Effect of diffuse fraction on gross primary productivity and light use efficiency in a warm-temperate mixed plantation

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Diffuse radiation (I_d) is one of important variables determining photosynthetic rate and carbon uptake of forest ecosystems. However, the responses of gross primary productivity (GPP) and light use efficiency (LUE) to diffuse fraction (DF) are still poorly understood. We used a 6-year dataset of carbon flux at a warm-temperate mixed plantation site in North China to explore the impacts of DF on GPP and LUE. During 2011–2017, ecosystem apparent quantum yield (α) and photosynthesis at photosynthetically active radiation (PAR) of 1800 µmol m⁻² s⁻¹ (P₁₈₀₀) on cloudy days were 63% and 17% higher than on clear days, respectively. Under lower vapor pressure deficit (VPD) and air temperature (T_a) conditions, canopy photosynthesis was significantly higher on cloudy skies than on clear skies. On half-hourly scale, increased DF enhanced α and P₁₈₀₀. Daily GPP peaked at a median DF (=0.5), while daily LUE significantly increased with DF (p<0.01). Both GPP and LUE were mainly controlled directly by DF and PAR. DF had an indirect effect on LUE and GPP mainly through PAR. At high DF levels (>0.5), the increase in LUE did not make GPP enhancement. The direct effect of DF on GPP and LUE under lower T_a and VPD was more sensitive than under higher T_a and VPD. When DF was incorporated into the Michaelis-Menten model, it performed well in the GPP estimation, and the determination coefficient increased by 32.61% and the root mean square error decreased by 25.74%. These findings highlight the importance of incorporating DF into carbon sequestration estimation in North China.

KEYWORDS
gross primary productivity, light use efficiency, diffuse fraction, environmental factors, mixed plantation
**Introduction**

GPP is an important indicator to characterize CO$_2$ uptake by ecosystems photosynthesis (Chapin et al., 2011) and accounts for the largest CO$_2$ flux in the carbon cycle of terrestrial ecosystems (Beer et al., 2010). Forest ecosystems contribute around 40–50% of terrestrial GPP flux, which is one of the important components of terrestrial carbon cycle (Cai et al., 2014). Solar radiation affects plant growth and terrestrial ecosystem productivity directly (Knöhl and Baldocchi, 2008; Mercado et al., 2009). It is reported that solar radiation has decreased by 15–30% in certain areas of the Northern Hemisphere since 1970 (Stanhill and Cohen, 2001; Zhang et al., 2011). Ecophysiological processes, especially carbon cycle, will be affected by the change of solar radiation in the future (Wang et al., 2008). Cloudiness and aerosols in the atmosphere reduce solar radiation but increase the diffuse fraction (DF) (Roderick et al., 2001; Oliphant et al., 2011; Yang et al., 2013).

Previous observational experiments have widely concluded that DF has an important influence on GPP and light use efficiency (LUE) in terrestrial ecosystems (Alton et al., 2007; Kanniah et al., 2013; Durand et al., 2021). The difference between direct and diffuse radiation impacts leaf photosynthesis generally depends on specific species and environmental conditions (Berry and Goldsmith, 2020), but direct radiation usually promotes more leaf photosynthesis under high radiation (Durand et al., 2021). Increased DF can enhance canopy photosynthesis, increasing LUE at ecosystem scales (Zhang et al., 2011; Wang et al., 2015; Wang et al., 2018). The mechanism of DF photosynthesis enhancement is mainly that, on one hand, the cloudiness leads to a more uniform distribution of light in the canopy, enhancing the photosynthesis of sunlit and shaded leaves (Steiner and Chameides, 2005; Park et al., 2018). On the other hand, $I_f$ from all directions can easily reach the bottom of the canopy, thereby improving canopy photosynthesis considerably (Urban et al., 2012; Kanniah et al., 2013). The increase in DF was accompanied by changes to light quality and quantity, which resulted in higher DF suppressing GPP in three forest ecosystems (Zhang et al., 2011), a temperate poplar plantation (Xu et al., 2017) and boreal coniferous and mixed forests (Ezhova et al., 2018). Moreover, the influence of DF on GPP and LUE in terrestrial ecosystems is related to vegetation type, canopy structure and leaf area index (LAI) (Alton et al., 2007; Knöhl and Baldocchi, 2008; Kanniah et al., 2012; Park et al., 2018). The increasing $I_f$ substantially improves CO$_2$ uptake of the forests with large LAI (Roderick et al., 2001; Zhang et al., 2011), whereas the effect of $I_f$ on carbon uptake in short or sparse vegetation is not significant (Niyogi et al., 2004; Lets et al., 2005; Park et al., 2018). Mean leaf tilt angle, canopy height and LAI dominated canopy structure and enhanced canopy heterogeneity, which improved canopy photosynthesis (Emmel et al., 2020). Therefore, it is necessary to clarify how the two opposing effects of GPP respond to DF in different ecosystems.

Both GPP and LUE were correlated with environmental factors at the ecosystem scale, such as air temperature ($T_a$) (Yamori et al., 2014), vapor pressure deficit (VPD) (Yuan et al., 2019) and soil water content (SWC) (Liu et al., 2020a), DF indirectly influences environmental factors to affect canopy photosynthesis (Kanniah et al., 2012; Han et al., 2019). By increasing DF, solar radiation is distributed evenly throughout the canopy, reducing $T_a$ and VPD, and thus improving canopy photosynthesis (Zhang et al., 2011; Xu et al., 2017). Other studies, however, indicated that $T_a$ and VPD had little effect on regulating the ecosystem photosynthesis response to $I_f$ (Jing et al., 2010; Kanniah et al., 2011; Oliphant et al., 2011). Changes in environmental conditions may affect GPP response to $I_f$ of forest and grassland ecosystems (Xu et al., 2017; Li et al., 2020). The coupling between DF and environmental factors will have complex effect on ecosystem photosynthesis (Kanniah et al., 2013; Gui et al., 2021). To date, our knowledge on the direct and indirect effect of DF on LUE and GPP is still limited, especially considering the constraints of environmental conditions.

LUE models have been developed to estimate photosynthetic production and investigate the impacts of environmental stresses on photosynthetic production (Nichol et al., 2010; Wang et al., 2017). Most LUE models treat vegetation canopy as a big single-leaf, and productivity linearly increases with the amount of incoming photosynthetically active radiation (PAR) (Pei et al., 2022). To estimate the effect of solar radiation on GPP accurately, considering the division of solar radiation into direct and diffuse parts in GPP simulations, such as MM$_{dif}$ Model (Cai et al., 2009), DIFFUSE Model (Donohue et al., 2014) and DTEC GPP Model (Yan et al., 2017). A top-down model of canopy photosynthesis (MM$_{dif}$ model) was developed by Cai et al. (2009) after the effect of DF on GPP was added into the Michaelis-Menten (MM) model, and there were lower systematic errors in GPP estimation on clear and cloudy days using the MM$_{dif}$ model. The effect of DF on GPP varies greatly in different ecosystems, influencing the accuracy of LUE models (Yuan et al., 2014; Wang et al., 2015; Yang et al., 2019). By effectively assessing the effect of DF on the accuracy of simulated GPP, and provides a scientific basis for subsequent improvement of LUE models. Here, we employed a big single-leaf model apprehending total and diffuse radiation control GPP physical mechanism under different environmental conditions.

