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EDITED BY

Haoran Zhou,
Yale University, United States

REVIEWED BY

Yonggang Chi,
Zhejiang Normal University, China
Mingjie Xu,
Shenyang Agricultural University, China

*CORRESPONDENCE

Tao Qi

✉ qitao@hebeu.edu.cn

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Leaf photosynthetic pigment as a predictor of leaf maximum carboxylation rate in a farmland ecosystem

Yue Li¹, Qingtao Wang², Taimiao Fu², Yunfeng Qiao³, Lihua Hao⁴ and Tao Qi^{2*}

¹School of Earth Science and Engineering, Hebei University of Engineering, Handan, China, ²School of Landscape and Ecological Engineering, Hebei University of Engineering, Handan, China, ³Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China, ⁴School of Water Conservancy and Hydropower, Hebei University of Engineering, Handan, China

The leaf maximum rate of carboxylation (V_{cmax}) is a key parameter of plant photosynthetic capacity. The accurate estimation of V_{cmax} is crucial for correctly predicting the carbon flux in the terrestrial carbon cycle. V_{cmax} is correlated with plant traits including leaf nitrogen (N_{area}) and leaf photosynthetic pigments. Proxies for leaf chlorophyll (Chl_{area}) and carotenoid contents (Car_{area}) need to be explored in different ecosystems. In this study, we evaluated the relationship between leaf maximum rate of carboxylation (scaled to 25°C; $V_{\text{cmax}25}$) and both leaf N_{area} and photosynthetic pigments (Chl_{area} and Car_{area}) in winter wheat in a farmland ecosystem. Our results showed that $V_{\text{cmax}25}$ followed the same trends as leaf Chl_{area} . However, leaf N_{area} showed smaller dynamic changes before the flowering stage, and there were smaller seasonal variations in leaf Car_{area} . The correlation between leaf $V_{\text{cmax}25}$ and leaf Chl_{area} was the strongest, followed by leaf Car_{area} and leaf N_{area} ($R^2 = 0.69$, $R^2 = 0.47$ and $R^2 = 0.36$, respectively). The random forest regression analysis also showed that leaf Chl_{area} and leaf Car_{area} were more important than leaf N_{area} for $V_{\text{cmax}25}$. The correlation between leaf $V_{\text{cmax}25}$ and N_{area} can be weaker since nitrogen allocation is dynamic. The estimation accuracy of the $V_{\text{cmax}25}$ model based on N_{area} , Chl_{area} , and Car_{area} ($R^2 = 0.75$) was only 0.05 higher than that of the $V_{\text{cmax}25}$ model based on Chl_{area} and Car_{area} ($R^2 = 0.70$). However, the estimation accuracy of the $V_{\text{cmax}25}$ model based on Chl_{area} and Car_{area} ($R^2 = 0.70$) was 0.34 higher than that of the $V_{\text{cmax}25}$ model based on N_{area} ($R^2 = 0.36$). These results highlight that leaf photosynthetic pigments can be a predictor for estimating $V_{\text{cmax}25}$, expanding a new way to estimate spatially continuous $V_{\text{cmax}25}$ on a regional scale, and to improve model simulation accuracy.

KEYWORDS

leaf chlorophyll content, leaf carotenoid content, leaf nitrogen content, maximum rate of carboxylation, photosynthetic capacity

1 Introduction

Farmland ecosystems play an important role in the carbon cycle of terrestrial ecosystems (Robertson et al., 2000). However, the carbon flux of farmland ecosystems is one of the main uncertainties in global terrestrial carbon cycle research and is significantly affected by human activities (Lal, 2001; Bondeau et al., 2007; Taylor et al., 2013). High-quality simulations of the carbon budget of farmland ecosystems are beneficial for future projections of climate change and crop yield (Houborg et al., 2015; Bonan and Doney, 2018). Process-based terrestrial biosphere models (TBMs) are effective tools for estimating changes in the ecosystem carbon budget. However, currently there is still significant uncertainty in simulating the impact of climate change on terrestrial carbon flux (Smith and Dukes, 2012; Anav et al., 2015; Li et al., 2018a). Approximately 90% of carbon and water fluxes in biosphere and atmospheric occur through photosynthesis, and the photosynthetic module is an important part of TBMs (Zhu et al., 2016). Photosynthetic rate is a primary source of uncertainty in terrestrial carbon dynamic modelling because of the lack of in-depth research on photosynthesis and field observation data (Dietze, 2014).

To simulate photosynthetic rate, most TBMs used a kinetic enzyme model based on Farquhar–von Caemmerer–Berry (FvCB) (Farquhar et al., 1980; Jin et al., 2023). The maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) are two key photosynthetic parameters in FvCB model. V_{cmax} represents the maximum rate of Ribulose-1,5-Bisphosphate (RuBP) carboxylation catalyzed by Rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) enzyme (Quebbeman and Ramirez, 2016). J_{max} is the rate of RuBP regeneration through the electron transport chain (Voncaemmerer and Farquhar, 1981; Sharkey et al., 2007). In process-based models, V_{cmax} plays a critical role in constraining photosynthetic rates (Lebauer et al., 2013). Previously, V_{cmax} was assumed to be a fixed value (at the temperature of 25°C; $V_{\text{cmax}25}$), which varied with plant functional type (PFT) in process-based models (Houborg et al., 2013; Zhang et al., 2014). Nonetheless, there are seasonal variations for $V_{\text{cmax}25}$ (Grassi et al., 2005; Medvigy et al., 2013; Alton, 2017; Croft et al., 2017). Even for the same PFT, the difference between species is great (Dillen et al., 2012; Croft et al., 2017). Previous studies have typically used leaf nitrogen content (N) to model the photosynthetic capacity to incorporate spatiotemporal changes in $V_{\text{cmax}25}$ (Kattge et al., 2009; Walker et al., 2014). However, it is not possible to accurately retrieve leaf nitrogen content based on remote sensing data (Knyazikhin et al., 2013). Additionally, a relationship between leaf N and $V_{\text{cmax}25}$ cannot be applied at large scales or to different PFTs because Rubisco-N, rather than total leaf nitrogen (photosynthetic and nonphotosynthetic nitrogen pools), is more related to $V_{\text{cmax}25}$ (Croft et al., 2017; Onoda et al., 2017; Effah et al., 2023). Nonphotosynthetic N pools can complicate the relationships between leaf $V_{\text{cmax}25}$ and leaf N.

In recent years, leaf chlorophyll content has been retrieved relatively accurately via remote sensing (Croft et al., 2013), which plays a crucial role in capturing light energy to drive photosynthetic reactions (Yang et al., 2014; Croft et al., 2020; Huang et al., 2023).

