ORIGINAL ARTICLE



The relationship between leaf and ecosystem CO₂ exchanges in a maize field

Zhenzhu Xu¹ · Guangsheng Zhou^{1,2} · Guangxuan Han^{1,3} · Yijun Li^{1,4}

Received: 18 September 2017 / Revised: 16 March 2018 / Accepted: 25 July 2018 © Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Kraków 2018

Abstract

The relationship between leaf photosynthetic rate (A) in a vegetation canopy and the net ecosystem CO₂ exchange (NEE) over an entire ecosystem is not well understood. The aim of the present study is to assess the coordinated changes in NEE derived with eddy covariance, A measured in leaf cuvette, and their associations in a rainfed maize field. The light response-curves were estimated for the carbon assimilation rate at both the leaf and ecosystem scales. NEE and A synchronically changed throughout the day and were greater around noon and persisted longer during rapid growth periods. The leaf A had a similar pattern of daytime changes in the top, middle, and bottom leaves. Only severe leaf ageing led to a significant decline in the maximum efficiency of photosystem II (PSII) photochemistry. The greater maximum NEE was associated with a higher ecosystem quantum yield. NEE was positively and significantly correlated with the leaf A averaged based on the vertical distribution of leaf area. The finding highlights the feasibility of assessing NEE by leaf CO₂ exchange because of most of experimental data obtained with leaf cuvette methods; and also implies that simultaneously enhancing leaf photosynthetic rate, electron transport rate, net carbon assimilation at whole ecosystem might play a critical role for the enhancement of crop productivity.

Keywords Eddy covariance \cdot Leaf photosynthetic rate \cdot Canopy \cdot Net CO₂ ecosystem exchange \cdot Photosynthetic quantum yield \cdot Photosystem II photochemistry \cdot Upscaling

Communicated by U. Feller.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11738-018-2732-6) contains supplementary material, which is available to authorized users.

Zhenzhu Xu xuzz@ibcas.ac.cn

Guangsheng Zhou gszhou@ibcas.ac.cn

- ¹ State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China
- ² Chinese Academy of Meteorological Sciences, Beijing 100081, China
- ³ Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai, China
- ⁴ National Meteorological Centre of China, Beijing, China

Introduction

An assessment of the consequences of climate change should monitor the carbon (C) cycle dynamic in an ecosystem because of its significance regarding the global carbon budget (Baldocchi 2003; Speckman et al. 2015; Waldo et al. 2016; Dold et al. 2017). Detailed information on the C budget of terrestrial ecosystems would improve the understanding of the ecosystems' functioning and responses to climatic change (Zha et al. 2004; Pielke et al. 2007; Ruiz-Vera et al. 2015). Carbon gas exchange has been assessed numerous times using individual methods, including the eddy covariance technique (EC), leaf cuvette, whole plant and soil and ecosystem chambers individually or together with different components of the ecosystem (e.g., Long and Bernacchi 2003; Vitale et al. 2007; Cleary et al. 2015; Kölling et al. 2015; Bloom et al. 2016; Anderson et al. 2017). However, the challenge may be how to corroborate ecosystem NEE measurement using other gas-exchange measurements (leaf, stem, and soil; see Moncrieff et al. 1996; Goulden

et al. 1996) or whole-plant chamber (e.g., Dore et al. 2003; Cleary et al. 2015; Malhi et al. 2017).

Measurement of CO₂ fluctuations using EC is a remarkable tool for monitoring gas and energy flux dynamics and has greatly contributed to our understanding of ecosystem carbon assimilation that occurs through photosynthesis and loss through respiration (e.g., Baldocchi 2003; Lasslop et al. 2010; Speckman et al. 2015; Vitale et al. 2016). More importantly, EC is a scale-appropriate method because it provides a relatively accurate net CO₂ exchange rate over an entire ecosystem (Baldocchi 2003; Speckman et al. 2015) including those with crop species (Jans et al. 2010; Schmidt et al. 2012; Wagle et al. 2017). However, many studies have assessed the net carbon exchange of ecosystem components using traditional tools, including the leaf cuvette (e.g., Field et al. 1982; Cleary et al. 2015) and whole-plant chamber (Denmeal et al. 1993; Tocquin and Périlleux 2004). The strength of the cuvette and chamber system is its ability to measure the diurnal variation of carbon fluxes and determines environmental response functions (Long and Bernacchi 2003; Jiang et al. 2004). However, a severe concern regarding measurement with a leaf chamber is the sampling required: a unit leaf area is chosen for measurement, even though leaves are not only different according to their physiological activity, age and position on the plant, but also according to their own photosynthetic capacity gradients (Tocquin and Périlleux 2004; Xu et al. 2011). Thus, the cuvette or chamber methods are limited in that only a small leaf area is considered and the environmental conditions may differ inside and outside the chambers (Law et al. 2001; Long and Bernacchi 2003; Lake 2004; Barron-Gafford et al. 2013). Building a bridge between the leafand ecosystem level gas-exchange processes is a key issue for improving a crop assimilation model's accuracy (Lizaso et al. 2005; Wang et al. 2015; Kölling et al. 2015). However, the relationship between the two methods (EC and cuvette) is not well understood (Barron-Gafford et al. 2013; Wang et al. 2015; Zhang et al. 2015). Additionally, because there is a relatively low cost when using leaf cuvette compare to EC systems (Long and Bernacchi 2003), the data at the leaf level often are more available than the data found when using EC technology. Thus, data captured by leaf cuvette may be useful when scaling up carbon exchange from leaf to ecosystem levels.

The older leaves of maize plants have lower *A*, chlorophyll and nitrogen contents compared to young leaves, indicating the obvious senescence in the older leaves (He et al. 2002; Chen et al. 2016). There is a negative relationship between *A* and leaf longevity (Wright and Cannon 2001; He et al. 2002; Xu et al. 2011). Thus, leaf position reflects the leaf growth stages, with the older leaves often located on closer to the ground in a canopy profile (Xu et al. 2011; Acciaresi et al. 2014). Nevertheless, the examination of

photosynthetic and photosystem function parameters, such as A and the maximum efficiency of PSII photochemistry (F_v/F_m) , where F_v is variable fluorescence and F_m is the maximum fluorescence yield), on different leaf positions, is of high importance to determine their relative contributions to photosynthetic capacity in an ecosystem.

In a field, most of the observed daily variations in photosynthesis could be largely attributed to environmental changes, such as radiation and temperature (Willianms and Gorton 1998; Muraoka et al. 2000; Lasslop et al. 2010; Barron-Gafford et al. 2013; Locke and Ort 2015). With measured photosynthetic photon flux density (PPFD) and other weather variables such as water and temperature, established empirical models may be able to estimate NEE and upscale CO_2 exchange from a leaf to the whole canopy (e.g., Hirose 2005; Yuan et al. 2007; Louarn et al. 2015; Terashima et al. 2016). Nevertheless, the changes in NEE derived from EC and their relationships with leaf A observed by leaf cuvette have received little attention. The present study used the EC method simultaneously combined with leaf cuvette measurement. We hypothesised that the daily and seasonal change of NEE pattern using EC over an entire ecosystem can be partly represented by those of A with a gas-exchange system in a leaf cuvette as a proxy, which depends on the change of PPFD and air temperature. Our specific object was to determine whether, and if so how, CO2 exchange rate with a leaf cuvette can represent EC over a rainfed maize ecosystem.