Plants cover about 80 million ha, which is 36% of the total forests in China (China’s Forestry Administration, 2018). The magnitude of carbon sequestration by planted forests was 47.8% of carbon sink of total forests in China during 1977–2008 (Guo et al., 2013). In north China, planted forests of the hilly region play a vital ecological barrier and carbon sink (Fang et al., 2007; Tong et al., 2012). Up to date, carbon sequestration and water use efficiency of plantations have been explored in this region (Tong et al., 2012; Guo et al., 2013; Tong et al., 2014; Xue et al., 2012).
et al., 2016; Xu et al., 2018). However, the impact of DF on LUE and GPP is not well understood. We hypothesize that the indirect effects of DF on temperate forest ecosystem LUE and GPP under different environmental conditions are mainly caused by PAR. Based on a 6-year carbon flux dataset of a mixed plantation, we used the path analysis method and a big single-leaf model to reveal the potential mechanisms of DF on LUE and GPP. To evaluate the performance of the MMdiff model combining DF into the GPP estimation.

Materials and methods

Site description

CO₂ flux and micrometeorological variables were measured at Xiaolangdi Forest Ecosystem Research Station of Jiyuan, Henan Province, China (36°01′N, 112°28′E, 410 m a.s.l.). The site is located at the south of the Taihang Mountain and the north of the Yellow River, with a warm-temperate continental monsoon climate. Annual average temperature is 13.4°C and the annual precipitation is 642 mm in recent three decades. During the growing season (April-September), the prevailing wind direction is the northeast. The dominant tree species is cork oak (Quercus variabilis), with an age of 47, average canopy height of 11.6 ± 1.2 m and average diameter at breast height of 16.8 ± 3.3 cm. Other two species are black locust (Robinia pseudoacacia L.) and arborvitae (Platycladus orientalis), with 43 and 45 years old, and average canopy heights of 10.5 ± 2.1 and 9.2 ± 1.6 m, respectively. The soil is classified as brown loam with high gravel content. Much detailed information of this site is reported by Tong et al. (2012).

Measurements of carbon flux and meteorological variables

Carbon flux was measured by the eddy covariance system with a 3-D sonic anemometer (Model CSAT3, Campbell Scientific Inc., USA) and an open-path and fast response infrared CO₂/H₂O analyzer (Model LI7500, Li-COR Inc., USA) at the height of 30 m above the surface. Raw data were collected at a frequency of 10 Hz, and the flux data were recorded by a data logger (Model CR5000, Campbell Scientific Inc., USA). Air temperature and humidity were monitored by psychrometers (Model HMP45C, Campbell Scientific Inc., USA). A Global solar radiometer (Model CM11, Kipp and Zonen Inc., NL) was installed at the 27 m height. PAR was measured by a quantum sensor (Model LI190SB, Li-COR Inc., USA). Direct solar radiation has been monitored by a radiometer (Model CSD3, Kipp and Zonen Inc., NL) since 2016. Soil moisture at the depths of 0, 5, 10 and 20 cm was monitored by time domain reflectometry (TDR) probes (Model CS615-L, Campbell Scientific Inc., USA). Soil temperature sensors were placed at the depths of 5, 10 and 20 cm. Additionally, precipitation was measured. All above data were sampled by the data loggers (Model CR10XT and CR23XTD, Campbell Scientific Inc., USA) at 5-min intervals. Observed data from the 2011 to 2017 growing seasons has been used, except for 2015.

Flux data proceeding

Half hourly CO₂ flux data was corrected by WPL algorithm (Webb et al., 1980) and 2-D coordination rotation (McMillen, 1988). CO₂ flux would be underestimated at night due to weak turbulence, and it should be deleted when u_∗ was lower than the threshold (0.35 m s⁻¹) (Tong et al., 2012). The data exceeded three times of the average variance value were removed. Due to instrument malfunction and unfavorable meteorological conditions, flux data should be deleted. During 2011-2017, the mean availability of valid CO₂ flux data was 66.7%, 34.3%, and 50.7% for daytime, nighttime and total, respectively. The small data gap (<2 h) was filled with the linear interpolation method (Falge et al., 2001). For the large gaps (>2 h), missing daytime fluxes were interpolated by using mean diurnal variation (MDV) with a 14-day moving window, and nighttime data gaps were filled by an exponential equation (Falge et al., 2001).

Calculation of LUE

GPP was calculated as:

$$GPP = NEP + R_{ec}$$

where NEP is net ecosystem productivity and it is measured by the eddy covariance system. $R_{ec}$ is ecosystem respiration, and it was estimated as:

$$R_{ec} = R_{o} \times Q_{10}^{(T_s/T_r)}$$

where $R_{o}$ is the base ecosystem respiration rate when soil temperature is at 0°C, $T_{s}$ is soil temperature at the depth of 10 cm, $Q_{10}$ is temperature sensitivity coefficient for $R_{o}$, and it represents respiration rate rising with every 10°C increment of temperature. The nighttime $R_{ec}$ (i.e. the nighttime net ecosystem carbon exchange) values were used to estimate $R_{o}$ and $Q_{10}$.

At the ecosystem level, LUE is the ratio of GPP to PAR reaching above the canopy:

$$LUE = \frac{GPP}{PAR}$$

Definition of clear skies

Clearness index (CI) can be used to represent the effect of the atmosphere on extraterrestrial radiation ($I_0$), and it is defined as:
where $I_g$ is global radiation (W m$^{-2}$), $I_0$ is the extraterrestrial radiation at a plane parallel to the earth surface (W m$^{-2}$) (Gu et al., 1999):

$$I_0 = I_{sc} + 0.33 \cos \beta$$

where $I_{sc}$ is solar constant (1370 W m$^{-2}$), $t_d$ is the day of the year, $b$ is solar elevation angle:

$$\sin b = \sin \phi \sin \delta + \cos \phi \cos \delta \cos \omega$$

where $\phi$ is local latitude, $\delta$ is solar declination and $\omega$ is hour angle.

