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The impact of diffuse light on gross ecosystem productivity over a winter wheat (*Triticum aestivum* L.) is related to the increase of incident light interception in the middle and lower canopy

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Abstract

Diffuse light has potential to increase ecosystem gross primary productivity without the confounding effect of other environmental factors. However, the magnitude of the importance of diffuse light for ecosystem carbon uptake and the mechanism behind the diffuse light-related photosynthetic enhancement is unclear. Here, 2 years of gross ecosystem primary productivity (GEP), assessed by eddy covariance technology over a (winter) wheat cropland, was used to determine whether diffuse photosynthetic active radiance (PAR_{dif}) affected wheat GEP. Additionally, the method of Artificial Neural Network combined with interference analysis and modelling were used to quantify the relative importance of diffuse light for GEP variations and to explore the underlying mechanism of diffuse light effect on GEP. Wheat GEP increased significantly with

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increase in PAR_{dif} in the absence of effect of total PAR. PAR_{dif} was found to be the most important factor for wheat GEP, making a contribution of 41.3% in 2011 and 35.7% in 2012 to GEP variations, which were greater than the contribution of total PAR, air temperature, vapor pressure deficit and friction velocity. The results of combination of model and measured data indicated that as PAR_{dif} increasing, the within canopy, especially the middle and lower canopy, intercepted more light, leading to photosynthetic increase in entire canopy. Over all, our study provided a new evidence for the importance of diffuse light for carbon uptake in agroecosystem, which is importance for predicting the response of ecosystem carbon budget to future light climate changes.

Key words: Diffuse radiance, ecosystem carbon exchange, mechanism, Artificial Neural Network, modeling.

1. Introduction

Solar radiation provides energy for plant photosynthesis and is an important factor influencing plant carbon production (Kanniah et al., 2012; Weber et al., 2009; Williams et al., 2014; Wohlfahrt et al., 2008). Terrestrial carbon assimilation rates on a leaf level response to sunlight nonlinearly and increase with solar radiation until leaves are light saturated (Falge et al., 2001; Law et al., 2002; Mercado et al., 2009). However, at the vegetative canopy scale, the photosynthetic response to solar radiation becomes more complex than on a leaf scale because of leaf arrangement and distribution within

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a canopy (Buckley et al., 2013; De Pury and Farquhar, 1997; Williams et al., 2014). The amount of solar radiance was often assumed to be stable because of simplicity for research and lack of better knowledge over the years. However, more and more evidences have indicated that there existing coherent periods and regions with prevailing "dimming" and "brightening" in solar radiance in the worldwide observational networks (Baldocchi, 2008; Knohl and Baldocchi, 2008; Wild, 2009; 2012). Thus, investigating the dependence of ecosystem-level carbon production on sunlight has important significance for global food security and predicting terrestrial carbon cycles under the background of light climate change.

When sunlight penetrates the Earth's atmosphere, it is scattered by clouds and aerosols, creating diffuse light (Durand et al., 2021; Urban et al., 2012; Zhang et al., 2011). Theory suggests that the relationships between canopy carbon exchange process and light climate differs under direct light and diffuse light or in sunny and cloudy days. Under direct light conditions, plant leaves are illuminated from a single direction, causing that the leaves of lower canopy are shaded heavily because of light interception of upper leaves. In comparison, canopy is illuminated from multi-directions under diffuse light conditions, and leaves that were previously shaded are now illuminated, leading to that the leaves of the within canopy intercept more light (Williams et al., 2014). Finally, the increase in light intercepted by canopy may lead to overall enhancement of canopy photosynthesis. According to these theory, one expects that canopy has greater photosynthetic capacity because of more light intercepted by the canopy under diffuse light condition compared with direct light condition.

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Measurements or modeling for carbon exchange process over ecosystems have confirmed the expectations for the enhancement of ecosystem carbon uptake with increase in diffuse light (Cheng et al., 2015; Emmel et al., 2020; Mercado et al., 2009; Oliphant et al., 2011; Rap et al., 2018; Zhou et al., 2021), but studies confirming the expectations for the underlying mechanism are scarce.

Diffuse light effect is not a separate process. The increase in level of diffuse light is accompanied with changes in total light (Knohl and Baldocchi, 2008). In cloudy days, total light tends to reduce, but diffuse light increases. This co–varying of the two elements may result in that the carbon uptake gain because of diffuse light increase is offset by photosynthetic reduction because of total light decline under cloudy conditions (Alton, 2005, 2007, 2008). Due to the balance of the two opposite carbon exchange processes, some ecosystems showed reduced carbon uptake under elevated diffuse light condition (Alton, 2008; Kanniah, et al. 2013), which contradicted with theory–based assumptions. This means that the diffuse light effect on ecosystem carbon exchange is unclear if the confounding effect of total light is not removed or minimized (Niyogi et al., 2004).

There are also some issues regarding the effect of diffuse light that need further explored, e.g., to what extent the diffuse light is important for canopy photosynthesis? Such analysis is important because if diffuse light contributes very little to photosynthetic variations, the effect of diffuse light on ecosystem may not be significant, although it can promote canopy photosynthesis. To date, only a few studies have quantified its relative importance. For example, one study on a forest ecosystem

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indicated that diffuse light is not as important as total light and vapor pressure deficit by calculating their separating contributions to net carbon uptake variations (Park et al., 2018). However, past research should be analyzed further by removing the potential effect of sun elevation angle, because solar elevation angle was found to play a significant modifying role to the effect of diffuse light on ecosystem photosynthesis (Cheng et al., 2015).

In this study, eddy covariance technique combined with modeling method were used to calculate the over-canopy variations in the gross ecosystem primary productivity (GEP) and simulated the within–canopy microclimate conditions and photosynthetic rate in a (winter) wheat (*Triticum aestivum* L.) crop in northern China from 2010 to 2012. Our aim was to 1) analyze the response of GEP to diffuse light without effect of total light, 2) quantify the relative importance of diffuse light for GEP, and 3) explore the underlying mechanism of effect of diffuse light on GEP. We hypothesize that wheat GEP will increase significantly along with diffuse light, and the increase is attributed to more light intercepted by the canopy when diffuse light increasing.