Methods

Site description

The research was conducted at Jinzhou Agricultural Ecosystem Research Station (41°09'N, 120°12'E, about 17 m.a.s.l.), Liaoning Province, in north-eastern China, which is located on the north-eastern maize production belt that accounts for 39 and 43% of China's total maize planting area and yield, respectively. The climate is a temperate monsoon with mild air temperature during the spring and autumn, cool and dry winters and hot and wet summers. The relevant climate variables in this experimental site are shown in Table 1. The field was surrounded by maize plants in all directions, and the entire area was flat. The rainfed maize sows and harvests conventionally in early May and late September, 2004. A composite fertilizer was applied (11.2 g N m⁻², 11.2 g $P_2O_5 \text{ m}^{-2}$ and 11.2 g $K_2O \text{ m}^{-2}$) 3–5 days before sowing. The site was a clay loam and medium type, a typical brown soil with a pH value of 6.3 in 0-40 cm soil layer. The soil's organic matter concentrations, total N, available N, available P_2O_5 , and available K₂O were 12, 0.69 g kg⁻¹, 60.0, 7.2 and 80.4 mg kg⁻¹, respectively. The measurements in situ

 Table 1
 Climate data in the site

 (Jinzhou Meteorological Station at the site)

Long-term (1951–2009)		Growing season during measurement (2004)						
		Months	May	Jun	Jul	Aug	Sep	
Mean annual air temperature (°C)	9.4	Mean monthly temperature	18.2	23.1	24.4	23.7	20.0	
Coldest monthly air temperature(°C)	- 8.2	Coldest daily air tempera- ture	12.3	17.3	19.4	16.7	12.6	
Hottest monthly air temperature (°C)	24.5	Hottest daily air tempera- ture	24.0	29.8	29.1	27.9	24.2	
Mean annual precipitation (mm)	564	Total monthly precipitation	33.4	194.7	214.6	131.0	47.6	

The long-term climate data are average values over the past 58 years (1951-2009) (Liang and Chen 2010)

showed that the row spacing was around 0.60 m with a plant density of 5.30×10^4 plant ha⁻¹.

Eddy covariance measurements

Carbon flux measurements were acquired using EC technique mounted at 3.5 m above the ground, about 1 m higher than the top of the maize plants. The flux system consisted of a three-dimensional sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, Utah, USA) and an open-path CO₂/ H₂O analyser with LI-7500 software (Li-Cor Inc., Lincoln, Nebraska, USA) with a CR500 measurement and control system. All EC data were collected at a 10 Hz sampling frequency. Half-hour CO₂ flux data were rejected if they met the following criteria: (1) the data were from an incomplete half-hour measurement, (2) they were periods during rain events, (3) there were relatively stable atmospheric conditions (u*, friction velocity = $< 0.2 \text{ m s}^{-1}$, see the threshold of 0.25 m s^{-1} set by Verma et al. 2005) and (4) the extreme values were derived from either the three-dimensional wind velocities or the scalars (Aurela et al. 2002; Wang et al. 2008; Li et al. 2009). Around 14-17% of the flux data were eliminated (Li et al. 2009). In the current study, the energy balance closure was considered an independent method to assess EC reliability (Li et al. 2009). Here, we avoided missing data in the measured time. Thus, interpolated values for filling gaps were not used (Wang et al. 2008). CO₂ fluxes monitored with the EC were obtained from a footprint upwind of the tower (covering at least 400 m²), which can calculate the NEE (i.e., CO₂ fluxes per second per unit ground area) collected with EC in this area during the measurement of leaf-gas exchange. The sampling area for the measurements of leaf area and leaf-gas exchange was also located within the EC tower's footprint. We simultaneously measured leaf-gas exchange within 30 min to complete one replicate (3-6 plants) to match the 30-min mean NEE at the same time. We separated the three groups to analyze the relationships of NEE with A at the leaf three positions (top, middle, bottom) at the three stages (silking, milking, and maturing). Each point for the photosynthesis measurement matched the NEE point within a 30-min measurement cycle.

A weather station was installed at about 15 m from the CO_2 flux measurement tower to record weather data. PPFD was measured at a height of 3.0 m above ground level with a Li-190SA quantum sensor (LI-COR, Inc., Lincoln, NE, USA). Surface temperatures were measured at 2.3 m above ground level (4000.4GL infrared temperature transducer, Everest Interscience, Inc., Tucson, USA).

Leaf net photosynthesis rate

Leaf-gas exchange measurements were made using an open gas-exchange system (LI-6400; LI-COR, Inc., Lincoln, NE, USA). The gas-exchange parameters were determined throughout the day at 1-2 h intervals under ambient conditions, and each measurement was taken within 30 min. The leaf temperature (T_{leaf}) was simultaneously measured on the leaf adaxial surface by a thermocouple. The leaf net photosynthetic rates (A) were measured using at least three plants chosen at random in around a 30-m radius of the meteorological tower. Before measurement, the leaves were acclimated in the cuvette for at least 40 s and then matched, under which the open gas measurement system can remain almost stable and obtain the ambient conditions of the field, such as PPFD, T_{leaf}, CO₂ concentration, and relative humidity (RH). Three-six leaves, that is, three-six replicates, were measured at each leaf position: top (1–2 leaves from the top of the plants), middle (ear leaf or the leaves above or below ear leaf) and bottom (relative elderly leaves). We measured every fully expanded leaf from each individual plant from 8:00 a.m.-11:30 a.m. on the three selected sunny days-which represents the three key plant growth stages: silking, milking, and maturing. The middle zone was measured in each leaf, which can represent the leaf's more actively physiological processes (Escobar-Gutiérrez and Combe 2012), and the main leaf's vein was avoided when measurement took place. We kept the measurement time for each plant to within 5 min to minimize the environmental variables such as radiation and temperature. Within a measurement period cycle, the measurement starting leaf was shifted between the top leaf and the most bottom leaf to minimize the environmental variables' effects.

Chlorophyll fluorescence

The measurements of chlorophyll fluorescence were conducted using an integrated fluorescence chamber head (LI-6400–40 leaf chamber fluorometer, LI-COR) with an open gas-exchange system (LI-6400F, LI-COR). The measured plant leaves were the same ones determined for *A*, after a 30-min dark adaptation at the ambient temperature; the minimal fluorescence yield (Fo) was measured using modulated light that was sufficiently low (<0.1 µmol m⁻² s⁻¹), and the maximal fluorescence yield (F_m) was determined with a 0.8 s saturating pulse at 7000 µmol m⁻² s⁻¹ in the darkadapted leaves. The fluorescence parameters were obtained from van Kooten and Snel (1990) formula, as follows:

The maximal efficiency of PSII photochemistry (F_v/F_m) = $(F_m - F_0)/F_m$.

where $F_{\rm o}$ and $F_{\rm m}$ are the minimal and maximal of fluorescence yields, respectively; $F_{\rm v}$ is the relative variable fluorescence.

Estimation for photosynthetic curves of light response

The parameters of the response of photosynthesis to light intensity were estimated by the following quadratic equation (Prioul and Chartier 1977; Long et al. 1993):

$$A = \left(\alpha \times \text{PPFD} + A_{\max} - \left(\left(\alpha \times \text{PPFD} + A_{\max}\right)^2 - 4\alpha \times \text{PPFD} \times \theta \times A_{\max}\right)^{0.5}\right) / (2\theta) - R_{d},$$

where *A* is the net photosynthetic rate (µmol m⁻² s⁻¹), A_{max} is the maximum CO₂ accumulation rate (µmol m⁻² s⁻¹), PPFD is the photosynthetic photon flux density (µmol m⁻² s⁻¹), α is the leaf maximum apparent quantum yield of CO₂ uptake, θ is the convexity of the transit from light-limited to light-saturated photosynthesis and $R_{\rm d}$ is the respiration rate. The parameter bounds were constrained to ensure the nonlinear curve regression estimation: $\alpha < 1$, $\theta < 1$, $R_{\rm d} < 10$, $\theta < 1$, $A_{\rm max} < 50$ (Long et al. 1993).