DF was estimated using the BRL-1 model (Liu et al., 2020b):

$$DF = \frac{1}{1 + \exp(a_0 + a_1 CI + a_2 AST + a_3 \sin b + a_4 \psi + a_5 RH)}$$

where $a_0$, $a_1$, $a_2$, $a_3$, $a_4$ and $a_5$ are fitted parameters, AST is apparent solar time, RH is relative humidity, $CI_d$ is daily CI and $\psi$ is a persistence of global radiation:

$$CI_d = \sum_{i=1}^{n} I_{g_i}$$

$$\psi = \begin{cases} CI_{t+1}, & \text{sunrise} < t < \text{sunset} \cr CI_{t+1}, & t = \text{sunrise} \cr CI_{t-1}, & t = \text{sunset} \end{cases}$$

where $t$ is time, $n$ is daylight hours.

The scatter plots of both measured and simulated DF with CI in 2017 are shown in Figure 1. The BRL-1 model performed well at 95% confidence level. During the period from 2011 to 2014, DF was estimated using the BRL-1 model. Diffuse radiation ($I_d$) and direct radiation ($I_t$) were calculated:

$$I_d = I_g \times DF$$

$$I_t = I_g - I_d$$

$TD_f$ is the ratio of diffuse PAR to PAR (Spitters, 1986; Gu et al., 1999):

$$TD_f = \frac{1 + 0.3(1 - q^2)}{1 + (1 - q^2) \cos^2(90^\circ - \beta) \cos^3 \beta}$$

where $q = I_f / I_g / CI$

We calculated diffuse PAR ($PAR_d$) and direct PAR ($PAR_t$) as:

$$PAR_d = PAR \times TD_f$$

$$PAR_t = PAR - PAR_d$$

Average CI ($CI_d$) was estimated at the half-day time scale, and the 2-month running mean $CI_{2m}$ was calculated. Clear skies were defined: $CI_d \geq 1.2CI_{2m}$; CI increased with $\sin b$ smoothly. We used the coefficient of 1.2 to make the proportion of clear skies to cloudy skies close to the long-term results of meteorological observations.

### Ecosystem photosynthesis-light response models

The response of ecosystem photosynthesis to PAR was fitted by the rectangle hyperbola equation (Michaelis and Menten, 1913):

$$GPP = \frac{\alpha P_{max}}{P_{max} + PAR}$$

where $\alpha$ is the ecosystem apparent quantum yield, $P_{max}$ is the maximum ecosystem photosynthetic capacity (mg CO$_2$ m$^{-2}$ s$^{-1}$). GPP under low light intensity ($P_{500}$ at PAR=600 μmol m$^{-2}$ s$^{-1}$) was compared with that under strong light intensity ($P_{1800}$ at PAR=1800 μmol m$^{-2}$ s$^{-1}$). DF was incorporated into the MM model (Cai et al., 2009):

$$GPP = \frac{\alpha P_{max} \left( PAR + kPAR_t \right)}{\left( PAR + kPAR_t \right) + P_{max}}$$

where ($PAR_t + kPAR_t$) is the effective incident PAR, $k$ is a measure of the contribution of PAR$_t$ to effective incident PAR, and it ranges from 0 to 1. The MM$_{dif}$ model can be expressed as the MM model when $k$ equals to 1. The $\alpha$, $P_{max}$ and $k$ values were fitted by the nonlinear Gauss-Newton algorithm. The differential responses of canopy photosynthesis to PAR$_t$ and PAR$_d$ were included in the MM$_{dif}$ model.
GPP had quadratic functions with $T_a$ and VPD, and it peaked at the optimum of $T_a=30\, ^\circ\text{C}$ and VPD=1.5 kPa (data not shown). Therefore, we analyzed the relationship between GPP and PAR under different sky conditions according to the classes VPD $\leq$ 1.5 kPa and VPD $>$ 1.5 kPa, and $T_a \leq 30\, ^\circ\text{C}$ and $T_a$ $>$ 30$^\circ$C classes. SWC was divided into water-stressed conditions (SWC $\leq$ 15%) and non-water-stressed conditions (SWC $>$ 15%).

Root mean squared error (RMSE), the relative error (RE) and the determination coefficient ($R^2$) were used to compare model performances:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(E_i - M_i)^2}{n}}$$

$$RE = \frac{M_i - E_i}{M_i} \times 100\%$$

$$R^2 = \frac{\left(\sum_{i=1}^{n}(E_i - \bar{E})(M_i - \bar{M})\right)^2}{\sum_{i=1}^{n}(E_i - \bar{E})^2 \sum_{i=1}^{n}(M_i - \bar{M})^2}$$

where $n$ is the data number, $E_i$ and $M_i$ are the simulated and measured values, respectively.

**Path analysis**

Path analysis was used to investigate the direct and indirect effect of environmental variables on GPP and LUE. It is a multiple regression model, which can deal with the casual relationships among correlated variables (Shipley, 2004):

$$r_{y}=r_{1,y}P_{1,2}+r_{2,y}P_{2,3}+\cdots+r_{i,y}P_{i-1,i}+\cdots+r_{n,y}P_{n-1,n} \quad (i=1,2,3,\ldots,n)$$

where $i$ is different independent variables, $r_{i,y}$ is the correlation coefficient between the independent variable $i$ and the dependent variable $y$, $r_{i,y}$ is the correlation coefficient between different independent variables, $P_{i,y}$ is the direct effect of the independent variable $i$ on the dependent variable $y$ (standardized regression coefficient), and $r_{i,n}P_{i,n}$ ($i \neq n$) is the indirect effect of independent variable $i$ affecting another independent variable $n$ which in turn affects the dependent variable $y$.

We used DF, PAR, $T_a$, VP and SWC in path analysis. Path analysis was performed by SPSS AMOS software (version 24.0, IBM Inc., USA). All input variables initially need to be standardized. Maximum likelihood method is applied in the calculation. Output results included direct impact (SDE, [-1,1]), indirect impact (SIE, [-1,1]) and total impact (STE, [-2,2]). Positive and negative values indicated positive and negative effects, respectively, and the absolute value of coefficient represented relative effect among variables.

**Results**

**Micrometeorological variables**

$I_{x}$ peaked in May-June in most years, except that it was highest in August in 2013 (Figure 2A). Annual $I_{x}$ in the years of 2011-2014 was lower than that in 2016 and 2017. $I_{x}$ peaked in June-July, and it varied from 939 to 1606 MJ m$^{-2}$ in the growing season, between 206 and 566 MJ m$^{-2}$ in the non-growing season. Monthly mean DF ranged from 0.10 to 0.64 during the 6-year period. Annual mean DF was about 0.41, and it was the largest in 2013 (0.52) and the lowest in 2014 (0.28). The strongest $I_{x}$ in August of 2013 led to its highest mean $T_a$ in the same period. However, in the other five years, monthly mean $T_a$ peaked in June-July (Figure 2C). Annual mean $T_a$ was lowest in 2011 (14.0$^\circ$C) and highest in 2017 (15.6$^\circ$C).