2. Materials and Methods

2.1 Study area and experimental measurements

The field experiment was conducted over a (winter) wheat (*Triticum aestivum* L.) cropland at the Luancheng Agroecosystem Experimental Station (37°50′N, 114°40′E; elevation: 50.1 m above sea level) in Hebei Province, China, during 2011–2012. The climate of the region is semi-humid and semi-arid, with a long winter (from November to next February) and a short spring (from March to April) (Yang et al., 2019). The long-term (from 1990 to 2008) mean annual temperature and precipitation were 12.8°C and 485 mm, respectively. Wheat was sown on October and harvested on June. The highest canopy heights were approximately 1.0 m. The maximal leaf area indexes (LAIs) for wheat were approximately 4.1 m^2 m^{-2} and 3.9 m^2 m^{-2} at the heading growing stage in 2011 and 2012, respectively.

The ecosystem CO_2 (carbon) and heat fluxes between the biosphere and atmosphere were measured using eddy covariance (EC) technology. The EC monitoring system consisted of a three-dimensional sonic anemometer (Model CSAT 3, Campbell Scientific Inc., USA) to monitor fluctuations in vertical wind velocity (ω') and an open-path and fast-response infrared gas analyzer (Model LI-7500, Li-Cor Inc., USA) to monitor the fluctuations in the CO_2 and water vapor concentrations (ρ') (Bao et al., 2022). The net ecosystem carbon exchange (NEE; mg CO_2 m^{-2} s^{-1}), latent heat flux (LE; W m^{-2} s^{-1}) and sensitivity heat flux (H; W m^{-2} s^{-1}) were calculated on line by the covariance between ω' and ρ'. Along with the flux measurements, variations in global radiation, net radiation, total photosynthetic active radiation (400–700 nm; hereafter denoted as PAR), air temperature (T_a), surface soil temperature, relative humidity, soil water content (SWC), precipitation and soil heat flux were also measured. A data logger collected the raw data at a rate of 10 Hz and stored them as 30 min averages. Details of other instruments for measuring and data collecting can be found in our published work (Bao et al. 2022).

The raw flux and meteorological data were experienced procedures of correcting,

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screening and rejecting (Falge et al., 2001; Webb et al., 1980). More information about the data processing has been described by Bao et al. (2022).

2.2 GEP estimation and light response curve

GEP is the difference between ecosystem respiration (ER) and NEE (GEP=ER–NEE). Nighttime ER (= nighttime NEE, because there is not photosynthesis in nighttime) gaps were interpolated by Lloyd & Taylor model (Lloyd and Taylor, 1994). Daytime ER was estimated by the method proposed by Reichstein et al. (2005). More information about ER interpolation can be found in Bao et al. (2020).

To obtain the entire time series for GEP during the whole growing seasons, the gaps of daytime NEE was also filled. The gaps had a time interval less than 2 hours were filled by linear interpolation method. The gaps longer than 2 hours were filled using marginal distribution sampling method, by which the "gaps" could be look up on the basis of relationships between flux and environmental factors (Reichstein et al., 2005).

Light is a crucial factor for ecosystem photosynthesis. There is often strong relationship between incident light and plant photosynthetic capacity, which can be described as a rectangular hyperbola light response model (Falge et al., 2001):

$$\mathrm{GEP} = \frac{\alpha A_{max} \mathrm{PAR}}{\alpha \mathrm{PAR} + A_{max}}, \tag{1}$$

where α represents the initial slope of the ecosystem light-response curve, i.e. the

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apparent quantum yield or the apparent light-use efficiency (mg CO_2 μmol photon^{-1}), A_{max} represents the maximum rate of ecosystem gross photosynthesis (mgCO_2 m^{-2} s^{-1}) at the infinite PAR (μmol photon m^{-2} s^{-1}).

2.3 PAR_{dif} estimation

The Luancheng site lacked the direct measurement of the diffuse component of solar radiance; consequently, the strength of diffuse light was estimated on the basis of the clearness index (CI) and the diffuse component of global solar radiation (S_d). According to Gu et al. (1999), CI is the ratio of the global solar radiation (S, W m^{-2}) received by the earth's surface to the extraterrestrial irradiance at a plane parallel to the Earth's surface (S_e, W m^{-2}) as follows:

$$CI = \frac{S}{S_e} \tag{2}$$

$$S_e = S_{sc}[1 + 0.003\cos(360t_d/365)]\sin\beta \tag{3}$$

$$\sin\beta = \sin\varphi \cdot \sin\delta + \cos\varphi \cdot \cos\omega, \tag{4}$$

where S_{sc} represents the solar constant (1,370 W m^{-2}), t_d represents the day of the year, β represents the solar altitude angle, φ represents the degree of latitude, δ represents the declination of the sun and ω represents the time angle (Gu et al. 1999).

The diffuse fraction of PAR (fDPAR) and diffuse PAR (PAR_{dif}) were calculated using the following relationships (Reindl et al., 1990):

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$$\mathrm{fDPAR} = \frac{\left[1 + 0.3\left(1 - q^2\right)\right]q}{1 + (1 - q)\cos^2(90 - \beta)\cos^3\beta} \tag{5}$$

$$q = \frac{S_d}{S_e \cdot CI} \tag{6}$$

because CI is the ratio of S to S_e, then,

$$q = \frac{S_d}{S} \tag{7}$$

when $0 \leq CI \leq 0.3$, restrain: $q \leq 1.0$,

$$q = 1.02 - 0.254CI + 0.0123\sin(\beta) \tag{8}$$

when $0.3 < CI < 0.78$, restrain: $0.1 \leq q \leq 0.97$,

$$q = 1.400 - 1.749CI + 0.177\sin(\beta) \tag{9}$$

when $CI \geq 0.78$, restrain: $q \geq 0.1$,

$$q = 0.486CI - 0.182\sin(\beta) \tag{10}$$

$$PAR_{dif} = PAR \times fDPAR$$

PAR and PAR_{dif} typically co-vary with each other, thus, the confounding effect of PAR should be removed to describe the response of GEP to PAR_{dif}. We first established the model using (total) PAR and the observed GEP (calculated using observed NEE) on the basis of Eq. 1, and GEP_{fitted} was obtained. Then, we calculated the residuals between observed GEP and GEP_{fitted}, which did not correlate with PAR. Finally, the

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relationships between these residuals and PAR_{dif} were examined because they represent the responses of GEP to PAR_{dif} that were not confounded by total light.