Here, we assumed NEE_{daytime} as net CO₂ assimilation rate at ecosystem level (the positive values indicate the net CO₂ uptake by the entire ecosystem) in terms of big leaf model (de Pury and Farquhar 1997). Thus, the parameters of the response of NEE_{daytime} to light were estimated accordingly from the following equation (Prioul and Chartier 1977; Long et al. 1993; de Pury and Farquhar 1997):

$$NEE_{daytime} = A = \left(e\alpha * PPFD + NEE_{daytime-max} - \left(\left(e\alpha \times PPFD + NEE_{daytime-max}\right)^{2} - 4 \times e\alpha \times PPFD \times \theta \times NEE_{daytime-max}\right)^{0.5}\right)$$
$$/(2\theta) - ER_{d},$$

where NEE_{daytime} is the net ecosystem exchange rate (µmol m⁻² s⁻¹), NEE_{daytime-max} is the maximum net ecosystem exchange rate (µmol m⁻² s⁻¹), $e\alpha$ is the ecosystem quantum yield and ER_d is the ecosystem respiration rate. The parameter bounds were constrained to ensure the nonlinear curve regression estimation: $e\alpha < 1$, $\theta < 1$, ER_d < 10, $\theta < 1$, NEE_{daytime-max} < 50 (Long et al. 1993).

Leaf area index (LAI)

1

For each plant measured for leaf–gas exchange, every leaf's maximum length and width (cm) were measured. The leaf area was calculated using an empirical equation: leaf area = leaf maximum length × leaf maximum width × 0.75. Total leaf area per plant was summed from every leaf area of the entire plant. LAI was assessed using total leaf area per plant divided by the ground area per plant (Francis et al. 1969). Whole plant leaves were equally divided into three vertical layers, from soil surface to plant top, to examine the LAI vertical distribution. Only green leaves were considered when calculating LAI.

Statistical analyses

All statistical analyses were performed using SPSS 20.0 software (SPSS Inc., Chicago, IL, USA). A two-way test on the effect of leaf positions (i.e., canopy layers) and measured time on these parameters, including leaf A, F_v/F_m , NEE and LAI, was conducted with a general linear model (GLM). We conducted nonlinear regression estimations for the responsecurves of the relationships between A at leaf scale or NEE at ecosystem scale with PPFD at the silking, milking, and maturing growth stages, respectively. The curve estimation method was determined by a sequential quadratic programming with a default maximum iteration—the program can use the iterative method to find the values of the parameters that fit best until the minimum sum of squares is found; the relevant parameters were constrained to a reasonable range to prevent iterative steps that could have led to an overflow issue (Gill et al. 1984). A linear regression of NEE with leaf A and a nonlinear regression of F_v/F_m with the days after sowing (DAS) were also made. Significance is at P < 0.05, otherwise stated.

Results

Relationship of net CO₂ exchange between leaf and ecosystem levels

The net ecosystem CO_2 exchange (NEE) was positively and significantly correlated with leaf *A* in the three leaf positions at the three key growth stages (*P* < 0.05; Fig. 1), except in the middle leaves at the milking stage (*F* = 1.60; *P* = 0.23, Fig. 1f). There were also positive and significant correlations between NEE and canopy *A* based on the leaf area vertical contribution at the three key stages (*P* < 0.05; Fig. 1d, h, 1).

Leaf area index (LAI) change and it distribution

The maize LAI increased gradually from early growth stage and reached a peak value of 4.3 m m⁻² at the middle growth stage, thereafter decreasing until maturity (Fig. 2). There was a maximum contribution to the total LAI in the top layer, followed by the middle and bottom layers, except at the late growth stage where the middle part had the maximum value. Following ANOVA, the effect of date on total LAI was significant (F=142.51, P<0.001). A two-way ANOVA indicated date and layer as the two main factors, and their interaction all had significant effects (P<0.001, see Supporting Information: Table SI1).

Leaf net photosynthetic rate

The diurnal variations in leaf net photosynthetic rates (A) of the top, middle and bottom leaves on the three chosen clear days were based on the determination in leaf cuvettes at the three growth stages (Fig. 3). The A peaked at 13:00 for all three leaf positions with a maximum value of 30.2 µmol $m^{-2} s^{-1}$ for the top leaf at the silking stage (Fig. 3a) and was greater in the top compared to both the middle and bottom leaves. At the milking stage (Fig. 3b), the peak values of 35.4 μ mol m⁻² s⁻¹ occurred at 10:00 a.m. but again peaked at 15:00. There was a lower A in the bottom leaf compared to the other two positions. At the later growth stage (26 September, Fig. 3c), the daily change of A was at a relatively stable level, and there were lower values relative to the early and middle growth stages. In the bottom leaves, A was approximately zero, even a negative value appeared. From the two-way (position and time) or three-way ANOVA (position, time and date), the main factor and the interactive effects were all significant (P < 0.05, Fig. 3a–c and see Supporting Information: Table SI2).

Net ecosystem CO₂ exchange (NEE)

Similar diurnal changes in NEE pattern were observed in the same 3 days, but they were more like the patterns of the diurnal leaf *A* in the top leaves, especially because the maximum values occurred at the same times of the day (Fig. 3a–c). NEE was higher than *A* of all the three layers at silking stage for most of the day, and NEE was higher at 11:00-14:00 around noon during midday at the milking stage. However, at the later growth stage (26 September), NEE was lower than the *A* of the top and middle leaves, but higher than those of the bottom leaves.

Chlorophyll fluorescence

There were quadratic curve patterns of the relationships between the maximum efficiency of PSII photochemistry (F_v/F_m) and days after sowing (DAS), particularly in the bottom leaves (P = 0.035) (Fig. 4). The F_v/F_m significantly decreased in the leaves located on the lower positions at the early and later stages (P < 0.05), whereas there were no significant differences along the three leaf positions during the middle stages. From the two-way ANOVA, the date, position and their interaction have all significant effects [P < 0.01, Table SI3].

Relationships of A and NEE with leaf and air temperature

Based on a linear regression analysis, there were often significant and positive relationships between leaf A and leaf temperature at the three growth stages (P < 0.05), except for the middle position at milking stage [see Supporting Information: Table SI4]. Daytime NEEs were also significantly and positively correlated with air temperature (T_a) at the three key growth stages ($R^2 = 0.94$, P < 0.001; $R^2 = 0.72$, P < 0.001; $R^2 = 0.47$, P = 0.009, respectively; Table SI4), showing a higher association between NEE and T_a during the peak growth periods.

Relationships of A and daytime NEE with PPFD

The maximum net photosynthetic rates (A_{max}) were the highest at the grain-milking stage, with the minimum being at the late grain-filling stage; the leaf photosynthetic quantum yield (α) decreased with plant and grain-filling development (Table 2).