Leaf chlorophyll can effectively eliminate the influence of nonphotosynthetic N, which refers to changes in the photosynthetic active N pool (Croft et al., 2017). Leaf chlorophyll contents have been adopted to represent photosynthetic capacity in some studies (Houborg et al., 2015; Croft et al., 2017). In farmland ecosystems, Houborg et al. (2013) adopted an intermediate variable (leaf N) to demonstrate a semi-empirical relationship between the leaf $V_{\text{cmax}25}$ and chlorophyll content. In temperate deciduous forests, Croft et al. (2017) found a direct correlation between leaf $V_{\text{cmax}25}$ and leaf Chl_{area} . Luo et al. (2018) incorporated Chl_{leaf} into terrestrial biosphere models to constrain $V_{\text{cmax}25}$ based on the relationship between $V_{\text{cmax}25}$ and Chl_{leaf} from the work of Croft et al. (2017), and improved the temporal correlations between the measured and the estimated fluxes in a temperate deciduous forest. Strong correlations between the field-measured leaf chlorophyll content and $V_{\text{cmax}25}$ have been reported in various PFTs (Qian et al., 2019; Lu et al., 2020; Wang et al., 2020; Qian et al., 2021; Lu et al., 2022; Liu et al., 2023b). Recent studies have found that leaf carotenoid, another major photosynthetic pigment, can improve the estimation precision for $V_{\text{cmax}25}$ based on leaf Chl_{area} . Leaf carotenoid content increases the capability of phenological monitoring, particularly in areas where seasonal variations in leaf chlorophyll content are not obvious (Wong et al., 2019). The functional relationship between the photosynthetic pigments (chlorophyll and carotenoid) and $V_{\text{cmax}25}$ plays an important role in regional model simulations (Croft and Chen, 2018; Luo et al., 2018; Luo et al., 2019). Therefore, leaf chlorophyll and carotenoid contents should be incorporated into the $V_{\text{cmax}25}$ model to improve the accuracy of TBMs in simulating C dynamics (Luo et al., 2019). However, the relationships between leaf pigment content (especially leaf carotenoid content) and $V_{\text{cmax}25}$ are still unclear. A large-scale spatial mapping of $V_{\text{cmax}25}$ requires understanding how these relationships change in different PFTs.

In this study, we estimated the relationships between $V_{\text{cmax}25}$ with leaf nitrogen and leaf pigments (chlorophyll and carotenoid) in a farmland ecosystem. Photosynthesis response curves, leaf nitrogen and leaf pigment content (chlorophyll and carotenoid contents) were observed at Yucheng (YC) Ecological Station during the 2021. We also investigated the correlations between $V_{\text{cmax}25}$ with leaf nitrogen, chlorophyll and carotenoid contents in a farmland ecosystem. We also analyzed the relationships among these driving variables associated with $V_{\text{cmax}25}$ and assessed their relative importance.

2 Materials and methods

2.1 Field site description

We carried out field experiments in Yucheng, Shandong Province, China (36°57' N, 116°38' E). The station is a wheat producing area in China, which located in a warm temperate zone. The annual average temperature and precipitation are 13.1°C and 610 mm, respectively. The average temperature in January is -3°C, and the average temperature in July is 26.9°C.

Precipitation occurs mainly from June to August, accounting for 69.1% of the total annual precipitation and shows a pattern of spring drought and summer floods (Zhu et al., 2020). The tidal soil is the main soil type in this area. The PH value is 8.0 and the soil organic matter content is 15.0 g kg⁻¹. Mass fraction of soil total nitrogen is 0.64 g kg⁻¹ (Hga et al., 2020).

2.2 Measurements of CO₂ response curve

Leaf gas exchange in winter wheat was measured in a 10 × 10m subset area within a larger field. We conducted winter wheat observation experiment from day of the year (DOY) 92 (April 2) to 147 (May 27) in 2021. Leaf samples were randomly selected approximately once every seven days (Table 1). Three to four winter wheat leaf samples were collected weekly during the 2021 growing season. The CO₂ response curves for leaves in winter wheat were measured by a portable gas-exchange system (Li 6400; Li-Cor, Inc., Lincoln, NE, USA).

CO₂ response curves were observed under saturated light conditions. It took about 40 minutes to observe CO₂ response curves. Adjust the photosynthetic photon flux density (PPFD) to 1,500 μmol m⁻² s⁻¹ (saturated light). The flow rate was maintained at 500 mmol s⁻¹, and the relative humidity was set in the range of 40–80% during the measurement period. The air CO₂ concentrations (C_a) gradients are 380, 300, 200, 100, 50, 380, 600, 800, 1,000, and 1,200 μmol CO₂ mol⁻¹ air. Leaf samples were acclimated in a 2 × 3 cm² leaf cuvette for 20 min at a temperature of 25°C and a CO₂ concentration of 380 μmol CO₂ mol⁻¹ before measuring CO₂ response curves. V_{cmax} and J_{max} values were estimated by an Excel tool (www.landflux.org/Tools.php) (Ethier and Livingston, 2004). Arrhenius equation (Equation 1 and Table 2) was used in our study to normalize V_{cmax} and J_{max} to V_{cmax25} and J_{max25} (Sharkey et al., 2007; Sharkey, 2016). The net photosynthetic rate (A_{sat}) was recorded at a PPFD of 1,500 μmol m⁻² s⁻¹ and a CO₂ concentration of 380 μmol mol⁻¹.

$$f(T_k) = k_{25} \exp(c \cdot \Delta H_a / RT_k) \quad (1)$$

TABLE 1 Leaf measurements stages and sample sizes of winter wheat at YC site in 2021.

Measurement DOY	Sample sizes	Growing stages
92 (April 2)	4	Elongation stage (≤95)
96 (April 6)	4	Booting stage (≤117)
105 (April 15)	3	Booting stage (≤117)
119 (April 29)	3	Flowering stage (≤131)
126 (May 6)	3	Flowering stage (≤131)
133 (May 13)	4	Filling stage (≤161)
140 (May 20)	4	Filling stage (≤161)
147 (May 27)	4	Filling stage (≤161)

TABLE 2 Parameters values referring to the temperature responses of leaf photosynthetic capacity.