Compared to the other five years, annual precipitation was highest (888 mm) in 2016 and lowest (437 mm) in 2013 (Figure 2B). During the 6-year period, annual precipitation was 654 ± 168 mm, close to the value (642 mm) in the recent 30-year. The average SWC in the growing season was largest (0.15 m$^3$ m$^{-3}$) in 2012 and lowest (0.09 m$^3$ m$^{-3}$) in 2013 owing to low precipitation. Monthly mean VPD peaked in May of 2014 and 2017, June of 2011, 2012, 2013 and 2016 due to low precipitation and high temperature in the same period (Figure 2C). Strong solar radiation and less precipitation were responsible for a higher mean VPD (1.24 kPa) in 2012.

**Seasonal patterns in GPP and LUE**

Monthly average GPP, PAR and LUE during the 6-year period are shown in Figure 3. In spring, GPP increased with the increase of PAR and $T_a$ (Figures 1, 3). With the decline of PAR and $T_a$ in autumn, GPP also dropped gradually. The maximum of monthly GPP appeared in late spring of 2014, but it occurred in summer of the other five years, ranging from 172 to 203 g C mol$^{-1}$ month$^{-1}$. The amount of GPP ranged between 925 g C m$^{-2}$ in 2016 and 1209 g C m$^{-2}$ in 2017. In 2016, low PAR and DF limited photosynthesis and therefore resulted in a reduction in GPP. Annual GPP of 2012 was higher than the other five years, which may be due to stronger PAR and larger SWC.

Monthly LUE varied from 0.01 to 0.21 g C mol$^{-1}$, and the maximum monthly average LUE occurred in July-August during the 6-year period. Annual mean LUE was highest (0.11 g C mol$^{-1}$) in 2011 and 2012 and lowest (0.09 g C mol$^{-1}$) in 2013, 2016 and 2017. During the 6-year period, the mean annual LUE was 0.10 ± 0.01 g C mol$^{-1}$.

**Diurnal patterns in GPP and LUE**

The diurnal patterns of GPP under clear and cloudy conditions are shown in Figure 4A. GPP was about 0.12 mg
CO₂ m⁻² s⁻¹ in the early morning and late afternoon, and it increased with solar radiation and peaked at noon. GPP was 13.93% higher under cloudy skies than under clear skies during the period of 10:00 am-14:00 pm. Though the overall amount of PAR reaching the canopy was normally lower under cloudy sky conditions (Figure 4C), there was an increase in GPP when the main component of the radiation moved from direct to diffuse above the canopy.

LUE was high in the early morning and late afternoon (Figure 4B). It was that PAR decreased more rapidly than GPP during the transition from light to dark (Figure 4C). During the period of 8:00 am-17:00 pm, LUE was low and maintained a value of 0.29 g CO₂ mol⁻¹ in the clear skies and 0.48 g CO₂ mol⁻¹ in the cloudy skies. LUE was 66% larger in the cloudy skies than in the clear skies.

**Light response of GPP under different sky and environment conditions**

Figure 5 illustrates the response of GPP to PAR under clear and cloudy sky conditions during the growing season.
Half-hourly GPP was averaged by PAR at a 100 μmol m⁻² s⁻¹ interval. At the same PAR level, GPP was larger in cloudy skies than in clear skies. Light response parameters (α and Pₚₚₚₚ) and Pₜₜₜₜ and P₁₈₀₀ derived from Eq.(16) are shown in Table 1. Compared with clear sky conditions, the values of α, Pₜₜₜₜ and P₁₈₀₀ under cloudy sky conditions increased by 16–132%, 18–57%, and 5–71%, with an average enhancement of 54%, 36%, and 27%, respectively. The Pₚₚₚₚ values ranged from 0.84 to 1.95 mg CO₂ m⁻² s⁻¹ under cloudy sky conditions, and from 0.82 to 1.64 mg CO₂ m⁻² s⁻¹ under clear sky conditions. During the 6-year period, Pₚₚₚₚ under cloudy skies was 21% higher than under clear skies. α, Pₜₜₜₜ, and P₁₈₀₀ values under higher DF (DF<0.4) were 198–202%, 82–115% and 19–54% higher than under lower DF (DF<0.2 and 0.2≤DF<0.4). α, Pₜₜₜₜ and P₁₈₀₀ values significantly increased with DF (p<0.05).

The responses of GPP to PAR under different Tₛ, VPD and SWC classes were calculated to consider the co-varying nature of environmental factors (Figure 6). Compared with clear sky conditions, α values under cloudy sky conditions increased by 54%, 71% and 42% at lower Tₛ, VPD and SWC, 38% and 47% at higher VPD and SWC, respectively. Under cloudy sky conditions, the P₁₈₀₀ value increased by 65%, 17% and 31% at lower Tₛ, VPD and SWC, and by 22%, 12% and 23% at higher Tₛ, VPD and SWC, respectively. At the mixed planted forest stand, the sensitivity of canopy photosynthesis to the change of SWC was low when the sky was covered by clouds. Lower Tₛ and VPD under cloudy sky conditions resulted in larger α and P₁₈₀₀ values (Figure 6 and Table 2).

### Effects of DF on GPP and LUE

The changes of LUE and GPP with DF are shown in Figures 7E, F. LUE increased significantly with increasing DF (p<0.01), and the values of LUE increased from 0.09 to 0.39 g C mol⁻¹, implying that cloud conditions were beneficial for LUE. GPP had a remarkable quadratic relationship with DF, and it peaked when DF was about 0.5 (p<0.01). It was indicated that partly cloudy sky conditions were favorable for carbon uptake. Both PAR and VPD decreased linearly with increasing DF (Figures 7A, C). At high DF (>0.5), Tₛ and SWC had significant decreasing and increasing trends, respectively (Figures 7B, D). Water conditions improved at high DF (>0.5), but the decreasing PAR and Tₛ mainly limited canopy photosynthesis, and hence the maximal GPP occurred with an optimal DF (0.5). Carbon assimilation increased when PAR was lower than 33.03 mol m⁻² d⁻¹, and any reduction in PAR may reduce GPP when light intensity is less than this value (Figures 7A, E).