It was indicated that NEE changes mainly depend on PPFD changes. When daytime NEE was regressed against PPFD (Table 2), the coefficients of determination were over 0.6 for the three key growth stages. There was a greater light-saturated rate of the net ecosystem CO_2 exchange (NEE_{daytime-max}) at the most rapid growing periods, with a



Fig. 1 Relationships of net ecosystem exchange rate (NEE, y) with leaf photosynthetic rate (A, x) at the leaf positions (top, **a**, **e**, **i**; middle, **b**, **f**, **j**; bottom, **e**, **g**, **k**; canopy values, **d**, **h**, **l**) at the three stages (Silking, **a**–**d**; milking, **e**–**h**; maturing, **i**–**l**) (n=13). *F* and *P* are given, respectively. Canopy values indicate average value weighted

by faction of leaf area index (LAI) each layer in total LAI. the negative NEE means the CO_2 release from ecosystem (i.e., the respiration rate at ecosystem level); meanwhile negative leaf A indicates the respiration rate at leaf level



Fig. 2 Changes in leaf area index (LAI) of three layers in maize plants. All values are mean \pm SE (n=3–5). The different lowercase letters indicate significant differences between the three layers at the same stage; and the different capital letters on the bars indicate significant differences between the three growth stages (P<0.05). Effects of layer and stage are significant (P<0.05)

maximum value of 48.7 μ mol m⁻² s⁻¹ at the grain-milking stage while the minimum value of 14.7 μ mol m⁻² s⁻¹ was found at the end of the grain-filling stage. The ecosystem quantum yield ($e\alpha$) decreased as the plant grew, with a maximum α of 0.039 at the milking stage and a minimum of 0.013 at the end of the grain-filling stage, indicating that the higher ecosystem quantum yield also occurred at the peak-growth period. The results also showed that a greater NEE_{daytime-max} was closely associated with a higher ecosystem quantum yield.

Discussion

The major aim of this research was to improve the understanding of the dynamics of carbon and water exchange between the atmosphere and biosphere using eddy covariance (EC) measurements (Baldocchi 2003; Zha et al. 2004; Béziat et al. 2009; Barron-Gafford et al. 2013; Sulman et al. 2016). Because EC technology can directly provide a reliable way to monitor net CO_2 exchange of an ecosystem (NEE), it may be asked whether those data using a commercial gas-exchange system in leaf cuvettes are still valid for assessing canopy carbon balance. Our results indicated that the maize ecosystem had a higher daytime maximum NEE and that NEE was closely associated with leaf photosynthetic rate (*A*) during the major plant growth season. Moreover, the present study indicated that NEE and *A*



Fig. 3 Diurnal changes in net ecosystem exchange rate (NEE) and net photosynthetic rate (A) in top, middle and bottom leaves at silking (a), milking (b), and maturing stages (c) (n=3-6). NEE or A are expressed on a m^2 ground or leaf area basis, respectively. F and P values are given for position (P) and time (T) effects and their interaction based on a two-way ANOVA

synchronously changed with daytime and decreased as the plant aged. In addition, decreases in the leaf and ecosystem photosynthetic quantum yield (α) with plant growing and grain-filling were also found.

The daytime maximum NEE was 4.8 μ mol m⁻² s⁻¹ in a Scot pine forest (Zha et al. 2004), and it ranged between 6.0 and 8.0 μ mol m⁻² s⁻¹ in a serpentine grassland in California (Valentini et al. 1995) and a *Stipa krylovii* steppe in northern China (Wang et al. 2008); the value reached up to 19.5 μ mol m⁻² s⁻¹ at the peak growth stage in a Mediterranean annual **Fig. 4** Relationships of maximum efficiency of PSII photochemistry (F_v/F_m , dimensionless) with DAS in top, middle and bottom leaves. DAS, day after sowing; Measured on 26 June (66 DAS), 24 July (103 DAS), 3 August (115 DAS), and 28 September (169 DAS), respectively



Table 2 Comparison of parameters derived from response-curves of the relationships of net leaf/ecosystem CO_2 exchange (A/NEE) with photosynthetic photon flux density (PPFD)

Stages A _{max}		α	Rd	θ	R^2	
Silking	40.26 (29.91)	0.060 (0.031)	1.44 (1.68)	0.270 (1.729)	0.904	
Milking	42.61 (24.19)	0.039 (0.008)	1.00 (1.19)	0.927 (0.231)	0.810	
Maturing	14.70 (13.93)	0.027 (0.024)	0.41 (0.93)	0.088(0.974)	0.944	
Stages	NEE _{daytime-max}	eα	ERd	θ	R^2	
Silking	40.90 (16.63)	0.039 (0.015)	6.13 (4.99)	0.984 (0.112)	0.838	
Milking	48.70 (24.03)	0.032 (0.038)	6.97 (12.34)	0.977 (0.809)	0.599	
Maturing	11.77 (7.89) 0.013 (0.008)		3.76 (1.02) 0.863 (0.558)		0.883	

The values in the parentheses represent the standard error. A_{max} , the maximum net photosynthetic rate (µmol m⁻² s⁻¹); *NEE*_{daytime-max} lightsaturated rate of the net ecosystem CO₂ exchange (µmol m⁻² s⁻¹); $\alpha/e\alpha$ leaf/ecosystem photosynthetic quantum yield; *Rd/ERd* is leaf/ecosystem respiration rate; θ a constant about convexity; R^2 coefficient of determination. Measured at silking (23 Jul), milking (2 Aug) and maturing stages (26 Sep), respectively

grassland (Xu and Baldocchi 2004). However, much higher maximum rates of CO₂ uptake (30–40 μ mol m⁻² s⁻¹) have been reported from a C₄ perennial grassland (Dugas et al. 1999). The daily peak NEE of soybean crops reached up to $34 \text{ CO}_2 \text{ } \mu\text{mol } \text{m}^{-2} \text{ s}^{-1}$ in a rainfed field (Verma et al. 2005); a peak CO₂ uptake of 23–35 CO₂ μ mol m⁻² s⁻¹ also occurred in another soybean field (Wagle et al. 2017). A maximum level of ~45 CO₂ μ mol ground m⁻² s⁻¹ (weighted by LAI) was found for maize plants (Jans et al. 2010), and a report by Vitale et al. (2007) indicated ~ 30 CO₂ μ mol ground m⁻² s⁻¹. These results are comparable to the present results (Table 2; Fig. 3). This may highlight that maize is one of the most productive agricultural staples (Dold et al. 2017). Moreover, NEE and A, as well as other photosynthetic capacity parameters such as leaf and ecosystem quantum yield, always are at their highest during the plant growth peak stage because the plants need more carbon for growth, canopy development and grain-filling (Wang et al. 2015; Zhang et al. 2015), which was confirmed by the current study (Table 2; Fig. 4).

Excess light, often occurring with high air temperatures or water deficits, is a major environmental stress, consequently causing midday depression of photosynthesis (Schulze et al. 1980; Muraoka et al. 2000; Locke and Ort 2015). Midday depression of assimilation and stomatal conductance of water vapour were remarkably deeper in shade leaves compared with sun leaves (Muraoka et al. 2000). It was assumed that precipitation might not have been a major environmental determinant of leaf and canopy CO_2 exchange at our site (Li et al. 2009). Thus, under the present environmental conditions, the higher air temperature and ample precipitation may have favoured maize plant growth and development. Although the light and air temperature were relatively higher in the middle of the day, the midday depression of photosynthesis was not observed, suggesting that the effects of a higher air temperature and light intensity combined with moderate soil water content did not constrain leaf and ecosystem carbon assimilation. In this region, PPFD may be a crucial factor in controlling CO_2 flux in the canopy when no drought occurs (also see Zhang et al. 2015) because it cannot reach the optimum level for photosynthesis in most plant growth periods.

Pattey et al. (1991) reported that the upper and middle parts of the maize canopy similarly contributed 38-44% of canopy assimilation rate around noon, whereas the lower part only contributed its 16%. Our results indicated the top and middle leaves had an almost similar leaf A but a reduction in the bottom leaves was observed around noon, which may link to decreased leaf photosynthetic activity such as PSII photochemistry efficiency (F_v/F_m) and accelerated leaf senescence in the bottom leaves. In addition, plant leaves in the canopy are largely different in terms of their ages, positions and nutrition status, consequently leading to their own photosynthetic potential gradients (Stirling et al. 1994; Tocquin and Périlleux 2004; Chen et al. 2016; Song et al. 2018), especially in direct solar radiation on a sunny day (Urban et al. 2007). Chen et al. (2016) reported that maize leaf A, stomatal conductance, and nitrogen content were higher in the upper leaves. Furthermore, leaf chlorophyll content and the chlorophyll/carotenoid ratio, as well as photosynthetic potentials, decrease as a leaf senesces, particularly at the very late stages of plant development (He et al. 2002; Acciaresi et al. 2014). In the present experiment, the F_v/F_m was greater in the top and middle leaves than in the bottom leaves, indicating a significant decline with severe leaf ageing. It also indicates that plant photosynthetic gradients can occur in a maize canopy's profile because the leaf' ages and the senescence severity differ with the plant's vertical profiles (Xu et al. 2011; Chen et al. 2016).