Parameter	Value at 25°C	c	ΔH _a
V _{cmax}	1	26.355	65.33
J	1	17.710	43.90

1 indicates the value of f(T_k)/k₂₅ at 25°C.

where k₂₅ and f(T_k) were, respectively, the values at 25°C and leaf surface temperature. c was a scaling constant (Table 2). ΔH_a referred to the activation energy. R was the molar gas constant (0.008314 kJ mol⁻¹ K⁻¹). T_k represented the absolute leaf temperature.

2.3 Leaf biochemistry measurements

We conducted leaf biochemical analyses (leaf nitrogen content, N_{area}; leaf chlorophyll content, Chl_{area}; and leaf carotenoid content, Car_{area}) on the same day as leaf A/Ci curves observations. The leaves of winter wheat were sampled from the same locations as for the A/Ci curves observations. For leaf photosynthetic pigment (chlorophyll and carotenoid) and nitrogen analyses, leaf samples were immediately packed in paper bags and were sent to chemistry laboratory. Fresh leaf weight was also recorded in chemistry laboratory. The leaf photosynthetic pigments were extracted using 95% ethanol. A Shimadzu UV-2600 spectrophotometer was used to calculate both leaf chlorophyll and carotenoid contents by measuring the absorbance at 665, 649, and 470 nm (Fargasova and Molnarova, 2010). We used the same leaves as those measured to determine the leaf photosynthetic pigments to calculate leaf nitrogen content. Dry the leaf samples at 80°C for 48 hours until a constant weight. Specific leaf area (SLA) was determined by leaf dry weights and leaf area. We ground the dried leaves into powder by a mixer mill (MM400, RETSCH, Germany). A Vario MAX CN elemental analyzer (Elementar Analyzer system, Hanau, Germany) was used to record leaf nitrogen content.

Fractions of leaf N allocated to photosynthetic components, i.e., active Rubisco (P_R), bioenergetics pools (P_B) and light-harvesting components (P_L), were determined based on V_{cmax}, J_{max} and leaf chlorophyll content, according to the equations reported by Niinemets and Tenhunen (1997).

$$P_R = \frac{V_{cmax}}{6.25 \times V_{cr} \times M_A \times N_{mass}} \quad (2)$$

$$P_B = \frac{J_{max}}{8.06 \times J_{mc} \times M_A \times N_{mass}} \quad (3)$$

$$P_L = \frac{C_C}{C_B \times N_{mass}} \quad (4)$$

where M_A referred to dry leaf mass per unit area (g m⁻²). C_C was leaf chlorophyll content (mmol g⁻¹). N_{mass} represented nitrogen content per dry leaf mass (g g⁻¹). The C_B value was 2.15 mmol g⁻¹. The values of V_{cr} and J_{mc} were 20.5 μmol CO₂ (g Rubisco)⁻¹ s⁻¹ and

156 $\mu\text{mol electrons } (\mu\text{mol cyt } f)^{-1} \text{ s}^{-1}$ at the temperature of 25°C, respectively (Niinemets et al., 1998).

2.4 Data analysis

In the correlation analyses, we used Pearson's correlation coefficients to demonstrate the linear correlation strength between two variables. Pearson correlation coefficient, also known as the Pearson product-moment correlation coefficient, is represented by R in this paper. The following function was used to calculate R :

$$R = \frac{\sum_{i=1}^n (x - \bar{x})(y - \bar{y})}{\sqrt{\sum_{i=1}^n (x - \bar{x})^2 (y - \bar{y})^2}} \quad (5)$$

where n is the sample size, and R is between -1 and +1. The larger the absolute value of R , the stronger the correlation. There may be a positive ($R > 0$) or negative ($R < 0$) correlation between two variables.

The relationships between leaf nitrogen content and leaf photosynthetic pigments (chlorophyll and carotenoid contents) were evaluated by simple linear regressions. We used the statistical package in Origin Pro 9.0 to conduct simple linear regressions. Analysis of variance (ANOVA) was adopted to evaluate the significance of the regression equations. The statistical significance of tests was set at 0.05. The prediction variables, leading to changes in $V_{\text{cmax}25}$, included leaf nitrogen, chlorophyll, carotenoid, and SLA. We adopted random forest regression analysis (Breiman, 2001) to discern the amount of changes in $V_{\text{cmax}25}$. The relative importance of each predictor was evaluated by random forest regression analysis (Delgado-Baquerizo et al., 2017), which can resolve the multicollinearity problems between prediction variables. The percentage increase in the mean square error (% IncMSE) indicates the influence of replacing a predictor with a random variable on the predicted outcome, which represents the effect of predictors on the dependent variable. The original variable was more important when the random variable changed the original variance significantly. Therefore, the higher the %IncMSE of predictor, the more importance it is. Random forest package (randomForest) in R was used in our study to perform the random forest regression (<http://www.r-project.org/>). Multiple linear regression models were constructed to explore the effects of leaf nitrogen and photosynthetic pigments (chlorophyll and carotenoid) on variations in $V_{\text{cmax}25}$. The performances of the $V_{\text{cmax}25}$ models were estimated using the coefficient of determination (R^2) between different leaf trait variables. We used SPSS[®] version 17.0 (SPSS Inc. Chicago, IL, USA) to perform multiple linear regression analysis in our study.

3 Results

3.1 Seasonal variations in leaf photosynthetic parameters and biochemical parameters

Winter wheat showed large temporal variations in leaf photosynthetic rate and $V_{\text{cmax}25}$ in 2021. At the elongation and booting stages, the leaf A_{sat} and $V_{\text{cmax}25}$ increased gradually before

the flowering stage (on average, 42% and 62% higher on DOY 126 than on DOY 92, respectively), reaching a peak of 28.63 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ and 133.46 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively, at the flowering stage. A_{sat} and $V_{\text{cmax}25}$ then declined rapidly during the filling stage (on average, 79% and 190% lower on DOY 147 than on DOY 126, respectively) (Figures 1A, C). Temporal variations in leaf $J_{\text{max}25}$ and $V_{\text{cmax}25}$ were consistent (Figure 1C). Leaf chlorophyll content had a similar temporal variation to $V_{\text{cmax}25}$, which gradually reached its peak at the flowering stage (on average, 68% higher on DOY 126 than on DOY 92) and rapidly declined at the filling stage (on average, 99% lower on DOY 147 than on DOY 126) (Figure 1B). Leaf A_{sat} and photosynthetic parameters appeared to follow the trends of leaf chlorophyll content. However, there were some differences in the seasonal patterns of leaf chlorophyll, nitrogen, and carotenoid contents. Leaf nitrogen content showed smaller dynamic changes before the flowering stage than leaf Chl_{area} (on average, 26% higher on DOY 126 than on DOY 92) and then declined rapidly at the late stage (on average, 83% lower on DOY 147 than on DOY 126) (Figure 1A). The peak value of leaf Car_{area} was, on average, 48% higher than that of Car_{area} on DOY 92. There were minor changes in leaf Car_{area} after the flowering stage (on average, 33% lower on DOY 147 than on DOY 126) (Figure 1B). Therefore, smaller seasonal changes were showed in leaf Car_{area} compared to leaf Chl_{area} in winter wheat, particularly after the flowering stage.