2.4 Artificial Neural Network

Before quantifying the effect of diffuse light, the factors affecting GEP using Artificial Neural Network (ANN) method were determined. ANN is a mathematical model that imitates the structure and function of a biological neural network. By learning the patterns of data samples, it explores nonlinearity and complex interactions among predictors without assumptions to simulate the internal mechanism between information (Jin et al., 2019). Many studies have indicated the effectiveness of ANN in data interpretation (Wagle et al., 2016; Zhou et al., 2021).

ANN models were established consisted of input layer, hidden layer and output layer by software package NeuroShell Easy Predictor, Version 2.0 (Ward Systems Group, Inc., Frederick, MD, USA). We considered PAR (μmol m^{-2} s^{-1}), PAR_{dif} (μmol m^{-2} s^{-1}), T_a (°C), vapor pressure deficit (VPD, Kpa), SWC (m^3m^{-3}) and friction velocity (u*, m s^{-1}) as input variables (neurons) in ANN modeling because they are the factors most often discussed in literature. Among these factors, we selected PAR, T_a and VPD as mandatory input variables because they are widely reported as affecting GEP. This empirical assumption was also supported by our analysis of the strong relationships between hourly GEP and PAR, T_a and VPD (data not shown). PAR_{dif}, SWC and u* were selected as optional input variables because their abilities to affect GEP are still debatable, according to past literature. This input variable setting resulted in eight

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models having different combinations of input parameters (Table 1). The number of hidden layer neurons was determined automatically by the software. The output layer consisted of one output variable of GEP (mg CO_2 m^{-2} s^{-1}). The raw GEP data (namely calculated by raw NEE) was divided into two parts: approximately 75% of the data samples were used to train samples and establish models, and the remaining 25% of the data samples were used to compare the model's accuracy according to two assessing indicators, i.e., the Nash–Sutcliffe efficiency index (R^2) and the root–mean–square error (RMSE). The calculation methods for these indicators were presented previously in Hu et al. (2008).

To quantify the relative effect of diffuse light on GEP, interference analysis method on the basis of ANN model was applied. Only when the model is relatively accurate can the results of the model-based interference analysis be reliable. For a certain input variable containing N groups of data, the corresponding output value is y(n). When adding 1% interference to the i*th* neuron (i = 1, 2, 3, 4….), the corresponding output value is y_i (n). If the neuron in the input layer has a large influence on GEP, then the output's simulated values after a small interference will deviate more from those without interference. We used S_i to indicate the influence of each neuron, as follows:

$$S_i = \frac{1}{N}\sum_{n=1}^{N}\frac{|y_i(n) - y(n)|}{|y(n)|} \tag{11}$$

The contribution of each variable to GEP can be estimated as follows:

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$$Q_i = \frac{S_i}{\sum_{n=1}^{i} S_i} \times 100\%. \tag{12}$$

Because the magnitude order of the input variables in original data set varied greatly, the input variables were normalized before interference analysis, and all the input data were converted into 0–1. The normalization formula is as follows:

$$Y = (X - x_{min})/(x_{max} - x_{min}), \tag{13}$$

where Y, X, x_{max} and x_{min} represent normalization values of the input variables, input variables, the maximum and minimal values of the input variables, respectively.

2.5 Biophysical multilayer canopy model

The eddy covariance technology only measures the above-canopy carbon flux. In order to obtain the CO_2 exchange rate within the canopy, we used a biophysical multilayer canopy model documented by Baldocchi and Wilson (2001). This model computes the biosphere-atmosphere exchange of water vapor, carbon and sensible heat flux and microclimate within and above the canopy at an hour timescale. The model consists of micrometeorological and physiological modules. The former computes leaf and soil energy exchange, scalar concentration profiles through the canopy. Environmental factors that were computed with the micrometeorological module drive the

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physiological modules that compute leaf photosynthesis. The model was driven by external variables that were measured above the canopy. The environmental inputs include incident PAR, air temperature, wind speed, relative humidity and CO_2 concentration. Plant structural variables include leaf area index, leaf angle orientation, a leaf clumping factor, and canopy height (Baldocchi et al., 1999). The key parameters of the model were collected by querying the site technicians and from literature. During the study period, the leaf area and plant height was relatively constant. The entire canopy was divided into ten layers on average by the model from canopy top to ground surface, and the meteorological conditions (mainly referring to the incident PAR) and photosynthetic rate of each layer was simulated. We then used mean value of photosynthetic rate and PAR in 1–3 layers, 4–7 layers and 8–10 layers to represented the upper, middle and lower of the canopy, respectively.

We used observed fluxes and radiation data during the study periods (introduced in next section) to validate the model. The slope of a linear relationship between model versus observed flux data (k) and the determination coefficient of the relationship (R^2) were used to describe the validation results. The results show that the multilayer canopy model predicted CO_2, LE flux and net radiation above the canopy well with k ≈ 1 and $R^2 > 0.85$ (Figure. 1).