How to properly assess the photosynthesis for both a leaf and canopy is a key issue when it comes to carbon balance (Stirling et al. 1994; Hollinger et al. 2005; Long et al. 2006; Kim et al. 2006; Barron-Gafford et al. 2013; Ma et al. 2017a, b). Currently, there are available tools such as EC to track changes in the canopy's photochemical activity in a field and to assess complex patterns of photosynthesis within and beyond the canopy (Chen et al. 2016; Pinto et al. 2016). EC technology serves as a scale-appropriate method because it provides ecosystem scientists with a method to assess and compare gas and energy exchange over a whole ecosystem (Baldocchi 2003; Rambal et al. 2004; Li et al. 2009; Lasslop et al. 2010). A main concern about leaf cuvettes is the sampling they require: a unit leaf area is chosen arbitrarily for measurement, even though leaves are not only different according to their ages and positions on the plants, but also because they have their own photosynthetic capacity

gradients (Tocquin and Périlleux 2004). For instance, a decrease in A at leaf-level because of photosynthetic acclimation under elevated CO₂ may not lead to any appreciable decline in photosynthetic capacity at the canopy, indicating the heterogeneity of the two scales under the predicted climatic change (Bagley et al. 2015). The different performances for CO₂ flux change were found at both leaf and ecosystem scales in different vegetation types (Barron-Gafford et al. 2013). However, in the present study, we found that NEE using EC technology was very closely associated with A with leaf cuvette, particularly at the top leaf position, suggesting a measurement with a small leaf chamber may still be more useful and feasible for assessing carbon balance and cycle in an ecosystem. It also indicated that the relationship of NEE by EC with PPFD is comparable to that of A in leaf cuvettes with PPFD in a maize field in southern Italy (Vitale et al. 2007). Liu et al. (2016) reported the close associations of the canopy CO₂ assimilation rate in a canopy chamber with the leaf A with a leaf cuvette in a wheat field. A consistent functional relationship across leaf-canopy-ecosystem scales in the photosynthetic responses to ambient temperatures has been confirmed by a long-term study in an oak-grass savanna (Ma et al. 2017a, b). This point is important for upscaling carbon fixation from a leaf to an ecosystem (Pielke et al. 2007; Cleary et al. 2015; Kölling et al. 2015), which may validate most of the data of the leaf-gas exchange measured in leaf cuvettes. A close relationship between leaf cuvette and chamber CO₂ assimilation rates were found only at the rapid growth stage in a sagebrush steppe ecosystem (Cleary et al. 2015). However, our results indicated the positive and tight correlations between NEE and A at the three stages—silking, milking, and maturing, although the values greatly differ at the different stages (Fig. 1). Nevertheless, whether and how leaf A at leaf level can precisely represent NEE at biosphere level at different plant growth stages and/or during entire period still need to be explored (Cleary et al. 2015; Chen et al. 2016). Nevertheless, the current finding indicated that the CO₂ exchange at a leaf level is analogous to field scale CO₂ flux in a singlecrop planting agricultural system at different stages, again highlighting there is a close relationship between leaf and ecosystem scales.

Carbon exchanges for leaves and ecosystems are crucial processes and important components in carbon balance and cycle (Stirling et al. 1994; Long et al. 2006; Barron-Gafford et al. 2013). The present findings concerning the close relationship of the carbon fluxes between the leaf and ecosystem scales during major plant growth could provide a credible insight into how to feasibly and accurately assess the carbon dynamics and cycles between leaf, canopy, and ecosystem scales. However, other components of the gas exchanges, such as plant stem and soil respiration, which are also important carbon exchange processes for assessing carbon cycle and budget (Goulden et al. 1996; Han et al. 2007; Cleary et al. 2015; Martínez-García et al. 2017; Malhi et al. 2017), were not considered in the current study.

Indeed, CO₂ exchange processes such as photosynthesis may not accurately predict plant dry matter accumulation yield. The relationships between photosynthesis and crop yield have been reported widely (e.g., Buttery et al. 1981; Gifford and Evans 1981; Zelitch 1982; Fischer et al. 1998a, b). However, the results are still not consistent: there are the positive, neutral, even negative relationships, depending on species/cultivars, growth stages, and environmental conditions (Buttery et al. 1981; Gifford and Evans 1981; Ashraf and Harris 2013; Yamori et al. 2016). Under environmental stresses like drought, the different relationships of growth or yield with photosynthetic performs were also found (Ashraf and Harris 2013): the positive in wheat (e.g., Fischer et al. 1998a, b) and maize (Ashraf et al. 2007), the neutral in wheat (Hura et al. 2006), and the negative in cotton (Levi et al. 2009). As reported, for instance, high photosynthetic rate did not lead to increases in both plant biomass and yield due to the sink limitation and the unmatched changes in the regulatory networks of metabolism determining metabolite levels to contribute to the regulation of biomass production (Sulpice et al. 2009; Rossi et al. 2015; de Oliveira Silva et al. 2018). Thus, enhancing photosynthetic capacity should be with synchronous improvement of the regulatory networks of metabolism related to biomass production.

In the present study, we found the positive correlations between NEE at ecosystem and leaf A throughout the day during rapid plant growth periods (Fig. 1). The NEE may indicate the net carbon accumulation rate at ecosystem in maize field, which may closely link to plant growth. Thus, the results may imply that the approaches for the enhanced A at leaf level may also promote NEE, and thus plant biomass (Long et al. 2006; Zhu et al. 2010; de Oliveira Silva et al. 2018). Moreover, the biotechnological approaches can be implemented to improve both photosynthesis and growth. For instance, the overexpression of the enzymes targeted to chloroplast development such as the cyanobacterial fructose-1,6-/sedoheptulose-1, 7-bisphosphatase can markedly increase the initial activity Rubisco, and hence enhancing both photosynthesis and growth (Miyagawa et al. 2001). The overexpression of the RieskeFeS protein for increasing electron transport rate also led to increases in Arabidopsis plant biomass and seeds (Simkin et al. 2018). The overexpression of C_4 -cycle enzymes in transgenic C_3 plant may improve C₃-photosynthesis and growth (Häusler et al. 2002); and the inhibited photorespiration via transferring of the *E. coli* glycolate catabolic pathway to chloroplasts has increased A. thaliana both photosynthesis and plant biomass (Kebeish et al. 2007; Peterhansel et al. 2013). It has been expected that introducing the CO₂ concentrating mechanism (CCM) from cyanobacteria would increase crop yield (Lin et al. 2014). These transplastomic tobacco lines with the improved photosynthetic metabolism has been obtained thought knocking out the native tobacco gene encoding the large subunit of Rubisco by inserting the large and small subunit genes of the Se7942 enzyme from the cyanobacterium Synechococcus elongatus PCC7942 (Lin et al. 2014). As anticipated, the synthetic CCMs in plant to markedly enhance both photosynthesis and growth may be established with artificial protein organelles such as the engineered encapsulin-based CO2-fixing organelles (Giessen and Silver 2017). Plant installed a complete cyanobacterial CCM with the low ATP cost of the cyanobacterial CCM and high enzymatic capacity per unit could bring a greater advantage under environmental presses such as climatic change (Yin and Struik 2017). Actually, the high plant biomass can be obtained by increasing photosynthetic assimilation and lessening respiratory losses over the growing season (Long et al. 2006; Reynolds et al. 2011; De Souza et al. 2017). Additionally, with genomic analyses, the identification of candidate genes regulating photosynthesis, primary metabolism and plant growth would provide new avenues for crop improvement (de Oliveira Silva et al. 2018). In terms of eco-physiological processes, balancing leaf A and stomatal behaviour to elevate water use efficiency (Xu and Zhou 2008; Xu et al. 2016) and shrinking the rapid decline in the photosynthetic capacity due to leaf senescence during grain-filling might be also useful to obtain higher yield (Dong et al. 1997; Xu et al. 2008, 2011; Song et al. 2018). Meanwhile optimizing canopy architecture in field to increase its light/nitrogen use efficiency would be helpful to increase plant production (Long et al. 2006; Zhang et al. 2015; Yuan et al. 2007; Hikosaka et al. 2016). Finally, the relationship of source and sink could be well regulated to improve harvest index and grain yield (Seebauer et al. 2010; Yang and Zhang 2010). In the present results, there were parallel increases in leaf $A_{\text{sat}}, F_{\text{v}}/F_{\text{m}}$, and NEE at peak growth stage (Table 2; Figs. 3, 4), implicated that simultaneously enhancing leaf photosynthetic rate, electron transport rate, net carbon assimilation at whole ecosystem may be an important avenue to improve crop productivity. A roadmap for the improvement of relationship between photosynthesis and crop production at multiple scales is proposed in Fig. 5.