3.2 Correlation of leaf photosynthetic parameters and leaf traits variables

There were positive correlations between the leaf photosynthetic parameters (A_{sat} , $V_{\text{cmax}25}$, and $J_{\text{max}25}$) and leaf trait variables (N_{area} , Chl_{area} , and Car_{area}) (Figure 2). The correlation coefficient between leaf $V_{\text{cmax}25}$ and leaf Chl_{area} was the highest (0.83), followed by leaf Car_{area} (0.68) and leaf N_{area} (0.60), all of which showed significant linear positive correlations ($p < 0.001$) (Figure 2). The correlations between Leaf $J_{\text{max}25}$ were also significantly correlated with leaf traits variables (N_{area} , Chl_{area} , Car_{area}), with correlation coefficients of 0.55 ($p < 0.01$), 0.79 ($p < 0.001$), and 0.70 ($p < 0.001$), respectively. Correlations were also observed between the three leaf trait variables (Figure 2).

Simple linear regressions were conducted between leaf photosynthetic capacity with leaf nitrogen content, and leaf photosynthetic pigments (Table 3). The results indicated that leaf Chl_{area} accounted for 69% and 63% of the temporal variation in $V_{\text{cmax}25}$ and $J_{\text{max}25}$, respectively ($p < 0.001$). Leaf Car_{area} accounted for 47% and 48% of the temporal variation in $V_{\text{cmax}25}$ and $J_{\text{max}25}$, respectively ($p < 0.001$). However, there was a weak relationship between leaf N_{area} and leaf photosynthetic capacity. Leaf N_{area} accounted for only 36% and 30% of the temporal variation in $V_{\text{cmax}25}$ and $J_{\text{max}25}$, respectively ($p < 0.001$) (Table 3). There were certain limitations to estimating $V_{\text{cmax}25}$ based on leaf N_{area} .

3.3 Changes in leaf nitrogen allocation

The ratios between leaf Chl_{area} and N_{area} indicate the allocation of leaf nitrogen between the Rubisco and leaf chlorophyll

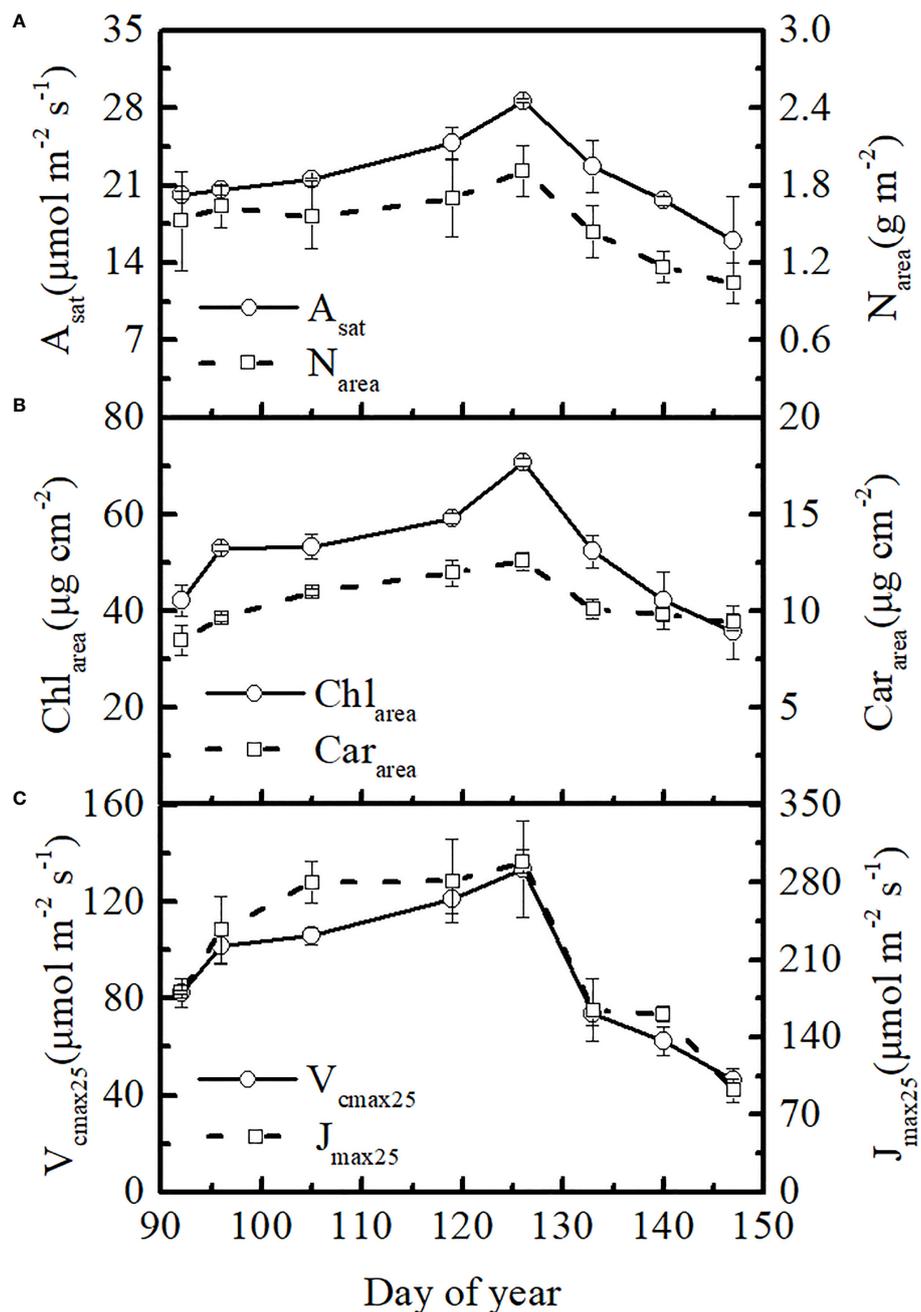


FIGURE 1

Seasonal changes in (A) photosynthetic rate and nitrogen content, (B) leaf chlorophyll and leaf carotenoid contents, and (C) $V_{\text{cmax}25}$ and $J_{\text{max}25}$ for winter wheat in 2021.

components (Kenzo et al., 2006). There was little seasonal variation in the ratios between leaf Chl_{area} to N_{area} (both units are $\mu\text{g cm}^{-2}$) after DOY 105 in 2021 (Figure 3A). The leaf $\text{Chl}_{\text{area}}/\text{N}_{\text{area}}$ ratios showed a rapidly increasing trend at the beginning stage (DOY 92 and DOY 96). The ratios were 0.23 and 0.32 at DOY 92 and 96, respectively. Leaf $\text{Chl}_{\text{area}}/\text{N}_{\text{area}}$ ratios were maintained at approximately 0.36 from DOY 105 to DOY 147 (Figure 3A).