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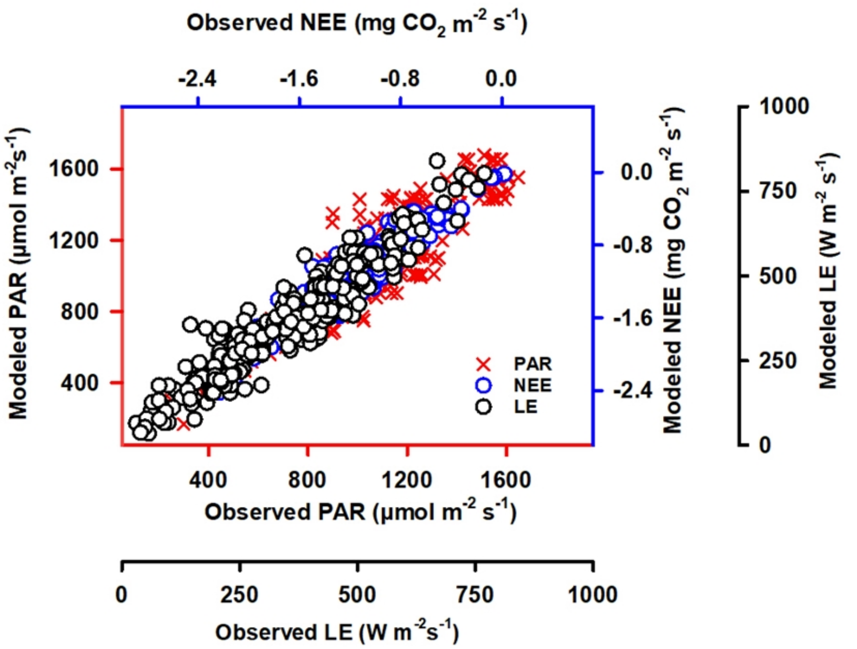

Figure 1. Validation for the multilayer canopy model. The unfilled observed data during the study periods was used. The fitted regression equation and determination coefficients (R^2) were $PAR_{modeled}$ = 0.99 $PAR_{observed}$ + 26.51, R^2=0.85; $NEE_{modeled}$ = 0.96 $NEE_{observed}$ – 0.02, R^2 = 0.88; $LE_{modeled}$ = 0.98 $LE_{observed}$ + 23.26, R^2=0.90. All the correlations were significant at the level of 0.01.

2.6 Analyzed periods

During growing seasons, the leaf areas of crops typically changed markedly along with plant growth. To minimize the impact of leaf area changes on carbon-exchange

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processes, data from April to middle May for wheat was selected. The periods mainly covered the stages from late jointing to heading for wheat, during which plants grew relatively steadily and the changes in leaf area index were not dramatic. In addition, due to that different solar zenith angles affect the responses of ecosystem carbon exchanges to light or the role of PAR_{dif} (Cheng et al., 2015), daytime data from 10: 00 am to 14:00 pm during the selected growing period were the focus. The GEP values estimated based on observed and unfilled NEE data were used.

3. Results

3.1 Weather conditions and GEP variations

The seasonal variations in meteorological factors and GEP are shown in Figure 2. During the whole growing seasons, the minimal monthly mean T_a values usually occurred in the following January, and then increased rapidly until harvest time (Fig.2a). Monthly mean VPDs exhibited a variation trend similar to that of T_a (data not shown). The rainfall during the wheat growing season was less. It mainly concentrated in May and July. The surface soil moisture condition showed a gently change (Fig. 2b). CIs varied obviously among months. It often reaches its maxima in February, indicating that the sky during this period was clearest (Fig. 2a). Solar radiation and its diffuse portion showed similar change trends (Fig. 2c). The PAR and PAR_{dif} values were low during winter, and then began to increase gradually from February.

Daily GEP of wheat was close to zero from sowing date in October to reviving stage in next February (Fig. 2d). In spring, daily GEP began to increase rapidly and reached its

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maximum values in May and then decreased because of plant senescence.

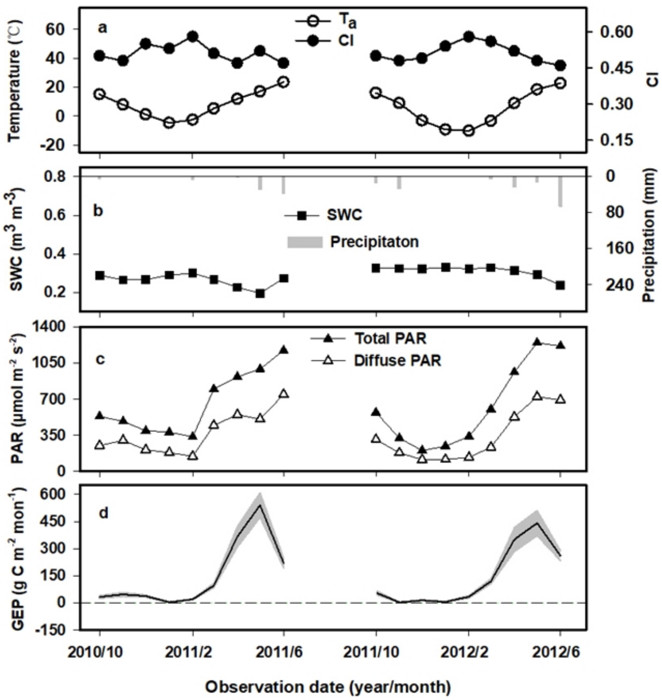

Figure 2. The seasonal variations in (a) monthly mean air temperature (T_a, °C), and clearness index (CI), (b) soil water content (SWC, m^3m^{-3}) and monthly summed precipitation (mm), (c) monthly mean PAR ($\mu mol\ m^{-2}\ s^{-1}$) and diffuse PAR (PAR_{dif}), and (d) monthly summed GEP ($g\ C\ m^{-1}\ mon^{-1}$) for the wheat during 2010–2012. The gray area in the panel (d) represents the uncertainty of the monthly values calculated according to the method described by Bao et al. (2022).