### Direct and indirect influences of environmental factors on GPP and LUE

The path analysis of the total and direct effect of environmental variables on GPP and LUE is illustrated in Table 3. There were significant correlations between GPP and PAR, DF, Tₛ and VPD during the growing season. PAR and DF had significant predictive power to predict the GPP value. LUE was significantly correlated with PAR, DF and VPD (p<0.05), but it was primarily regulated by DF. The negative direct impact of VPD on GPP and LUE was evident under higher Tₛ and VPD conditions, and the small positive direct impact of Tₛ was found for lower Tₛ and VPD conditions. Compared with higher Tₛ and VPD conditions, the direct effect of PAR on GPP was more pronounced under lower Tₛ and VPD conditions. Under water or temperature-limited conditions, both GPP and LUE were mainly controlled by PAR and VPD. In addition, SWC had little effect on LUE and GPP. It is likely because the deep root system of the forest can supply sufficient water for top soil when water in the top soil is depleted (Wu et al., 2012; Wang et al., 2018), and SWC did not limit plant photosynthesis at this site. The direct effect of DF on GPP and LUE was greater in low Tₛ and VPD than in high Tₛ and VPD.

Table 4 shows the indirect effect of DF on GPP and LUE, which describes how GPP and LUE are affected by DF via other environmental factors. DF primarily interacted with PAR to affect GPP and LUE. Under high Tₛ conditions, DF positively interacted with VPD and PAR to impact GPP and LUE. The indirect effect of DF through Tₛ and SWC on GPP and LUE was not significant. Compared with higher Tₛ and VPD conditions, the indirect effect of DF through PAR on GPP and LUE was more significant under lower Tₛ and VPD conditions.

### Comparison of GPP estimated by the MM and MM₆diff models

The MM₆diff and MM ecosystem photosynthesis-light response models were used to estimate GPP during the growing season. The parameter k of the MM₆diff model ranged between 0.12 and 0.62, with an average of 0.38. The low k indicated the significant impact of Iᵣ on GPP and the fraction of light-limited sunlit leaves. The relationships between k and DF, Tₛ, VPD and SWC are shown in Figure 8. The k value significantly increased with DF and SWC. Conversely, higher Tₛ and VPD reduced the k value. Forest canopies received more PAR under cloudy sky conditions with higher SWC, lower Tₛ and VPD, which was beneficial to canopy photosynthesis.

The MM₆diff model performed better than the MM model (Figure 9). The R² value increased by 32.61% and the RMSE decreased by 25.74% after the impact of DF on GPP was included in the MM₆diff model. The RE of the MM and MM₆diff models were compared under different environmental conditions (Figure 10). In general, the estimates of GPP produced by the MM₆diff model were less biased than the MM model under different environmental conditions. Compared with the MM₆diff model, the MM model significantly
overestimated GPP value at high PAR, $T_a$, VPD and low DF levels. Under high and low DF conditions, the performance of the MM$_{dif}$ model was better than that of the MM model. This discrepancy may be because the MM model tends to represent median DF conditions. The RE of MM$_{dif}$ and MM models were $1.5–1.8\%$ and $5.6–7.0\%$ in low $T_a$ and VPD, respectively. In case for high $T_a$ and VPD, the RE of MM$_{dif}$ and MM models were respectively $-14.2–9.2\%$ and $-29.2–19.3\%$. These results employed that ecosystem photosynthesis-light response model performed better after DF was incorporated into the GPP simulation.

Discussion

Response of photosynthesis to different sky conditions

Canopy photosynthesis increased under cloudy sky conditions (Gu et al., 2002; Knohl and Baldocchi, 2008; Zhang et al., 2011; He et al., 2013; Ezhova et al., 2018; Zhou et al., 2021). Under clear sky conditions, sunlit leaves of the canopy receive more direct solar radiation, causing photosynthesis saturation. However, shaded leaves receive low solar radiation under clear sky conditions and are sensitive to radiation changes (Roderick et al., 2001; Gu et al., 2002; Alton et al., 2007). The enhancement of LUE was $36\%$ under cloudy skies (Figure 4B), close to the results reported for the tropical broadleaf (33%) (Alton et al., 2007), higher than obtained in a sparse canopy (6–18%) (Alton et al., 2007), but lower than the crops (110%) (Choudhury, 2001) and the old-growth temperate forest (50%) (Hollinger et al., 1994). The value of $\alpha$ under cloudy sky conditions was $63\%$ higher than under clear sky conditions (Table 1), close to the finding of Rocha et al. (2004) in a northern hardwood forest. Under thick cloud conditions, $\alpha$ increased by 21% in a tropical savanna forest (Kanniah et al., 2013).

In the mixed plantation, GPP significantly enlarged on cloudy days in comparison to clear days (Figures 5, 6). The values of $P_{600}$ and $P_{1800}$ were 36% and 17% larger under cloudy skies than those under clear skies, respectively (Table 1). On cloudy days, the $\alpha$ and $P_{1750}$ values of a subtropical coniferous plantation increased by 19.2% and 23.4%, respectively (Han et al., 2019). Under different environmental classes, the values of $\alpha$ and $P_{1800}$ were also higher on cloudy days than on clear days (Table 2). Under cloudy sky conditions, the vertical distribution of PAR in the whole forest canopy was more even and additional $I_r$ reaches the below canopy, and hence enlarging photosynthetic rates of shaded leaves (Kanniah et al., 2011; Urban et al., 2012; Dengel et al., 2015). Moreover, the blue/red light ratio is high under cloudy sky conditions, which is conducive to stimulating photochemistry and stomatal opening (Matsuda et al., 2004; Dengel and Grace, 2010; Urban et al., 2012). On cloudy days, the enhancement of $\alpha$ and $P_{1800}$ in low $T_a$ and VPD were higher than in high $T_a$ and VPD (Table 2). It is similar to those results that were found in a poplar plantation (Xu et al., 2017) and a desert steppe (Li et al., 2020). Under cloudy sky conditions, low $T_a$ and VPD were more conducive to enhancing canopy photosynthesis. It was because water or temperature-unlimited conditions reduce stomatal resistance and promote leaf carbon dioxide uptake (Zhang et al., 2021).

Impacts of DF on LUE and GPP

Previous studies reported that DF enhanced ecosystem photosynthesis in a broad-leaved forest (Oliphanh et al., 2011), a subtropical coniferous forest (Han et al., 2019), and three forest canopies (a sparse boreal needle-leaved, a temperate broad-leaved, and a dense tropical broad-leaved) (Alton et al., 2007). Increasing DF led to a large enhancement of photosynthesis at
FIGURE 5
Light response curves of half-hourly gross primary productivity (GPP) to photosynthetically active radiation (PAR) under different sky conditions. All data with standard error bars are averaged at a 100 µmol m\(^{-2}\) s\(^{-1}\) interval under the same sky condition.

