945 and 1.270 m for pea, wheat, barley and rapeseed, respectively, but individual plants could be taller.*

Discussion

In our study we investigated the effect of diffuse *vs.* direct light conditions on penetration depth in the canopy and the associated GPP enhancement. Our aims were to (1) determine the effect of diffuse light on crop photosynthesis at stand level whilst considering the full range of fractions of diffuse to total PAR for six different crop and cover species, and (2) identify the role of canopy architecture on such a photosynthesis enhancement.

Light response with diffuse light fraction

Increases in diffuse fraction led to the largest relative enhancement of photosynthesis (expressed with GPP) at lowest light levels, but the relative enhancement decreased exponentially with increasing PAR (Fig. 5). Initial light response α was higher under diffuse than direct light for all crop and cover species (Fig. 2a,b,e,f,i,j, Table S3), whereas maximum assimilation A_{max} was lower under diffuse than direct light conditions, except for pea and cover crop (Table S3). The latter nicely agrees with well-established knowledge at leaf-level (see Fig. 5.9 in Chapin, Matson, & Mooney, 2002) but partially contrasts with other studies that found not only increasing α but also increasing A_{max} with increasing fraction of diffuse light (Gu et al., 2002; Dengel and Grace, 2010; Urban et al., 2011). The strongest enhancement of photosynthesis with increasing DF was found in rapeseed (Fig. 5f), which was the crop with the largest h_c out of the six species investigated in this study. To the best of our knowledge this is the first study that investigated the relationship between h_c and photosynthesis enhancement due to diffuse *vs.* direct light. Photosynthesis increased linearly with h_c (since both $A_{2000,dir}$ and $A_{2000,dif}$ in Fig. 2g,h increased significantly with h_c, whereas α_{dir} and α_{dif} in Fig. 2e,f remained rather constant irrespective of h_c) in all six crop and cover species. This dependence on h_c is an indication that canopy volume and not primarily canopy LAI (Fig. 2a–d) is essential for the theoretic asymptotic assimilation maximum. Our LMM however assigned more explained variance in light response

parameters to MTA than h_c. Our interpretation is that at a given locality there is a strong correlation between a selected crop variety and its maximum seasonal h_c. It is however not unlikely that if a larger-scale analysis could be performed with a wider selection of varieties of a specific crop species, so that there is more within-species variation of h_c than in our study, then h_c might obtain the same or even more importance than MTA as a predictor for light response parameters. Thus, we recommend to measure MTA (which can be done via optical LAI measurements), but also h_c, a simple-to-measure canopy architecture parameter, which might be important for global comparisons of studies. Future studies should also investigate whether internodal lengths of the plants might be an even better explanatory measurement than MTA, LAI, and h_c. Canopy height correlates to the ratios of initial quantum yield $\alpha_{dif}/\alpha_{dir}$ and $A_{max,dif}/A_{max,dir}$ rather well (Fig. 8) and thus deserves further investigation with a more detailed assessment that goes beyond the maximum seasonal h_c approach used in this study.
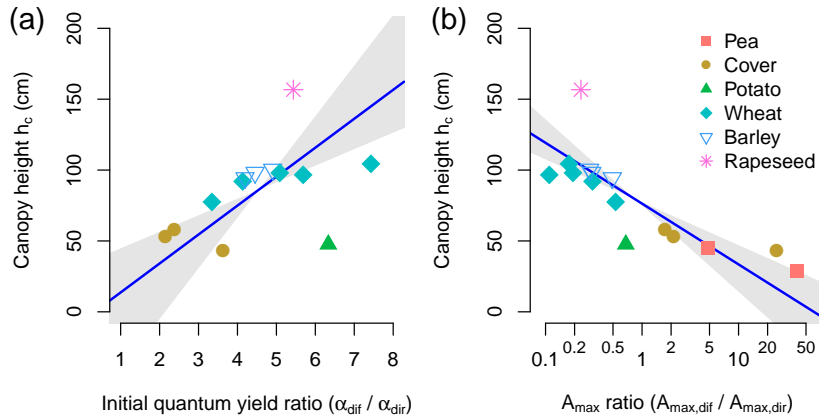

FIGURE 8: Ratio between diffuse and direct light response curve parameter estimates (a) for initial quantum yield, and (b) for asymptotic maximum assimilation rate as a function of canopy height (h_c). Standardized major axis (SMA) regressions (orthogonal regression approach; Legendre and Legendre 2012) are shown with the best estimate (blue line) and the

95% confidence interval (gray area). Note the log-transformed x-axis in (b). SMA regressions are the same if x and y axes are switched, hence we plotted canopy height along the vertical axis for better legibility of the graph.