P_R , P_B , and P_L showed seasonal patterns that first increased and then decreased (Figures 3B–D). The growing stage at which leaf P_B reached its highest point in winter wheat differed from that of P_R and P_L . Temporal variations in leaf P_R and P_L were coordinated,

reaching their highest points at the flowering stage. In general, changes in leaf N allocation to different N pools were dynamic (Figures 3B–D), which may have led to a weak correlation between leaf nitrogen and $V_{\text{cmax}25}$ (Table 3).

3.4 Relationships among leaf nitrogen, chlorophyll and carotenoid contents

A significant linear relationship between leaf nitrogen and leaf chlorophyll contents ($R^2 = 0.90$, $p < 0.001$) was observed in our study.

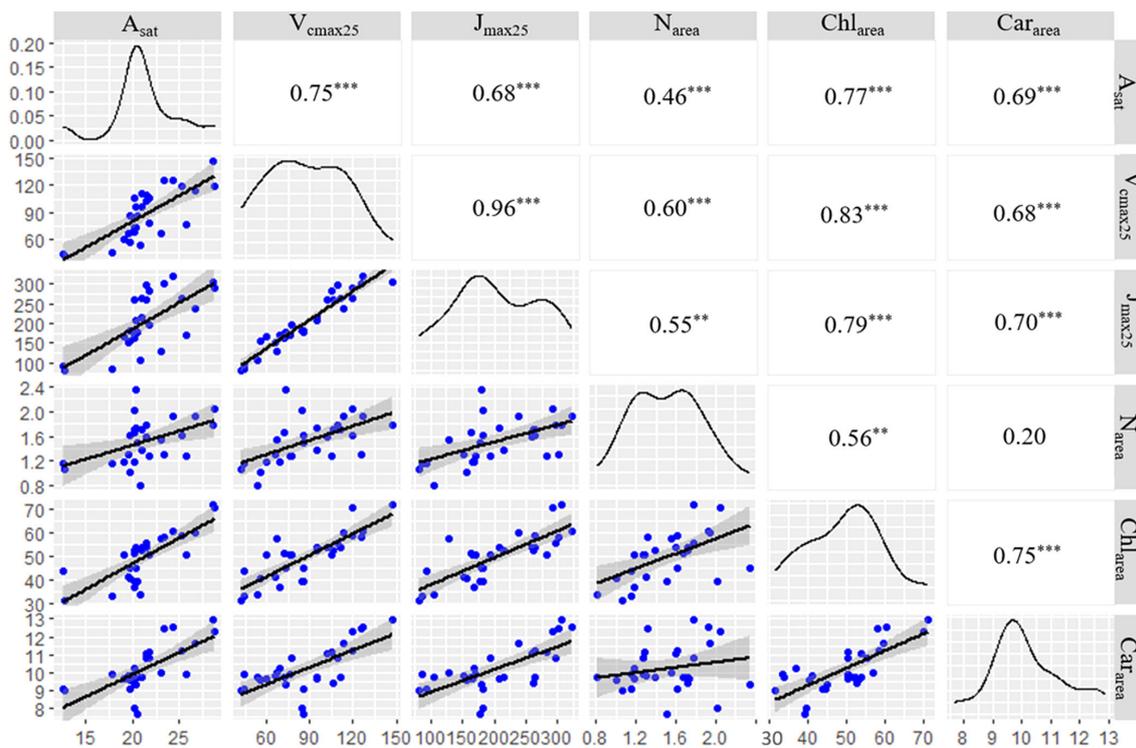


FIGURE 2 Correlation between both leaf photosynthetic rate and leaf photosynthetic capacity with different leaf traits variables. ***, ** and * represent $p < 0.001$, $p < 0.01$ and $p < 0.05$, respectively. The caption describes all significant situations of correlation between parameters, including significant correlation (*) and extremely significant correlation (** and ***). The results in Figure 2 showed that the parameters were highly correlated (** and ***) or uncorrelated.

The observations on DOYs 92 and 96 were outside the 95% confidence intervals of the regression (Figure 4A), which may be attributed to the significant variations in nitrogen allocation to the leaf chlorophyll fractions on these two days (Figure 3A). Leaf Chl_{area} was also strongly correlated with Car_{area} ($R^2 = 0.71$, $p = 0.005$) (Figure 4B). However, a weaker relationship between leaf N_{area} and Car_{area} was observed ($R^2 = 0.43$, $p = 0.05$) in winter wheat in 2021 (Figure 4C).

3.5 The importance of each prediction variable to V_{cmax25}

We used a random forest regression analysis to evaluate the relative importance of each prediction variable for V_{cmax25} . Leaf Car_{area} , Chl_{area} , and leaf N_{area} were all main prediction variables for

V_{cmax25} in our study (Figure 5). Leaf Chl_{area} (%IncMSE = 22.60%) was the most important driver of V_{cmax25} , followed by leaf Car_{area} (%IncMSE was 21.47%), and leaf N_{area} (%IncMSE = 19.08%). The importance of SLA (%IncMSE = 15.66%) to V_{cmax25} was far below the importance of leaf photosynthetic pigment and nitrogen content (Figure 5).

3.6 Optimization of V_{cmax25} model by multiple regression models

Multiple linear regression models were established to improve the accuracy of the V_{cmax25} models using leaf N_{area} , Chl_{area} , and Car_{area} (Equations 6-9). The estimation accuracies of the binary linear regression models for V_{cmax25} ($R^2 = 0.72$, 0.70, and 0.69, respectively, for $f(N_{area}, Chl_{area})$, $f(Chl_{area}, Car_{area})$, and

TABLE 3 Coefficients of determination for simple linear regressions between photosynthetic parameters with both leaf nitrogen and leaf photosynthetic pigment during 2021.