TABLE 1 Light response parameters estimated by the MM model under different sky conditions.

| Year | Sky condition | α    | \(P_{\text{max}}\) (mg CO\(_2\) m\(^{-2}\) s\(^{-1}\)) | \(P_{600}\) (mg CO\(_2\) m\(^{-2}\) s\(^{-1}\)) | \(P_{1800}\) (mg CO\(_2\) m\(^{-2}\) s\(^{-1}\)) | \(R^2\) | n  |
|------|---------------|------|---------------------------------|-----------------|-----------------|------|----|
| 2011 | Clear         | 0.019| 0.96                            | 7.47             | 13.30            | 0.61 | 1273|
|      | Cloudy        | 0.027| 0.87                            | 8.83             | 14.00            | 0.50 | 1019|
| 2012 | Clear         | 0.015| 1.64                            | 7.07             | 15.38            | 0.72 | 824 |
|      | Cloudy        | 0.023| 1.89                            | 10.28            | 20.86            | 0.70 | 486 |
| 2013 | Clear         | 0.019| 0.89                            | 7.31             | 12.71            | 0.59 | 1093|
|      | Cloudy        | 0.024| 1.16                            | 9.27             | 16.30            | 0.57 | 728 |
| 2014 | Clear         | 0.016| 0.86                            | 6.56             | 11.77            | 0.60 | 1359|
|      | Cloudy        | 0.023| 0.84                            | 8.10             | 13.16            | 0.48 | 1020|
| 2016 | Clear         | 0.018| 0.82                            | 6.73             | 11.75            | 0.55 | 1402|
|      | Cloudy        | 0.020| 1.95                            | 9.57             | 20.05            | 0.67 | 1162|
| 2017 | Clear         | 0.015| 1.03                            | 6.47             | 12.50            | 0.56 | 1286|
|      | Cloudy        | 0.035| 0.87                            | 10.14            | 15.05            | 0.52 | 707 |
| 2011-2017 | Clear     | 0.016| 1.04                            | 6.73             | 12.84            | 0.70 | 7237|
|      | Cloudy        | 0.026| 0.97                            | 9.16             | 15.00            | 0.55 | 5122|
| DF interval  | <0.2        | 0.009| 1.48                            | 4.59             | 10.81            | 0.44 | 1020|
|      | 0.2-0.4       | 0.014| 1.26                            | 6.61             | 13.57            | 0.55 | 2611|
|      | 0.4-0.6       | 0.019| 1.10                            | 7.78             | 14.41            | 0.64 | 2117|
|      | 0.6-0.8       | 0.021| 1.23                            | 8.58             | 15.97            | 0.69 | 2258|
|      | >0.8          | 0.027| 1.12                            | 9.85             | 16.63            | 0.63 | 4353|

All regressions are significant at the level of \(p<0.05\).
DF is diffuse fraction, \(\alpha\) is ecosystem apparent quantum yield, \(P_{\text{max}}\) is the maximum ecosystem photosynthetic capacity, \(P_{600}\) is GPP at high PAR (1800 µmol m\(^{-2}\) s\(^{-1}\)) and \(P_{1800}\) is GPP at low PAR (600 µmol m\(^{-2}\) s\(^{-1}\)).
light levels (Table 2). LUE was positively correlated with DF, and DF explained 34–41% of the variation in LUE (Table 3). It was found that LUE had positive linear relations with DF in a poplar plantation (Xu et al., 2017) and a wheat cropland (Yang et al., 2019). Increased DF improved photosynthetic rate by improving photosynthesis of shade leaves but limiting light saturation of sunlit leaves (Gu et al., 2002). Higher DF corresponded to a large value of $k$ because increasing clouds reduced the limitation of strong light on ecosystem photosynthesis (Figure 8).

GPP had a significant relationship with DF, and 8–28% of the variation in GPP could be explained by DF (Table 3), consistent with the finding in a temperate deciduous beech forest (Wang et al., 2018). Similarly, DF explained 41% and 17% of seasonal GPP variation in a cropland and temperate forest, respectively (Cheng et al., 2015).

Though the interaction between DF and PAR enhanced LUE, GPP decreased due to low PAR. GPP initially increased and then decreased with increasing DF, and it peaked under moderate cloudy sky conditions (DF=0.5) in the mixed plantation (Figure 7). In forests, croplands and global FLUXNET sites, GPP peaked at a median of DF (Oliphant et al., 2011; Huang et al., 2014; Yang et al., 2019; Zhou et al., 2021). It is indicated that an increase of clouds may weaken the “diffuse fertilization effect” when light intensity is lower than a specified level. The path analysis showed that DF regulated GPP mainly by the indirect effect of radiation (Table 4). The quantity of radiation is still a critical factor for GPP despite a higher fraction of $I_f$ can enhance LUE (Alton et al., 2007; Kanniah et al., 2013). Due to the reduction in PAR (Figure 7), LUE enhancement under diffuse sunlight was insufficient to increase GPP at a high DF level (>0.5). Therefore, the net effect of DF on GPP depends on the balance between the increase in photosynthesis for shade leaves resulting from the rise of the diffuse fraction of the PAR and the weakening of the photosynthetic rates for sunlit leaves due to reducing total PAR (Mercado et al., 2009; Kanniah et al., 2013). Moreover, compared with cloud water droplets, the scattering of aerosols prefers for forward direction, and it is more conservative with

| Environmental condition | Sky condition | $\alpha$ | $P_{\text{max}}$(mg CO$_2$ m$^{-2}$ s$^{-1}$) | $P_{600}$(mg CO$_2$ m$^{-2}$ s$^{-1}$) | $P_{1800}$(mg CO$_2$ m$^{-2}$ s$^{-1}$) | $R^2$ | n |
|-------------------------|---------------|---------|-------------------------|-------------------------|-------------------------|-------|---|
| $T_a \leq 30^\circ C$   | Clear         | 0.016   | 1.10                    | 0.31                    | 0.60                    | 0.65  | 5342 |
|                         | Cloudy        | 0.025   | 1.93                    | 0.50                    | 0.99                    | 0.66  | 4329 |
| $T_a > 30^\circ C$      | Clear         | 0.036   | 0.53                    | 0.34                    | 0.45                    | 0.39  | 1895 |
|                         | Cloudy        | 0.029   | 0.72                    | 0.37                    | 0.55                    | 0.55  | 793  |
| VPD $\leq$ 1.5 kPa     | Clear         | 0.014   | 2.27                    | 0.31                    | 0.73                    | 0.71  | 2953 |
|                         | Cloudy        | 0.023   | 1.59                    | 0.44                    | 0.85                    | 0.65  | 3312 |
| VPD $>$ 1.5 kPa         | Clear         | 0.023   | 0.68                    | 0.32                    | 0.49                    | 0.51  | 4286 |
|                         | Cloudy        | 0.031   | 0.70                    | 0.38                    | 0.55                    | 0.45  | 1810 |
| SWC $\leq$ 15%          | Clear         | 0.021   | 0.75                    | 0.32                    | 0.52                    | 0.59  | 3738 |
|                         | Cloudy        | 0.029   | 0.96                    | 0.43                    | 0.68                    | 0.54  | 2426 |
| SWC $>$ 15%             | Clear         | 0.018   | 0.90                    | 0.31                    | 0.55                    | 0.59  | 3499 |
|                         | Cloudy        | 0.027   | 1.00                    | 0.41                    | 0.68                    | 0.55  | 2696 |