Mean leaf tilt angle had a relevant influence on all light response parameters, which is in agreement with earlier findings from a temperate deciduous forest (Knohl & Baldocchi 2008). This view is also in line with Chen et al. (2014), who found, via explicit 3D canopy architecture modeling, that diffuse light improved light interception of leaves that are directly shaded by other leaves. They argued that this is the reason why more heterogeneous canopies experience a higher GPP enhancement via diffuse radiation than homogeneous canopies such as pea in our study, or soybean canopies in e.g. Cheng et al. (2015). Although MTA is an easy-to-measure variable when using a LAI2000 (or newer) analyser, many assumptions are involved in the calculations. Thus, a better quantification of MTA using 3D scanners in the future may substantially increase the quality of MTA estimates, which in turn could provide a statistically more robust information on the relationship between MTA and light response parameters.

Residual analysis (Figs S7–S12) generally showed that Eq. (1) provided a good fit to measured data. In a few seasons and crops, however, this model tended to overestimate GPP at high DF. In future studies it is recommended to specifically investigate why the variability in GPP at high DF at a given PAR level was much greater than under moderate or low DF. At our field site, frequent fog during the early growth phase in autumn and in spring might be the reason, but specific measurements of horizontal visibility or fog droplet concentration will be required to investigate this aspect in more depth.

Light interception across canopy profiles

The light interception measurements across plant canopies carried out in four out of the six crops used in this study provided additional insights into light absorption. All crops

investigated in our study indicated that canopies with high LAI (i.e., wheat, barley, rapeseed) were more sensitive to the DF than those with low LAI (i.e., pea). This supports the expectation of a modeling study by Greenwald et al. (2006), which has not been validated with empirical measurements so far. Potato, which was only covered by one season in our study, deviates somewhat from other crops and shows higher sensitivity to DF at low PAR levels than at high levels (Fig. 5b). For the pea canopies, the PAR interception distribution was mostly affected by changes in DF at very low DF ranges (Fig. 6e). Similarly, the photosynthesis enhancement of pea was also only affected at low DF (Figs 4a, 5a). Pea had the lowest maximum h_c of the studied crops and its LAI of 2.4 to 3.3 m^2 m^{-2} was close to the limit for the photosynthesis enhancement effect reported by Wohlfahrt et al. (2008) for a grassland (between 2 and 4 m^2 m^{-2}). Cover crop, which is more comparable to grassland due to a mixture of grasses, legumes and forbs, showed a larger photosynthesis enhancement than pea (Figs 4c, 5c) despite its comparatively low maximum LAI of 3.23 m^2 m^{-2} during the 2005 season. During this cover crop season, h_c was clearly larger (0.70 m) than during both pea seasons (0.20 m and 0.45 m). This made us hypothesize that the combination of h_c and LAI is relevant for the photosynthesis enhancement. However, our linear mixed model indicated that only α_{dir} (i.e., not the other three light response model parameters) was related to the interaction between h_c and LAI (Table 1). According to Timlin et al. (2014), planting density could also have had an effect on the photosynthesis enhancement. Planting density tends to correlate with LAI and was therefore only indirectly represented in our study. However, we have shown that LAI had no significant effect on α_{dif} and $A_{2000,dif}$, whereas MTA was the only canopy architecture variable that turned out to be relevant for the explanation of all four light response parameters (Table 1).

A non-uniform vertical distribution of nitrogen across the plant canopies is known to modify light absorption. Because our study did not involve accounting for variability in the distribution of nitrogen (N) in the canopy, this aspect was not included in our linear mixed