	N_{area}		Chl_{area}		Car_{area}	
	R^2	p	R^2	p	R^2	p
V_{cmax25}	0.36	***	0.69	***	0.47	***
J_{max25}	0.30	***	0.63	***	0.48	***

The caption describes all significant situations of correlation between parameters, including significant correlation (*) and extremely significant correlation (** and ***). The results in Table 3 showed that the parameters were highly correlated (***). ***, ** and * represent $p < 0.001$, $p < 0.01$ and $p < 0.05$, respectively.

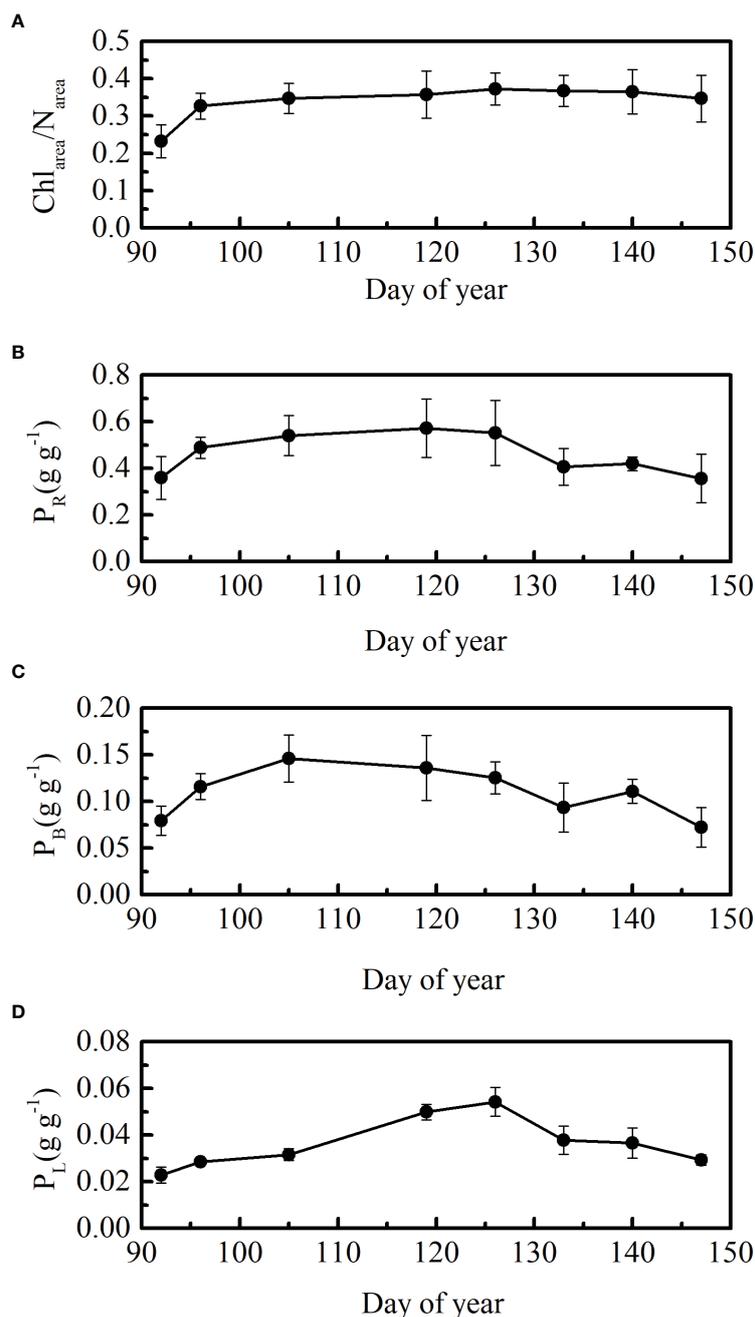


FIGURE 3
Seasonal patterns in (A) leaf Chl_{area} to N_{area} ratios, (B) P_R , (C) P_B , and (D) $P_L \pm \text{SD}$, in 2021.

$f(\text{N}_{\text{area}}, \text{Car}_{\text{area}})$) were all significantly higher than those of the two simple linear regression models for $f(\text{N}_{\text{area}})$ and $f(\text{Car}_{\text{area}})$ ($R^2 = 0.36$ and 0.47 , respectively) in our study (Tables 3, 4). However, the estimation accuracy of the simple linear regression models for $f(\text{Chl}_{\text{area}})$ ($R^2 = 0.69$) was not significantly different from that of the binary linear regression models (Tables 3, 4). The model based on leaf N_{area} , Chl_{area} , and Car_{area} had the highest accuracy in estimating $V_{\text{cmax}25}$ ($R^2 = 0.75$, $p < 0.001$), which was only 0.06 higher than that of the simple linear regression models for $f(\text{Chl}_{\text{area}})$ ($R^2 = 0.69$) (Tables 3, 4). Thus,

leaf Chl_{area} was a better predictor for $V_{\text{cmax}25}$ than leaf N_{area} in winter wheat at the YC site (Tables 3, 4). Incorporating leaf photosynthetic pigments (chlorophyll and carotenoid content) into photosynthetic models can significantly improve the estimation accuracy of $V_{\text{cmax}25}$ model based on leaf nitrogen for winter wheat.

$$V_{\text{cmax}25} = 15.17\text{N}_{\text{area}} + 1.99\text{Chl}_{\text{area}} - 34.43 \quad (6)$$

$$V_{\text{cmax}25} = 1.99\text{Chl}_{\text{area}} + 3.13\text{Car}_{\text{area}} - 43.51 \quad (7)$$

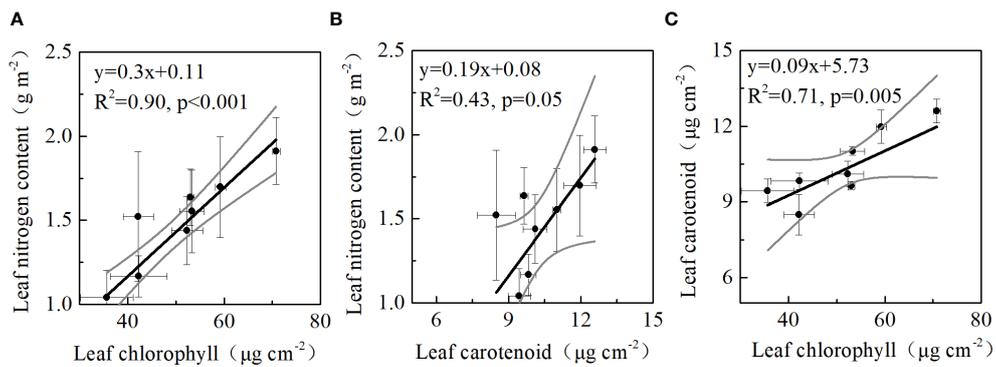


FIGURE 4
 Relationships between (A) leaf nitrogen and chlorophyll contents, (B) leaf nitrogen and carotenoid contents, (C) leaf carotenoid and chlorophyll contents in 2021. Horizontal error bars denote standard deviation of leaf chlorophyll and leaf carotenoid. Vertical error bars refer to standard deviation of leaf nitrogen and leaf carotenoid.