3.2. Effect of diffuse light

The responses of wheat GEP to PAR_{dif} without confounding effect of PAR are shown in Figure 3. The residual GEP increased along with PAR_{dif} significantly in both years,

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indicating that PAR_{dif} had a positive effect on the GEP. Results of ANN analyses shows that the most efficient simulation model for wheat GEP in 2011 was MD.2, which was without SWC but had the largest R^2 and lowest RMSE (Table 1). There were also models having the same R^2 and RMSE values, e.g., MD1 and MD4, and MD.5 and MD.7. Both pairs of models did not incorporate SWC, further indicating that SWC did not affect wheat GEP in 2011, so the main affecting factors were PAR, T_a, VPD, PAR_{dif} and u* in 2011. Similar to wheat GEP in 2011, SWC also did not affect wheat GEP in 2012 because of the highest R^2 and lowest RMSE occurred in MD.2 and the same magnitudes of assessing parameters between models that differed in their incorporation of SWC (i.e., MD.3 and MD.6, for wheat GEP in 2012).

The interference analysis indicated that the change magnitudes in GEP when interfering independence variables compared with those when no interference occurred among variables are different among different variables (Fig. 4). The simulated GEP having interfering u* deviated the least from the initial values in the absence of interference. Further computations (Eq. 12–13) on the basis of the changes magnitude caused by the interference indicated that PAR_{dif} was the most important factor affecting wheat GEP during the study periods, making a contribution of 41.3% in 2011 and 35.7% in 2012 to GEP variations (Fig. 5). PAR was the second important factor for wheat GEP, making contributions of 28.2% and 26.9% in 2011 and 2012, respectively. The effects of T_a and VPD were nearly equal and played medium level roles in affecting GEP. u* affected GEP the least, contributing less than 10% to GEP variation.

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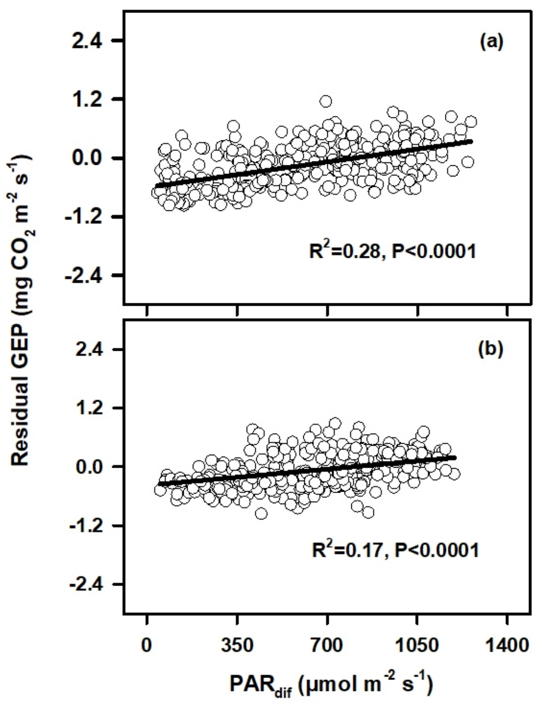

Figure 3. The relationships between residual GEP (mg CO_2 m^{-1} s^{-1}) (the difference between observed GEP and fitted GEP by PAR using Eq. (1)) and diffuse PAR (PAR_{dif}, μmol m^{-2} s^{-1}) for wheat in (a) 2011 and (b) 2012. R^2 represents the determination coefficient of the relationships.

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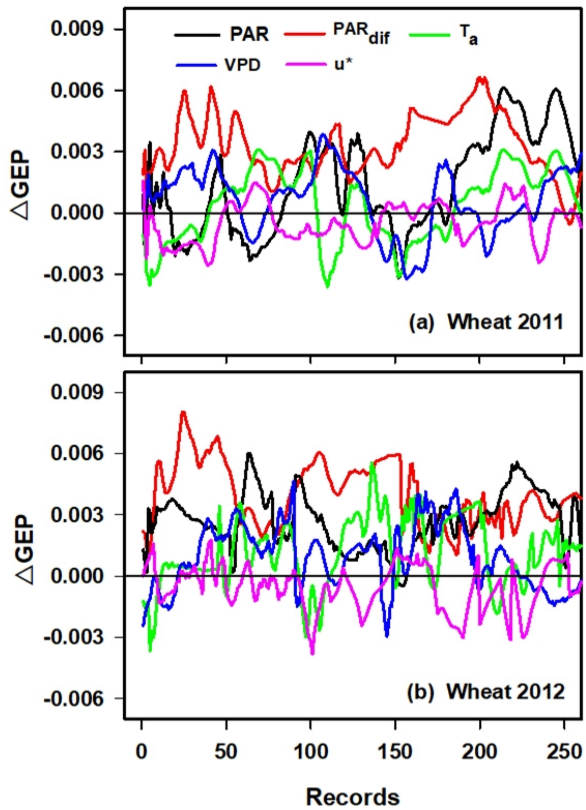

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318 Figure 4. Comparisons of changes in output GEP values with and without artificial

319 interference within recorded regime.

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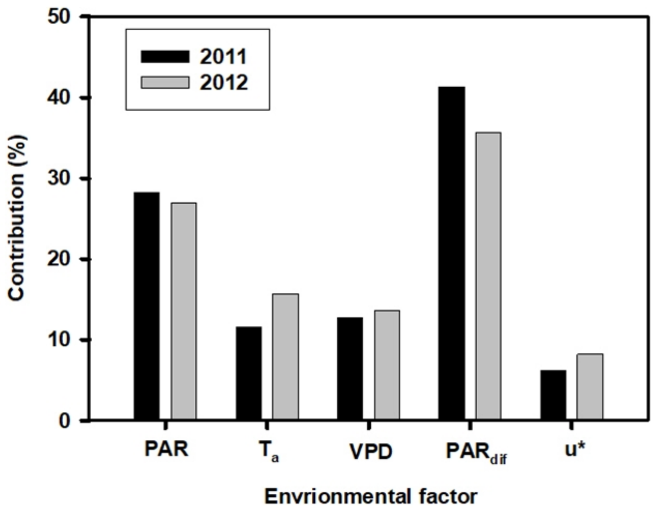

Figure. 5 Relative contributions of environmental factors to wheat GEP during study periods in 2011 and 2012.