Conclusion

EC technology can directly provide a reliable way to test whether those data from leaf cuvettes are still valid for assessing canopy carbon balance. The present results indicated that NEE and A synchronically changed throughout the day during rapid plant growth periods. The leaf A performed similar daytime change patterns in the top, middle and bottom leaves. A significant decline in the



Fig. 5 A diagrammatic representation of the improvement of relationship between photosynthesis and crop production at multiple scales. Note: at molecular level, the photosynthesis could be improved by the overexpression of the proteins targeted to photosynthetic processes and its organelles (1, Miyagawa et al. 2001; Simkin et al. 2018), by introducing the CO₂ concentrating mechanism (CCM) (2, Lin et al. 2014), by knockdown of photorespiration via transferring the *E. coli* glycolate catabolic pathway (3, Kebeish et al. 2007; Peterhansel et al. 2013), and by identification of candidate genes regulating photosynthesis and the relevant metabolisms (4, de Oliveira Silva et al. 2018). At leaf level, the photosynthesis-improved paths might be to shrink rapid decline in photosynthetic capacity due to leaf senescence (5,

maximum photochemistry efficiency of PSII was found as leaf severely ageing. A tight association was observed between the greater maximum NEE and ecosystem quantum yield. Further, we found that NEE was positively and significantly correlated with the leaf *A* averaged based on the leaf area vertical distribution patterns. Our results may provide better understanding of the behaviours of carbon exchanges between the atmosphere and biosphere at different scale levels using both leaf cuvette and EC measurements. Nevertheless, in these major terrestrial ecosystems, how to properly assess and integrate various carbon balance components at different scales in the field needs to be addressed further; this should be done based on more appropriate and integrative measurement technologies and more feasible modelling methods (Bloom et al. 2016;

Dong et al. 1997; Xu et al. 2008, 2011; Song et al. 2018), to balance leaf A and stomatal behavior to elevate water use efficiency (WUE) (6, Xu and Zhou 2008; Xu et al. 2016). At canopy level, optimizing canopy architecture in field to increase its light/nitrogen use efficiency is helpful (7, Long et al. 2006; Zhang et al. 2015; Yuan et al. 2007; Hikosaka et al. 2016). Relationship of source and sink could be well regulated to promote harvest index and grain yield (8, Seebauer et al. 2010; Yang and Zhang 2010). The parallel increases in both net leaf photosynthetic rate (A) and net ecosystem CO₂ exchange rate (NEE) are also suggested to improve crop production (9, Table 2; Figs. 3, 4)

Chen et al. 2016; Malhi et al. 2017). It also implicated that simultaneously enhancing leaf photosynthetic rate, electron transport rate, net carbon assimilation at whole ecosystem level may be important to increase crop productivity, which needs further study.

Author contribution statement ZX and GZ conceived and designed the study. ZX, GH, and YL performed the experiment. ZX and GZ wrote the manuscript. All authors read and approved the final manuscript.

Acknowledgements We are greatly indebted to Shi Chunqiao, Yang Yang, Liu Jingli, Wang Yunlong for their work during the experiment.

Funding National Natural Science Foundation of China (41330531), and China Special Fund for Meteorological Research in the Public Interest (GYHY201506001-3; GYHY201506019).

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

References

- Acciaresi HA, Tambussi EA, Antonietta M, Zuluaga MS, Andrade FH, Guiamét JJ (2014) Carbon assimilation, leaf area dynamics, and grain yield in contemporary earlier-and later-senescing maize hybrids. Eur J Agron 59:29–38
- Anderson RG, Alfieri JG, Tirado-Corbalá R, Gartung J, McKee LG, Prueger JH et al (2017) Assessing FAO-56 dual crop coefficients using eddy covariance flux partitioning. Agric Water Manag 179:92–102
- Ashraf A, Harris PJC (2013) Photosynthesis under stressful environments. An overview. Photosynthetica 51:163–190
- Ashraf M, Nawazish S, Athar HR (2007) Are chlorophyll fluorescence and photosynthetic capacity potential physiological determinants of drought tolerance in maize (*Zea mays L.*). Pak J Bot 39:1123–1131
- Aurela M, Laurila T, Tuovinen JP (2002) Annual CO₂ balance of a subarctic fen in northern Europe: importance of the wintertime efflux. J Geophys Res Atmos 107(D21). https://doi. org/10.1029/2002JD002055
- Bagley J, Rosenthal DM, Ruiz-Vera UM, Siebers MH, Kumar P, Ort DR, Bernacchi CJ (2015) The influence of photosynthetic acclimation to rising CO_2 and warmer temperatures on leaf and canopy photosynthesis models. Global Biogeochem Cycles 29:194–206
- Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Glob Change Biol 9:479–492
- Barron-Gafford GA, Scott RL, Jenerette GD, Hamerlynck EP, Huxman TE (2013) Landscape and environmental controls over leaf and ecosystem carbon dioxide fluxes under woody plant expansion. J Ecol 101:1471–1483
- Béziat P, Ceschia E, Dedieu G (2009) Carbon balance of a three crop succession over two cropland sites in South West France. Agric For Meteorol 149:1628–1645
- Bloom AA, Exbrayat JF, van der Velde IR, Feng L, Williams M (2016) The decadal state of the terrestrial carbon cycle: global retrievals of terrestrial carbon allocation, pools, and residence times. PNAS 113:1285–1290
- Buttery BR, Buzzell RI, Findlay WI (1981) Relationships among photosynthetic rate, bean yield and other characters in field-grown cultivars of soybean. Can J Plant Sci 61:190–197
- Chen Y, Wu D, Mu X, Xiao C, Chen F, Yuan L, Mi G (2016) Vertical distribution of photosynthetic nitrogen use efficiency and its response to nitrogen in field-grown maize. Crop Sci 56:397–407
- Cleary MB, Naithani KJ, Ewers BE, Pendall E (2015) Upscaling CO_2 fluxes using leaf, soil and chamber measurements across successional growth stages in a sagebrush steppe ecosystem. J Arid Environ 121:43–51
- de Pury DGG, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ 20:537–557