All regressions are significant at the level of $p<0.05$. $T_a$ is air temperature, VPD is vapor pressure deficit and SWC is soil water content. $\alpha$ is ecosystem apparent quantum yield, $P_{\text{max}}$ is the maximum ecosystem photosynthetic capacity, $P_{600}$ is GPP at low PAR (600 μmol m$^{-2}$ s$^{-1}$) and $P_{1800}$ is GPP at high PAR (1800 μmol m$^{-2}$ s$^{-1}$).
respect to \( I_g \) (Farquhar and Roderick, 2003; Alton et al., 2007). In recent years, the increasing aerosols due to human activities and climate change have enlarged the photosynthetic rate (Zhang et al., 2021). Changes of clouds and aerosols will become the source of uncertainty affecting carbon sink of forest ecosystems in the future (Boucher et al., 2013; Melnikova and Sasai, 2020). In addition, the responses of LUE and GPP to increasing DF depend on plant species, canopy structure, LAI and environmental factors (Kanniah et al., 2012; Cheng et al., 2015). The forest with stratified layers canopy was much more tightly correlated with \( I_g \) (Cheng et al., 2015) than croplands and grasslands with open canopies (Hollinger et al., 1994; Niyogi et al., 2004). Plant LAI varies seasonally, and leaf nitrogen increases with LAI, which further influences the changes in canopy photosynthesis (Reich, 2012). The effect of DF on photosynthesis increased with seasonally increasing LAI in the deciduous broadleaf forest (Knohl and Baldocchi, 2008) and the evergreen coniferous forest (Cheng et al., 2015).

Different environmental conditions may affect the response of GPP to cloudiness in forest ecosystems (Park et al., 2018; Gui et al., 2021). The direct effects of environmental factors showed that the increase of GPP and LUE responses to DF was influenced by the

**TABLE 3** Total effect (TE) and direct effect (DE) of environmental factors on gross primary productivity (GPP) and light use efficiency (LUE).

| Environmental condition | PAR | DF | VPD | \( T_a \) | SWC |
|-------------------------|-----|----|-----|---------|-----|
|                         | TE  | DE | TE  | DE      | TE  | DE |
| GPP \( T_a \leq 30^\circ C \) | 0.59 | 0.78 | -0.26 | 0.23 | 0.17 | -0.12 | 0.22 | 0.09 | 0.08 | 0.06 |
| \( T_a > 30^\circ C \) | 0.50 | 0.50 | -0.21 | - | -0.31 | -0.37 | -0.03 | 0.14 | 0.29 | 0.21 |
| VPD \( \leq 1.5 \) kPa | 0.62 | 0.78 | -0.24 | 0.27 | 0.28 | 0.01 | 0.27 | 0.07 | 0.09 | 0.05 |
| VPD > 1.5 kPa | 0.54 | 0.60 | -0.23 | 0.08 | -0.18 | -0.27 | -0.03 | 0.08 | 0.19 | 0.16 |
| SWC \( \leq 15\% \) | 0.63 | 0.80 | -0.24 | 0.26 | 0.24 | -0.04 | 0.22 | 0.04 | 0.09 | - |
| SWC > 15\% | 0.62 | 0.76 | -0.25 | 0.28 | 0.32 | 0.03 | 0.30 | 0.09 | 0.09 | 0.06 |
| LUE \( T_a \leq 30^\circ C \) | -0.30 | -0.07 | 0.39 | 0.31 | -0.25 | -0.07 | -0.08 | 0.04 | 0.09 | 0.09 |
| \( T_a > 30^\circ C \) | -0.37 | -0.32 | 0.34 | 0.08 | -0.35 | -0.33 | -0.07 | 0.12 | 0.29 | 0.25 |
| VPD \( \leq 1.5 \) kPa | -0.24 | -0.05 | 0.34 | 0.32 | -0.16 | - | -0.05 | 0.05 | 0.05 | 0.08 |
| VPD > 1.5 kPa | -0.34 | -0.24 | 0.35 | 0.17 | -0.25 | -0.23 | -0.06 | 0.08 | 0.19 | 0.20 |
| SWC \( \leq 15\% \) | -0.31 | -0.07 | 0.41 | 0.29 | -0.32 | -0.14 | -0.22 | - | - | 0.04 |
| SWC > 15\% | -0.34 | -0.15 | 0.39 | 0.25 | -0.25 | -0.15 | -0.09 | 0.13 | 0.16 | 0.13 |

PAR is photosynthetically active radiation, \( T_a \) is air temperature, VPD is vapor pressure deficit and SWC is soil water content. "-" means that it is insignificant. Others are significant at the level of \( p<0.05 \).
discrepancy in the effect of different $T_a$ and VPD on canopy photosynthesis (Table 3), and the role of cloudiness in regulating GPP and LUE needs to be taken into different environmental conditions. Under water (VPD $\leq 1.5$ kPa) or temperature ($T_a \leq 30$ °C)-unlimited conditions, the effect of cloudiness on canopy photosynthesis was more obvious in the mixed plantation (Figure 6). The average value of $k$ decreased under water or temperature-limited conditions (Figure 8), indicating that extreme environmental factors reduced the effective incident radiation demand for photosynthesis. Under high VPD conditions, stomatal closure avoids water loss but limits canopy photosynthetic rate (Körner, 1995). $T_a$ can promote ecosystem photosynthesis because increased $T_a$ enhances enzyme activity and photosynthetic electron transfer efficiency (Berry and Bjorkman, 1980), but high $T_a$ above an optimum can also limit photosynthetic rates (June et al., 2004). These results revealed that

| Environmental condition | Indirect effect from DF via | PAR | VPD | $T_a$ | SWC |
|-------------------------|-----------------------------|-----|-----|------|-----|
| $T_a \leq 30°C$         | GPP                         | -0.534 | 0.062 | -0.017 | 0.000 |
|                         | LUE                         | 0.045 | 0.034 | -0.007 | -0.002 |
| $T_a > 30°C$            | GPP                         | -0.289 | 0.122 | -0.033 | -0.002 |
|                         | LUE                         | 0.181 | 0.111 | -0.029 | -0.006 |
| VPD $\leq 1.5$ kPa     | GPP                         | -0.502 | -0.001 | -0.007 | -0.004 |
|                         | LUE                         | 0.033 | 0.003 | -0.005 | -0.007 |
| VPD $> 1.5$ kPa        | GPP                         | -0.363 | 0.062 | -0.004 | -0.009 |
|                         | LUE                         | 0.140 | 0.056 | -0.004 | -0.013 |
| SWC $\leq 15\%$        | GPP                         | -0.479 | 0.056 | -0.004 | -0.012 |
|                         | LUE                         | 0.112 | 0.007 | 0.061 | 0.007 |
| SWC $> 15\%$           | GPP                         | -0.564 | 0.093 | -0.059 | 0.005 |
|                         | LUE                         | 0.119 | 0.039 | -0.040 | 0.008 |

PAR is photosynthetically active radiation, $T_a$ is air temperature, VPD is vapor pressure deficit and SWC is soil water content. The values are significant at the level of $p<0.05$.