Table 1 Comparison of ANN in predicting GEP using different input variable combinations

Crop	Model number	Optional Input variable			Evaluation Indicators			
					2011		2012	
		PAR_{dif}	SWC	u*	R^2	RMSE	R^2	RMSE
Wheat	MD.1	N	Y	Y	0.754	0.1267	0.787	0.1265
	MD.2	Y	N	Y	0.875	0.1032	0.876	0.1020
	MD.3	Y	Y	N	0.824	0.1167	0.841	0.1108
	MD.4	N	N	Y	0.754	0.1267	0.835	0.1248
	MD.5	N	Y	N	0.817	0.1293	0.827	0.1237
	MD.6	Y	N	N	0.848	0.1143	0.841	0.1108
	MD.7	N	N	N	0.817	0.1293	0.806	0.1285
	MD.8	Y	Y	Y	0.826	0.1105	0.842	0.1266

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Notes: Y or N indicates that the ANN model includes or excludes the variable, respectively. Because all the models included PAR, T_a and VPD, these variables are not shown in the table. R^2 represents the Nash-Sutcliffe efficiency index. RMSE represents root-mean-square error.

3.3 Mechanism of diffuse light effect

To illustrate the reason for the GEP enhancement with diffuse light increase, the incident light and photosynthetic rate within the canopy were simulated by the canopy model at varied diffuse light levels. Results shows that the simulated incident PAR into upper canopy was almost constant when diffuse light increasing, while the simulated incident PAR into middle and lower canopy increased significantly along with diffuse light (Fig. 6). This reflects that the incident light within canopy distributed more deeply and that the within canopy intercept more light when PAR_{dif} increasing. The light distribution caused vertical variations in photosynthetic rate within the canopy. Fig.7 shows that the simulated photosynthetic rate of upper canopy did not differ significantly under different PAR_{dif} levels, while the photosynthesis of middle and lower canopy was enhanced significantly with increase in PAR_{dif}, with the determination coefficient of 0.80 and 0.87 for middle and lower canopy, respectively. When PAR_{dif} increase from its minimal level to maximal level, the entire canopy photosynthesis (represented as the sum of photosynthetic rate for three parts of canopy) increased by ~53%, middle and lower canopy contributed ~60% and ~40% for this increase, indicating that as PAR_{dif} increasing, the within canopy, especially the middle and lower canopy, intercepted

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more light, leading to photosynthetic increase in middle and lower canopy, consequently, the photosynthesis of entire canopy enhanced.

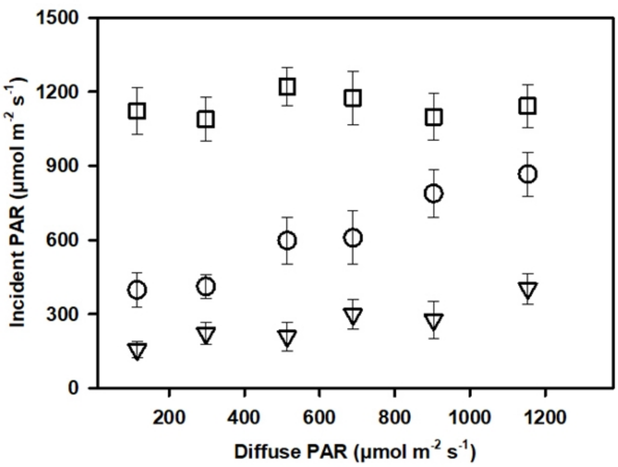

Figure. 6 Response of simulated incident PAR into upper canopy (square), middle canopy (circle) and lower canopy (inverted triangle) to PAR_{dif} over PAR_{dif} bins of 200 μmol m^{-2} s^{-1}. The error bars indicate the standard deviations of incident PAR of each PAR_{dif} bin. The incident PAR into middle and lower canopy increased with diffuse PAR in linearly pattern, with determination coefficient of 0.96 ($P<0.01$) and 0.86 ($P<0.05$), respectively.

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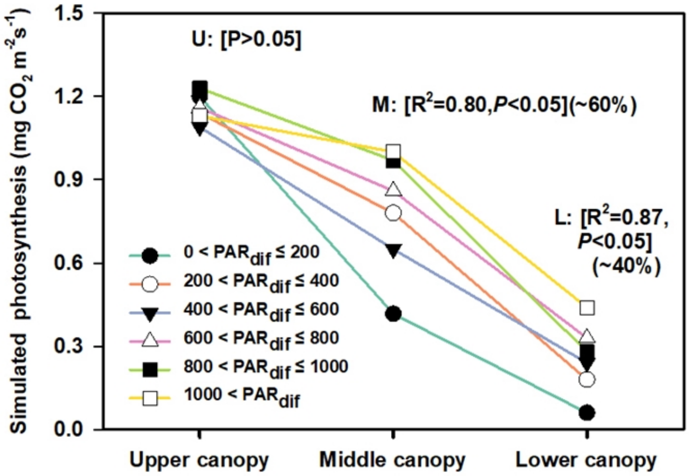

Figure 7. Gross photosynthetic rate for upper (U), middle (M) and lower wheat canopy layer (L) simulated by multiple canopy model. The averaged values over PAR_{dif} bins of 200 μmol m^{-2} s^{-1} were presented. R^2 represents the determine coefficient of the linear regression equation between the simulated photosynthetic rate and PAR_{dif} for different canopy part, P represents the significance of the correlations. The percentage in the parentheses is the ratio of changes in photosynthesis of the corresponding canopy part to the total change in photosynthesis of entire canopy when PAR_{dif} increased from minima to maxima.