- De Souza AP, Massenburg LN, Jaiswal D, Cheng S, Shekar R, Long SP (2017) Rooting for cassava: insights into photosynthesis and associated physiology as a route to improve yield potential. New Phytol 213:50–65
- de Oliveira Silva MF, Lichtenstein G, Alseekh S, Rosado-Souza L, Conte M et al (2018) The genetic architecture of photosynthesis and plant growth-related traits in tomato. Plant Cell Environ 41:327–341
- Denmeal OT, Dumin FX, Wong SC (1993) Measuring water use efficiency of Eucalpyt tree with chambers and micrometeorological techniques. J Hydrol 150:649–664
- Dold C, Büyükcangaz H, Rondinelli W, Prueger JH, Sauer TJ, Hatfield JL (2017) Long-term carbon uptake of agro-ecosystems in the Midwest. Agric For Meteorol 232:128–140
- Dong ST, Gao RQ, Hu CH, Wang QY, Wang KJ (1997) Study of canopy photosynthesis property and high yield potential after anthesis in maize. Acta Agron Sin 23:318–325
- Dore S, Hymus GJ, Johnson DP, Hinkle CR, Valentini R, Drake BG (2003) Cross validation of open-top chamber and eddy covariance measurements of ecosystem CO₂ exchange in a Florida scrub-oak ecosystem. Glob Change Biol 9:84–95
- Dugas WA, Heuer ML, Mayeux HS (1999) Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum. Agric For Meteorol 93:121–139
- Escobar-Gutiérrez AJ, Combe L (2012) Senescence in field-grown maize: from flowering to harvest. Field Crops Res 134:47–58
- Field CB, Berry JA, Mooney HA (1982) A portable system for measuring carbon dioxide and water vapor exchange of leaves. Plant Cell Environ 5:179–186
- Fischer RA, Rees D, Sayre KD et al (1998a) Wheat yield progress is associated with higher stomatal conductance, higher photosynthetic rate and cooler canopies. Crop Sci 38:1467–1475
- Fischer RA, Rees D, Sayre KD, Lu ZM, Condon AG, Saavedra AL (1998b) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. Crop Sci 38:1467–1475
- Francis CA, Rutger JN, Palmer AFE (1969) A rapid method for plant leaf area estimation in maize (*Zea mays* L.). Crop Sci 9:537–539
- Giessen TW, Silver PA (2017) Engineering carbon fixation with artificial protein organelles. Curr Opin Biotechnol 46:42–50
- Gifford RM, Evans LT (1981) Photosynthesis, carbon partitioning, and yield. Ann Rev Plant Physiol 32:485–509
- Gill PE, Murray WM, Saunders MA, Wright MH (1984) Procedures for optimization problems with a mixture of bounds and general linear constraints. ACM Trans Math Softw 10:282–296
- Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC (1996) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Glob Change Biol 2:169–182
- Han G, Zhou G, Xu Z, Yang Y, Liu J, Shi K (2007) Biotic and abiotic factors controlling the spatial and temporal variation of soil respiration in an agricultural ecosystem. Soil Biol Biochem 39:418–425
- Häusler RE, Hirsch HJ, Kreuzaler F, Peterhänsel C (2002) Overexpression of C₄-cycle enzymes in transgenic C₃ plants: a biotechnological approach to improve C₃-hotosynthesis. J Exp Bot 53:591-607
- He P, Osaki M, Takebe M, Shinano T (2002) Changes of photosynthetic characteristics in relation to leaf senescence in two maize hybrids with different senescent appearance. Photosynthetica 40:547–552
- Hikosaka K, Anten NP, Borjigidai A, Kamiyama C, Sakai H, Hasegawa T et al (2016) A meta-analysis of leaf nitrogen distribution within plant canopies. Ann Bot 118:239–247

- Hirose T (2005) Development of the Monsi–Saeki theory on canopy structure and function. Ann Bot 95:483–494
- Hollinger SE, Bernacchi CJ, Meyers TP (2005) Carbon budget of mature no-till ecosystem in North Central region of the United States. Agric For Meteorol 130:59–69
- Hura T, Grzesiak S, Hura K et al (2006) Differences in the physiological state between triticale and maize plants during drought stress and followed rehydration expressed by the leaf gas exchange and spectrofluorimetric methods. Acta Physiol Plant 28:433–443
- Jans WW, Jacobs CM, Kruijt B, Elbers A, Barendse S, Moors EJ (2010) Carbon exchange of a maize (*Zea mays* L.) crop: Influence of phenology. Agric Ecosyst Environ 139:316–324
- Jiang D, Cao WX, Dai TB, Jing Q (2004) Diurnal changes in activities of related enzymes to starch synthesis in grains of winter wheat. Acta Bot Sin 46:51–57
- Kebeish R, Niessen M, Thiruveedhi K, Bari R, Hirsch HJ, Rosenkranz R et al (2007) Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. Nat Biotechnol 25:593–599
- Kim S-H, Sicher RC, Bae H, Gitz DC, Baker JT, Timlin DJ, Reddy VR (2006) Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription profiles of maize in response to CO₂ enrichment. Glob Change Biol 12:588–600
- Kölling K, George GM, Künzli R, Flütsch P, Zeeman SC (2015) A whole-plant chamber system for parallel gas exchange measurements of *Arabidopsis* and other herbaceous species. Plant Methods 11:48
- Lake JA (2004) Gas exchange: new challenges with *Arabidopsis*. New Phytol 162:1–4
- Lasslop G, Reichstein M, Papale D, Richardson AD, Arneth A, Barr A et al (2010) Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. Glob Change Biol 16:187–208
- Law BE, Kelliher FM, Baldocchi DD, Anthoni PM, Irvine J, Moore D, Van Tuyl S (2001) Spatial and temporal variation in respiration in a young Ponderosa pine forest during a summer drought. Agric For Meteorol 110:27–43
- Levi A, Ovnat L, Paterson AH, Saranga Y (2009) Photosynthesis of cotton near-isogenic lines introgressed with QTLs for productivity and drought related traits. Plant Sci 177:88–96
- Li Y, Zhou L, Xu Z, Zhou G (2009) Comparison of water vapour, heat and energy exchanges over agricultural and wetland ecosystems. Hydrol Process 23:2069–2080
- Liang T, Chen M (2010) Analysis of characteristics of climate change from 1951 to 2009 at Jinzhou city. Meteorol Environ Res 1:53–56
- Lin MT, Occhialini A, Parry MAJ, Hanson MR, Andralojc PJ (2014) A faster Rubisco with potential to increase photosynthesis in crops. Nature 513:547–550
- Liu T, Wang Z, Cai T (2016) Canopy apparent photosynthetic characteristics and yield of two spike-type wheat cultivars in response to row spacing under high plant density. PLoS One 11:e0148582
- Lizaso JI, Batchelor WD, Boote KJ, Westgate ME, Rochette P, Moreno-Sotomayor A (2005) Evaluating a leaf-level canopy assimilation model linked to CERES-Maize. Agron J 97:734–740
- Locke AM, Ort DR (2015) Diurnal depression in leaf hydraulic conductance at ambient and elevated [CO₂] reveals anisohydric water management in field-grown soybean and possible involvement of aquaporins. Environ Exp Bot 116:39–46
- Long SP, Bernacchi CJ (2003) Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. J Exp Bot 54:2393–2401
- Long SP, Bake NR, Raines CA (1993) Analysing the responses of photosynthetic CO₂ assimilation to long-term elevation of atmospheric CO₂ concentration. Vegetatio 104/105:33–45
- Long SP, Zhu XG, Naidu SL, Ort DR (2006) Can improvement in photosynthesis increase crop yield? Plant Cell Environ 29:315–330