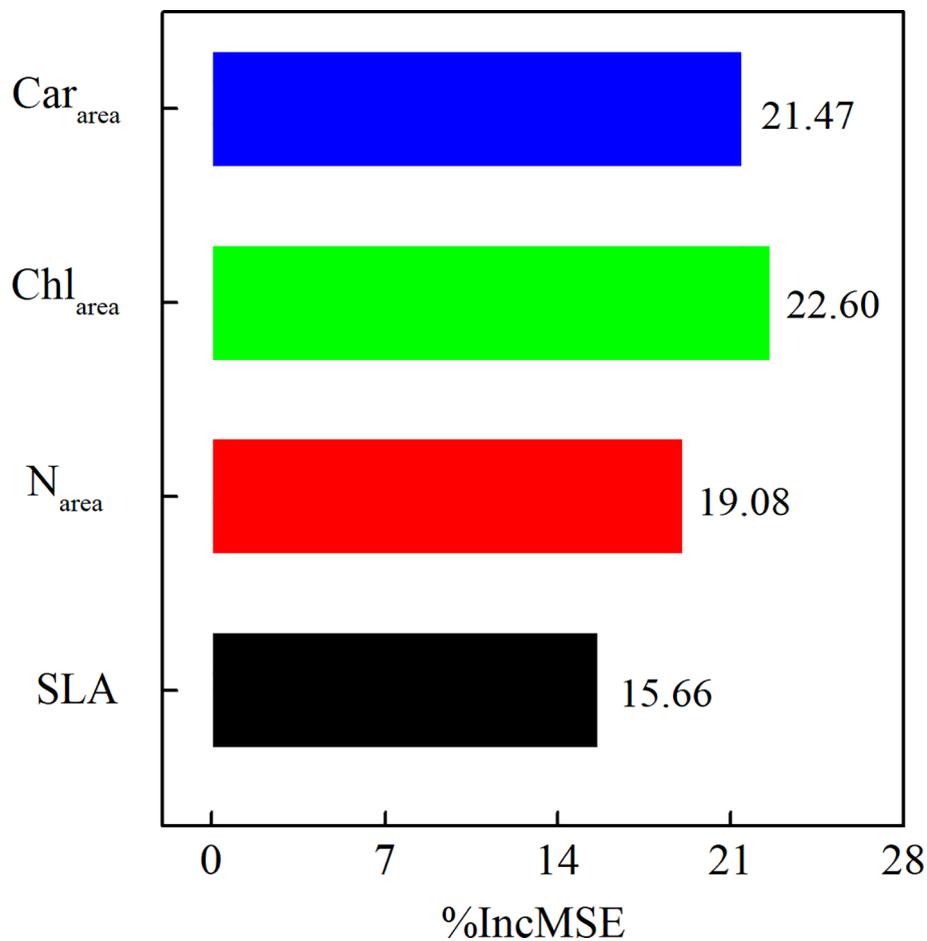


FIGURE 5
 The importance of leaf Car_{area}, leaf Chl_{area}, leaf N_{area}, and SLA to V_{cmax25} in 2021.

TABLE 4 Coefficient of determination (r^2) of $V_{\text{cmax}25}$ models based on different leaf traits variables.

$V_{\text{cmax}25}$ models	R^2	p-value
$f(N_{\text{area}}, \text{Chl}_{\text{area}})$	0.72	<0.001
$f(\text{Chl}_{\text{area}}, \text{Car}_{\text{area}})$	0.70	<0.001
$f(N_{\text{area}}, \text{Car}_{\text{area}})$	0.69	<0.001
$f(N_{\text{area}}, \text{Chl}_{\text{area}}, \text{Car}_{\text{area}})$	0.75	<0.001

$$V_{\text{cmax}25} = 37.48N_{\text{area}} + 12.68\text{Car}_{\text{area}} - 98.92 \quad (8)$$

$$V_{\text{cmax}25} = 22.30N_{\text{area}} + 1.26\text{Chl}_{\text{area}} + 6.18\text{Car}_{\text{area}} - 71.99 \quad (9)$$

4 Discussion

4.1 Differences in seasonal trends of photosynthetic parameters

In our study, leaf A_{sat} and photosynthetic parameters appeared to follow trends in leaf chlorophyll content. However, there were some differences in the seasonal patterns of leaf chlorophyll, nitrogen, and carotenoid contents. Leaf N_{area} was relatively high at the elongation stage relative to leaf Chl_{area} (Figures 1A, B), which may be attributed to the inorganic nitrogen present in buds before leaf flushing. The different trends in leaf nitrogen and leaf chlorophyll maybe attributed to dynamic changes in leaf nitrogen partitioning among photosynthetic pools (Croft et al., 2017; Liu et al., 2023a). Fertilization management can also maintain high leaf nitrogen content at the start of season (Lu et al., 2020). Leaf Car_{area} showed smaller seasonal variations compared to leaf Chl_{area} in winter wheat, particularly after the flowering stage (Figure 1B). As there is massive loss of leaf chlorophyll in winter wheat during senescence in the filling stage, carotenoids are retained in the leaves for a much longer time (Wong et al., 2019). In the early growth stage, the leaf Chl_{area} is higher than the leaf Car_{area} . The leaves appear green because green light is almost completely reflected. In the late stage, leaf chlorophyll is heavily damaged, but leaf carotenoids are only slightly affected, causing the leaves to turn yellow (Stylinski et al., 2002; Garrity et al., 2011). Flowering stage is an important physiological stage for winter wheat, since all the photosynthetic parameters have inflection point in this period. The results are consistent with Lu et al. (2020). The temperature rises gradually after the greening period. At this period, plant root is vigorous, enzyme activity and plant photosynthetic capacity increases. Thus, leaf photosynthetic parameters increase gradually and reach the maximum point at the flowering stage. The reproductive growth of winter wheat is dominant after flowering stage. Leaf and other vegetative organs gradually stop growing and aging. Therefore, leaf photosynthetic parameters decrease gradually (Yang et al., 2020).