model. However, as a follow-up to our modeling study by Revill et al. (2019) for the same site we simulated the effect of an even *vs.* uneven N distribution across the canopy for the taller crops: wheat, barley, and rapeseed (Fig. S13). Model canopy height was set to 0.8 m, and nitrogen distribution for the case of unevenly distributed N was taken from measurements presented in D'Odorico et al. (2019). For the evenly distributed N simulation the average across the bottom and top canopy measurements in D'Odorico et al. (2019) was used. Although the uneven N distribution has an effect on GPP, which reflects the difference in light absorption under diffuse *vs.* direct light, the differences are within the statistical uncertainty of comparison (see error bars in Fig. S13). It is interesting to note that while the modeled effect of even *vs.* uneven N distribution across the canopy had very little effect on all three species considered (Fig. S13; wheat, barley and rapeseed), Fig. 7 clearly showed a different behaviour of wheat (Fig. 7e–h) as compared to barley (Fig. 7i–l) and rapeseed (Fig. 7m–p): light absorption in wheat was almost independent of DF, whereas it strongly depended on DF in barley and rapeseed. This is in agreement with findings from a meta-analysis carried out by Hikosaka et al. (2016) who found that the photosynthetic nitrogen distribution coefficient in wheat mainly depended on LAI, whereas it was also depending on the light extinction coefficient in non-wheat species. (MTA was not available for the Hikosaka et al. 2016 meta-analysis.) In our study, leaf N content was only measured by D'Odorico et al. (2019) during one season and thus it was not possible to include this aspect in further detail in our study for all 13 years.

Variations of diffuse and direct light inside the canopy

Earlier studies (Urban et al., 2011; Li et al., 2014) found that average PAR$_{rel}$ at a certain height within the canopy was higher under diffuse than under clear-sky conditions. Under diffuse light conditions, PAR$_{rel}$ was vertically more evenly distributed within the canopy than under direct light, and a higher fraction reached the lower canopy layers (Kanniah et

al., 2012). Contrastingly in our study, we found that average absolute PAR was not larger at any height under diffuse than under clear-sky conditions (not shown). Moreover, we found that PAR_{rel} was usually not enhanced at any height within the canopy under diffuse conditions (Figs 6a–d and 7). Instead, the region of highest PAR absorption was rather found in the upper part of the canopy (Fig. 6e–h). Thus, with respect to our hypothesis (1) the absorbed fAPAR in the lower part of the canopy was clearly higher during clear-sky conditions (DF < 0.2) in pea, barley, and rapeseed, whereas only wheat showed no difference in fAPAR at different DF levels (Fig. 6e–h). Thus, our first hypothesis cannot be retained given our field measurements. While wheat did not show an effect of DF on fAPAR, the absorption of PAR in the rapeseed canopy became more vertically uniform with more diffuse light when DF exceeded the threshold of 0.2.

The shift from a unimodal to a bimodal distribution at intermediate heights within the canopy of barley and rapeseed, and the lowest canopy layer of pea (Fig. 7), indicates that PAR was horizontally more evenly distributed under diffuse than under clear-sky conditions. This means that under clear-sky conditions some leaves were exposed to sun flecks while others were in the deep shade (Gu et al., 2002), creating strong within-canopy contrasts in light levels. When one leaf is in the full sunlight and another is in the deep shade, the average photosynthesis rate of the two leaves is likely to be lower than if both leaves had been exposed to intermediate light/shade levels (Farquhar and Roderick, 2003). Moreover, D'Odorico et al. (2019) showed that crop plants at this site reached light saturation in the lower canopy at lower PAR than in the higher canopy, which indicates a high plasticity of the plants to adapt to their local environment. Therefore, the plant leaves can benefit from a shift of the peak in the fAPAR distribution as observed in the upper canopy layers of barley and rapeseed by adapting to these light conditions. In pea canopies with smaller photosynthesis enhancement than in other crops (Fig. 5), there was no pronounced change in the PAR distribution between clear and diffuse conditions.

Further implications

In our study of six major arable crops, we found that the canopy architecture variables MTA and h_c were good predictors of the effect that DF has on the light response parameters at high DF (Table 1). At low DF, when direct PAR dominated, also LAI, GDD and DI, and the interactions among the three canopy architecture variables, contributed with 4.4% to 26.3% to the total explained variance of α_{dir} and $A_{2000,dir}$ (Table 1).

We conclude that at least canopy height and MTA, two relatively easily measured canopy architecture variables, should be quantified in field studies addressing the photosynthesis enhancement of crop species. Considering canopy architecture and diffuse light conditions will greatly reduce uncertainty in global GPP of cropping systems estimated by models, the improvement of which is still strongly limited by the low number of validation datasets from different crop and cover species and climatic environments worldwide. At the same time, quantitative information on crop photosynthesis enhancement under diffuse light conditions will improve our ability to make an adequate evidence-based selection of major crop species for food security under future conditions with different cloudiness and thus diffuse fraction of light.

Acknowledgements

Data availability

The data used in this study can be downloaded from the ETH Zurich Research Data Respository via doi:10.3929/ethz-b-000381776.

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