4. Discussion

4.1 Diffuse light and other factors

This study found that the increase in PAR_{dif} enhanced wheat GEP significantly without the confounding effect of total light, and thus confirming our first initial hypothesis. This result was consistent with previous studies. Cheng et al., (2015) indicated that the

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GEP of forest ecosystems and a rainfed soybean cropland increased along with PAR_{dif} by removing the effect of direct PAR. By integrating flux data at >200 sites, Zhou et al. (2021) reported that ecosystems gross primary productivity responded positively to increase PAR_{dif} under heavy sky cloud condition, i.e., when radiation condition was dominated by diffuse light (diffuse light fraction was larger than 0.8). We did not use the method that Zhou et al. (2021) applied to ignore the effect of direct or total radiation, because the data pairs under the condition of diffuse light fraction > 0.8 was far less than that during the study period in the current study. The limited data may bring uncertainties and the analysis results may not be convincing. It is worth noting that T_a and VPD also change together with diffuse light, so the effect of T_a and VPD on GEP should be removed when exploring effect of diffuse light on GEP. In this study, T_a and VPD were estimated to contribute much less (10–15%) than total light to GEP changes, so we believed that the confounding effect of the two factors for dependence of GEP to PAR_{dif} can be ignored.

There were also studies drew inconsistent conclusion with the current study. Using a normalized method, Knohl and Baldocchi (2008) minimized the confounding effect of PAR, T_a and VPD and found a significant relationship between above-canopy carbon exchange rate and diffuse light fraction (fDIF). In reality, fDIF differs from PAR_{dif}, i.e., a higher fDIF is not meaning a stronger PAR_{dif}. When the relationship between diffuse fraction of PAR and PAR_{dif} was analyzed, we found that PAR_{dif} initially increased and then decreased with increasing diffuse fraction of PAR (Fig. 8). High level of diffuse light fraction are commonly caused by heavy atmospheric aerosols and clouds, in which

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case total radiation is much weak and its diffuse component is also weaker. Thus, the increase in net ecosystem carbon uptake along with diffuse light fraction in study of Knohl and Baldocchi (2008) indicated that the ecosystem carbon uptake was strongest when diffuse and total radiation was weakest (highest diffuse fraction), which contradicted our initial assumption.

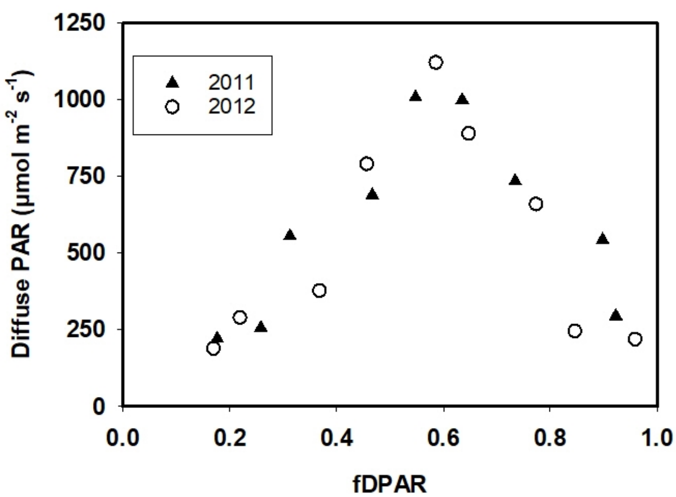

Figure. 8 Relationship between diffuse PAR and diffuse PAR fraction (fDPAR) in 2011 and 2012.

By estimating the contributions of the considered factors to GEP variations, PAR_{dif} was found to be the predominant driver among the factors this study considered. To date, studies on determining the extent of importance of diffuse light for ecosystem carbon exchange are scarce. By combining eddy covariance measurement and modelling, Park et al. (2018) explored the drivers for net ecosystem carbon uptake in a forest and

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concluded that diffuse light fraction explained less than total light and VPD. Cheng et al. (2015) also used above–canopy measurements and reported that diffuse light explained approximately 41% of GEP variance in croplands and 17% in forests they studied. These studies indicated that the importance of diffuse light to ecosystem productivity is not constant and may depend on plant species and different analysis methods.

T_a and VPD typically impact photosynthesis by influencing photosynthetic enzyme activity levels (Li et al., 2014; Wohlfahrt et al., 2008) and leaf stomatal behavior (Farquhar and Sharkey, 1982; Souza et al., 2004). Increase in T_a may promote photosynthesis, but sometimes inhibit photosynthesis because of the stomatal closure caused by high level of VPD that typically co-vary with temperature. The simple correlation analysis in our study indicated that GEP increased along with T_a and VPD, indicating that the weather conditions favored crop growth, with little water stress occurring. The role of the two factors were not as important as light for GEP variations (Fig. 5), which is consistent with previous studies indicating that temperature and VPD played unimportant roles in affecting plant productivity (Alton, 2008; Alton et al., 2007; Oliphant et al., 2011; Urban et al., 2007; Park et al. 2018). u*, which is mainly related to transporting carbon dioxide into the internal canopy, was the least important driver of GEP. This is probably because an increase in u* may reach a threshold at which the carbon dioxide concentration was saturated, leading to canopy productivity not being further impacted by wind speed. Although soil moisture was reported to impact ecosystem photosynthesis in past studies (e.g., Zhang et al., 2007), we did not find that

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SWC affect wheat GEP variations in either year as assessed by ANN model comparisons. Tong et al. (2014) indicated that ecosystem photosynthetic parameters hardly varied at different soil moisture conditions and was related to sufficient irrigation and abundant rainfall. In this study, wheat was irrigated twice per season, and the precipitation amount was moderate during the main growing season, and thus guaranteeing adequate water for crop growth and development during the study period and leading to GEP being insensitive to SWC variations.