4.2 Relationships among leaf $V_{\text{cmax}25}$, nitrogen and photosynthetic pigments

Leaf nitrogen was closely correlated with leaf chlorophyll in previous studies, with a fixed value of leaf $\text{Chl}_{\text{area}}/N_{\text{area}}$ ratio (Sage et al., 1987; Evans, 1989; Houborg et al., 2013). Our results also showed a strong linear relationship between leaf Chl_{area} and N_{area} ($R^2 = 0.90$; $p < 0.001$) (Figure 3A). The robustness of the linear correlation between leaf nitrogen and chlorophyll contents was influenced by changes in leaf nitrogen allocation to chlorophyll (Lu et al., 2020). A relatively stable allocation of leaf nitrogen to leaf chlorophyll ($\text{Chl}_{\text{area}}/N_{\text{area}}$ ratio of approximately 0.36) was found in our study for winter wheat (Figure 4A), which contributed to a good linear relationship between leaf Chl_{area} and N_{area} (Figure 3A).

$V_{\text{cmax}25}$ was closely related to leaf N_{area} , leaf Chl_{area} , and SLA in previous studies (Houborg et al., 2013; Houborg et al., 2015; Croft et al., 2017; Watanabe et al., 2018; Miner and Bauerle, 2019; Qian et al., 2021; Lu et al., 2022). However, the results are inconsistent in different studies, indicating that these relationships vary among species and are difficult to apply at large scales. Qian et al. (2021) showed a stronger linear relationship between $V_{\text{cmax}25}$ and Chl_{area} than between leaf $V_{\text{cmax}25}$ and N_{area} across 13 species. In other ecosystems, a strong relationship exists between leaf $V_{\text{cmax}25}$ and N_{area} and the slopes vary among species (Walker et al., 2014; Quebbeman and Ramirez, 2016). However, the slopes of the relationship in $N_{\text{area}}-V_{\text{cmax}25}$ varies greatly with environmental conditions and PFTs (Walker et al., 2014; Rogers et al., 2017). A weaker correlation between leaf $V_{\text{cmax}25}$ and leaf N_{area} than between leaf $V_{\text{cmax}25}$ and Chl_{area} were showed in our study (Figure 2; Table 3), which is in agreement with Qian et al. (2021). Rubisco-N allocation (P_R), rather than the total leaf nitrogen content, was more related to V_{cmax} based on the meta-analysis (Ali et al., 2015). P_R showed significant seasonal variation during the growing season in our study (Figure 4B). The weak correlation between leaf N_{area} and $V_{\text{cmax}25}$ may also be attributed to variations in P_R (Figures 2, 4B; Table 3). Therefore, leaf N_{area} is not an ideal predictor for $V_{\text{cmax}25}$ in the present study. The temporal variations in leaf P_L coordinated with changes in P_R , which indicated that the allocation of leaf nitrogen to leaf carotenoids was dynamic. Consequently, A weak correlation between the leaf N_{area} and leaf Car_{area} for winter wheat area was showed in our study (Figure 3B).

4.3 Physiological mechanism for the relationships between leaf photosynthetic pigments and $V_{\text{cmax}25}$

Our results showed a stronger correlation between $V_{\text{cmax}25}$ with both leaf Chl_{area} ($R^2 = 0.69$) and Car_{area} ($R^2 = 0.47$) than with leaf N_{area} ($R^2 = 0.36$) (Figure 2; Table 3). Leaf photosynthetic pigments are a better predictor for $V_{\text{cmax}25}$ in winter wheat. The underlying mechanism of this phenomenon is the driving role of leaf pigment in light harvesting of photosynthesis (Zhang et al., 2009; Gitelson et al.,

2014; Li et al., 2018b). The random forest regression analysis also showed leaf chlorophyll and carotenoid contents were more important than leaf nitrogen content for $V_{\text{cmax}25}$ (Figure 5). Compared with other leaf traits, $V_{\text{cmax}25}$ can be accurately retrieved based on leaf chlorophyll content from remote sensing data (Gitelson et al., 2006; Croft et al., 2013). Moreover, leaf chlorophyll can effectively eliminate the influence of nonphotosynthetic nitrogen since it only reflects the changes of photosynthetic active N pool (Alton, 2017; Croft et al., 2017). Carotenoid, which is important component of plant photosynthesis, participate in the collection of sunlight, especially at wavelengths where leaf chlorophyll molecules are not absorbed strongly (Ritz et al., 2000). Leaf carotenoid also protect chlorophyll molecules from photo-oxidation. Carotenoid is commonly referred to as “auxiliary pigments” in light harvesting center, promoting the transfer of excitation energy to the reaction center (Niyogi et al., 1997). Leaf chlorophyll and carotenoid molecules are usually arranged in clusters to maximize the capture of light energy (Croft and Chen, 2018).

Leaf chlorophyll and carotenoid contents are the most important factors determining photosynthetic rate, owing to their important roles in light capture and absorption of photosynthetic effective radiation (Zhang et al., 2009; Zhang et al., 2011; Kooistra and Clevers, 2016). Therefore, leaf photosynthetic pigments play an important role in simulating vegetation productivity processes (Croft et al., 2017; Luo et al., 2018). The construction of a $V_{\text{cmax}25}$ model based on photosynthetic pigments can improve the accuracy of ecological process model simulations (Luo et al., 2019; Liu et al., 2023b). The multiple linear regression models established in our study showed that $f(N_{\text{area}}, \text{Chl}_{\text{area}}, \text{Car}_{\text{area}})$ had the highest optimization accuracy for the $V_{\text{cmax}25}$ model ($R^2 = 0.75$), which represents different information expressed by the leaf N_{area} and leaf photosynthetic pigment. The estimation accuracy of the $V_{\text{cmax}25}$ model based on $N_{\text{area}}, \text{Chl}_{\text{area}}$ and Car_{area} ($R^2 = 0.75$) was only 0.05 higher than that of the $V_{\text{cmax}25}$ model based on Chl_{area} and Car_{area} ($R^2 = 0.70$). However, the estimation accuracy of the $V_{\text{cmax}25}$ model based on Chl_{area} and Car_{area} ($R^2 = 0.70$) was 0.34 higher than that of the $V_{\text{cmax}25}$ model based on N_{area} ($R^2 = 0.36$). Leaf photosynthetic pigments can significantly improve the estimation accuracy of $V_{\text{cmax}25}$ based on leaf nitrogen in winter wheat.

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Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

YL analysed data and wrote the manuscript. The experiments were designed by TQ. QW and TF performed the experiments. YQ and LH revised the manuscript. 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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