TABLE 4 The indirect effect from diffuse fraction (DF) through other environmental factors to gross primary productivity (GPP) and light use efficiency (LUE).
the promotion of canopy photosynthesis by DF reached its maximum when water or temperature conditions were unlimited. High temperatures and wet summers as well as heat stress may limit the response of GPP and LUE to cloudiness (Figure 2 and Table 3). Furthermore, under VPD>1.5 kPa or $T_a$>30°C conditions, high VPD was the important factor restricting GPP in the mixed plantation (Table 3). It is demonstrated that the primary environmental element limiting GPP changed with the environmental conditions.

Comparison of GPP derived from the MM and MM$_{dif}$ models

Quantitative estimation of GPP is necessary for understanding the response of terrestrial ecosystems to the change in the quality of incoming radiation (Wang et al., 2015; Yan et al., 2020). The MM$_{dif}$ model described the response of canopy photosynthesis to light as a nonlinear process. In the GPP estimation, the MM$_{dif}$ model performed better than the MM model when DF was incorporated into the MM$_{dif}$ model (Figure 9). The MM$_{dif}$ model can be regarded as a single big-leaf model, it avoids some errors of the previous single big-leaf models of canopy photosynthesis (Sellers et al., 1996). A previous study found that the performance of a joint "top-down" GPP and ET model was improved when the cloudiness index was taken into the simulation, and RMSE decreased by 11.7% in GPP for a high latitude temperate deciduous forest (Wang et al., 2018). The LUE model significantly underestimated GPP on cloudy days due to ignoring the effect of DF on canopy photosynthesis (Yuan et al., 2014). Similarly, if the impact of $I'$ is ignored, the LUE model will underestimate GPP increasing trend in China (Yan et al., 2020). Half-hourly CO$_2$ flux is measured over a large flux footprint, making the MM$_{dif}$ model effective for overcoming the spatial heterogeneity of canopy radiation regime and suitable for simulating canopy photosynthesis at the regional scale (Cai et al., 2009). Additionally, SIF (solar-induced chlorophyll fluorescence) is also usually used to estimate GPP and it is an optical signal directly emitted by plants during the light reactions of photosynthesis (Wu et al., 2022). Cloudy sky conditions affect SIF-GPP relationships by enhancing photosynthesis in light-limited leaves (Yang et al., 2018). The canopy escape fraction increases with PAR$_r$ fraction due to the variation of near-infrared reflectance and radiation (Kim et al., 2021). Therefore, the connection between different sky conditions and the SIF-GPP relationships should not be neglected in improving the estimation of terrestrial GPP.

There are differences in the simulation performance of the MM and MM$_{dif}$ models under different environmental conditions in this study. Under different DF conditions, GPP estimated by the MM$_{dif}$ model was much closer to the measured GPP in comparison with that determined by the MM model. It was attributed to the inclusion of direct and diffuse components in the MM$_{dif}$ model (Figure 10D), consistent with the results in a hemisphere bog (Goodrich et al., 2015) and a deciduous forest (Wang et al., 2018). There are lower systematic errors in GPP estimated by the MM$_{dif}$ model under clear and overcast sky conditions (Cai et al., 2009). Compared with the MOD17 model, the CI-LUE model less underestimated GPP under cloudy sky conditions after cloudiness was incorporated into the simulation (Wang et al., 2015). Since PAR$_r$ and PAR$_p$ were simulated separately, the MM$_{dif}$ model performs well under lower $T_a$ and VPD conditions (Figures 10B, C). At higher $T_a$ and VPD, the weak effect of DF and PAR on GPP may lead to limit the performance of the MM$_{dif}$ model. We found that MM$_{dif}$ model significantly overestimated GPP value in high $T_a$ and VPD, which may affect the applicability of LUE models in areas with extreme environmental conditions. LUE models should quantify environmental stresses to realistically capture environmental controls on ecosystem functions. Because the effect of environmental variables on photosynthesis varies in different ecosystems (Gui et al., 2021), more studies under various
environment conditions are needed to identify the optimal parameters of the LUE models. Moreover, water factors have complex effects on GPP simulation, so multiple indicators may be needed to capture the diverse responses of plants to water stress (Pei et al., 2022). Besides environmental factors, leaf optical parameters (reflectance and transmittance) influence the response of GPP to DF (Durand et al., 2021). Therefore, GPP will be estimated accurately if these associated variables are incorporated into the simulation in the future.

**Conclusions**

We explored the impact of DF on GPP and LUE of a temperate mixed plantation in North China during a 6-year period. Both GPP and LUE were larger under cloudy sky conditions than under clear sky conditions at the half-hourly scale. On cloudy days, the enhancement of $\alpha$ and $P_{1800}$ in low $T_a$ and VPD was higher than in high $T_a$ and VPD. DF explained 34–41% and 8–28% of the variation in LUE and GPP, respectively. GPP initially increased and then decreased with increasing DF, and it peaked under moderate cloudy sky conditions (DF=0.5). Daily LUE significantly increased with DF. Meanwhile, PAR was the major intermediate variable of the regulation of DF on LUE and GPP. The trade-off effect between DF and PAR on GPP is linked with sky conditions, canopy structure and environmental conditions. In low $T_a$ and VPD, canopy photosynthesis is more easily increased with DF in the mixed plantation. These findings highlight the importance of incorporating DF into GPP estimation, and the performance of the MM$_{dif}$ model in estimating GPP was better than that of the MM model, especially under low $T_a$ and VPD conditions. Under future climate change and human activities, the responses of ecosystem productivity to sky and environmental conditions are nonlinear. Thus, additional factors (e.g. aerosols, vegetation phenology, leaf optical parameters and environmental factors) interacting with GPP should be taken into account in the GPP simulation.

**Data availability statement**

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

**Author contributions**

PL and XT carried out the data processing and analysis and wrote the manuscript. JSZ and PM contributed to the conception and design of the study. PL and JL organized the data and performed the statistical analysis.
analysis. JRZ and YZ carried out data collection. All authors participated in the manuscript editing and approved the final version. All authors contributed to the article and approved the submitted version.

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**Conflict of interest**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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