4.2 About the mechanism

With the combination of over-canopy flux measurements and modeling method, our study indicated that as PAR_{dif} increasing, the middle and lower canopy intercepted more incident light, leading to their photosynthetic increase, consequently, the photosynthesis of entire canopy was enhanced, thus confirming our second hypothesis regarding the underlying mechanism of the effect. To our knowledge, studies illustrating the reasons for the enhancement due to diffuse light increase are scarce. Urban et al., (2012) indicated that the leaves in middle and lower spruce canopy assimilate more carbon in cloudy days compared with in sunny days because of more even vertical distribution of light among leaves across the canopy. Williams et al., (2014) investigated the linkage between light conditions and canopy photosynthesis within a tundra canopy and found that the proportion of deep shade within canopy is significantly much greater under direct conditions than that under diffuse conditions, resulting greater photosynthesis under diffuse conditions. However, these studies explored the mechanism by measuring leaves at different canopy layers to represent canopy part, i.e., upper, middle or lower canopy. Because one canopy part commonly includes several leaf layers, using photosynthesis of only one leaf layer to represent that of a certain canopy part may bring some uncertainties.

Our study found that the incident light into upper canopy was almost constant when diffuse light changing (Fig. 6). Because both clear sky condition and heavy cloud condition can lead to low PAR_{dif}, the values of incident PAR under low PAR_{dif} conditions (~ < 600 μmol m^{-2} s^{-1}) was the balance (or the average) of strong incident PAR under clear sky conditions and weak incident PAR under heavy sky conditions. Thus, the nearly stable change trend in incident light along with diffuse light in upper wheat canopy was occurred. For the middle canopy, under low PAR_{dif} conditions, the leaves could not receive or receive less direct light when the sky was clear because they were shaded by upper leaves. This caused that the incident light into middle canopy was dominated by weak diffuse light produced by heavy cloud. The PAR_{dif} into lower canopy declined compared with middle canopy, possibly because that the diffuse light that previously illuminated lower canopy was intercepted by middle canopy. Because it is widely accepted that light availability is a major affecting factor of photosynthesis (Glenn et al., 2010; Suyker et al., 2005), we believed that the enhanced primary productivity with diffuse light increasing was mainly attributed to the increased incident light into middle and lower canopy.

Although this study has revealed that the enhancement of canopy photosynthesis with diffuse light increase is related to more light intercepted by canopy, there exists other hypothesis for the possible reasons. One is that diffuse light has a greater ratio of blue to red light, which may stimulate photochemical reactions and stomatal opening; thereby, promoting canopy carbon exchange (Dengel and Grance, 2010; Urban et al., 2012). The other is that diffuse light tends to eliminate photoinhibition in sunlit leaves at the top of the canopy (Gu et al., 2002) and thus increases entire-plant photosynthesis. The latter hypothesis indicates that canopy photosynthesis is inhibited under strong incident light condition and promoted under diffuse light condition. It was unclear whether strong light (under weak diffuse light condition) depress GEP in upper canopy in the current study, because the GEP values corresponding to low PAR_{dif} caused by strong light and that caused by heavy clouds were averaged. Even if photosynthetic depression under strong light was found, the chemical reactions and enzymatic activity related to photosynthesis at leaf scale should be analyzed without destroying the natural state of the vegetation to test whether the photosynthetic decline is related to photoinbitition. Overall, the increase in light absorption of canopy with diffuse light increase may not be the only one mechanism for the enhancement of canopy photosynthesis under diffuse light condition. In order to fully understand the affecting mechanism, research on relationships between photosynthetic physiological and ecological processes and light climate changes at cell, leaf and canopy scales are needed in future.

4.3 Implications

This study showed that diffuse light enhances canopy photosynthesis in a wheat ecosystem and played a predominant role compared with other affecting factors, thus, our study provided new supporting data for the importance of diffuse light for

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ecosystem productivity and for the necessity to consider diffuse light into carbon models to predict the ecosystem carbon uptake dynamics accurately. Moreover, the ecosystem photosynthetic enhancement could be interpreted by the increased light interception by the canopy, and thus giving a first report to reveal the mechanism of diffuse light–related enhancement in agroecosystem productivity.

In order to investigate the response of photosynthesis to diffuse light, the confounding effect of total light was removed in this study. However, the real ecosystem carbon uptake is the result of the combined effect of total and diffuse light. This means that the response pattern of ecosystem photosynthesis to sky cloud cover or aerosols concentration depends on which light element the ecosystem is sensitive to. Studies have shown that canopy structure characteristics, such as canopy height, leaf inclination angle and green leaf area index, can influence the sensitivity of canopy photosynthesis to diffuse light (Cheng et al., 2015; Emmel et al., 2020; Kanniah et al., 2012). Thus, different crop species response to change in sky cloud cover or aerosols concentration differently. Future studies should be conducted in a wide range of cropland types at site scale to summarize which croplands are sensitive to diffuse light and which are sensitive to total light. Based on these information, it is valuable to analyze what canopy structure features do they have in common, and whether there are spatial distribution patterns in the sensitivity across continents or even globe. The answer to these questions are of great significance for accurately predicting the carbon budget dynamics in farmland ecosystems under the background of light climate changes.

5. Conclusions

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In this study, we explored the effect of PAR_{dif} on GEP and the affecting mechanism in a wheat cropland based on the eddy covariance measured over canopy carbon flux data. Wheat GEP increased significantly with PAR_{dif} increase in the case of absence of total light effect. In addition to its positive effect, diffuse light was also found to be the most important affecting factors for GEP among the considered factors, according to the quantified contribution of different factors to GEP variations. As PAR_{dif} increasing, the middle and lower canopy intercepted more incident light, making the photosynthesis in these canopy parts become greater, and thus the entire canopy photosynthesis enhanced. This indicated that the impact of diffuse light on canopy photosynthesis was related to the light interception of the canopy at least.

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Author contribution: Conceived and designed by Xueyan Bao and Xiaomin Sun, Performed by Xueyan Bao and Xiaomin Sun, Aanlyzed data by Xueyan Bao, Worte paper by Xueyan Bao.

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