- Louarn G, Frak E, Zaka S, Prieto J, Lebon E (2015) An empirical model that uses light attenuation and plant nitrogen status to predict within-canopy nitrogen distribution and upscale photosynthesis from leaf to whole canopy. AoB Plants 7:plv116. https ://doi.org/10.1093/aobpla/plv116
- Ma S, Osuna JL, Verfaillie J, Baldocchi DD (2017a) Photosynthetic responses to temperature across leaf–canopy–ecosystem scales: a 15-year study in a Californian oak-grass savanna. Photosynth Res 132:277–291
- Ma SY, Osuna JL, Verfaillie J, Baldocchi DD (2017b) Photosynthetic responses to temperature across leaf–canopy–ecosystem scales: a 15-year study in a Californian oak-grass savanna. Photosynth Res 132:277–291
- Malhi Y, Girardin CA, Goldsmith GR, Doughty CE, Salinas N, Metcalfe DB et al (2017) The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. New Phytol 214:1019–1032
- Martínez-García E, Dadi T, Rubio E, García-Morote FA, Andrés-Abellán M, López-Serrano FR (2017) Aboveground autotrophic respiration in a Spanish black pine forest: Comparison of scaling methods to improve component partitioning. Sci Total Environ 580:1505–1517
- Miyagawa Y, Tamoi M, Shigeoka S (2001) Overexpression of a cyanobacterial fructose-1, 6-/sedoheptulose-1, 7-bisphosphatase in tobacco enhances photosynthesis and growth. Nat Biotechnol 19:965–969
- Moncrieff JB, Malhi Y, Leuning R (1996) The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. Glob Change Biol 2:231–240
- Muraoka H, Tang Y, Terashima I, Koizumi H, Washitani I (2000) Contribution of diffusional limitation, photoinhibition and photorespiration to middy depression of photosynthesis in Arisaema heterophyllum in natural high light. Plant Cell Environ 23:235–250
- Pattey E, Rochette P, Desjardins RL, Dube PA (1991) Estimation of the net CO₂ assimilation rate of a maize (*Zea Mays* L.) canopy from leaf chamber measurements. Agric For Meteorol 55:37–57
- Peterhansel C, Blume C, Offermann S (2013) Photorespiratory bypasses: how can they work? J Exp Bot 64:709–715
- Pielke SR, Adegoke RA, Chase JO, Marshall TN, Matsui CH, Niyogi T D (2007) A new paradigm for assessing the role of agriculture in the climate system and in climate change. Agric For Meteorol 142:234–254
- Pinto F, Damm A, Schickling A, Panigada C, Cogliati S, Müller-Linow M et al (2016) Sun-induced chlorophyll fluorescence from highresolution imaging spectroscopy data to quantify spatio-temporal patterns of photosynthetic function in crop canopies. Plant Cell Environment 39:1500–1512
- Prioul JL, Chartier P (1977) Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. Ann Bot 41:789–800
- Rambal S, Joffre R, Ourcival J-M, Cavender-Bares J, Rocheteau A (2004) The growth respiration component in eddy CO₂ flux from a *Quercus ilex* Mediterranean forest. Glob Change Biol 10:1460–1469
- Reynolds M, Bonnett D, Chapman SC, Furbank RT, Manes Y, Mather DE, Parry MA (2011) Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. J Exp Bot 62:439–452
- Rossi M, Bermudez L, Carrari F (2015) Crop yield: challenges from a metabolic perspective. Curr Opin Plant Biol 25:79–89
- Ruiz-Vera UM, Siebers MH, Drag DW, Ort DR, Bernacchi CJ (2015) Canopy warming caused photosynthetic acclimation and reduced seed yield in maize grown at ambient and elevated [CO₂]. Glob Change Biol 21:4237–4249

- Schmidt M, Reichenau TG, Fiener P, Schneider K (2012) The carbon budget of a winter wheat field: An eddy covariance analysis of seasonal and inter-annual variability. Agric For Meteorol 165:114–126
- Schulze E-D, Lange OL, Evenari M, Kappen L, Buschbom U (1980) Long-term effects of drought on wild and cultivated plants in the Negev desert. II. Diurnal patterns of net photosynthesis and daily carbon gain. Oecologia 45:19–25
- Seebauer JR, Singletary GW, Krumpelman P, Ruffo ML, Below FE (2010) Relationship of source and sink in determining kernel composition of maize. J Exp Bot 61:511–519
- Simkin AJ, McAusland L, Lawson T, Raines CA (2018) Over-expression of the RieskeFeS protein increases electron transport rates and biomass yield. Plant Physiol https://doi.org/10.1104/ pp.17.00622
- Song H, Li YB, Zhou L, Xu ZZ, Zhou GS (2018) Maize leaf functional responses to drought episode and rewatering. Agric For Meteorol 249:57–70
- Speckman HN, Frank JM, Bradford JB, Miles BL, Massman WJ, Parton WJ, Ryan MG (2015) Forest ecosystem respiration estimated from eddy covariance and chamber measurements under high turbulence and substantial tree mortality from bark beetles. Glob Change Biol 21:708–721
- Stirling CM, Aguilera C, Baker NR, Long SP (1994) Changes in the photosynthetic light response curve during leaf development of field grown maize with implications for modelling canopy photosynthesis. Photosynth Res 42:217–225
- Sulman BN, Roman DT, Scanlon TM, Wang L, Novick KA (2016) Comparing methods for partitioning a decade of carbon dioxide and water vapor fluxes in a temperate forest. Agric For Meteorol 226:229–245
- Sulpice R, Pyl ET, Ishihara H, Trenkamp S, Steinfath M, Witucka-Wall H et al (2009) Starch as a major integrator in the regulation of plant growth. Proc Natl Acad Sci USA 106:10348–10353
- Terashima I, Tang Y, Muraoka H (2016) Spatio-temporal variations in photosynthesis. J Plant Res 129:295–298
- Tocquin P, Périlleux C (2004) Design of a versatile device for measuring whole plant gas exchanges in *Arabidopsis thaliana*. New Phytol 162:223–229
- Urban O, Janouš D, Acosta M, Czerný R, Markvá I, Navrátil M, Pavelka M, Pokorný R, Šprtová M, Zhang R, Špunda V, Grace J (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. Glob Change Biol 13:157–168
- Valentini R, Gamon JA, Field CB (1995) Ecosystem gas exchange in a California grassland: seasonal patterns and implications for scaling. Ecology 76:1940–1952
- van Kooten O, Snel JFH (1990) The use chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth Res 25:147–150
- Verma SB, Dobermann A, Cassman KG, Walters DT, Knops JM, Arkebauer TJ et al (2005) Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. Agric For Meteorol 131:77–96
- Vitale L, Di Tommasi P, Arena C, Fierro A, Virzo De Santo A, Magliulo V (2007) Effects of water stress on gas exchange of field grown Zea mays L. in Southern Italy: an analysis at canopy and leaf level. Acta Physiol Plant 29:317–326
- Vitale L, Di Tommasi P, D'Urso G, Magliulo V (2016) The response of ecosystem carbon fluxes to LAI and environmental drivers in a maize crop grown in two contrasting seasons. Int J Biometeorol 60:411–420
- Wagle P, Gowda PH, Anapalli SS, Reddy KN, Northup BK (2017) Growing season variability in carbon dioxide exchange of irrigated and rainfed soybean in the southern United States. Sci Total Environ 593:263–273

- Waldo S, Chi J, Pressley SN, O'Keeffe P, Pan WL, Brooks ES et al (2016) Assessing carbon dynamics at high and low rainfall agricultural sites in the inland Pacific Northwest US using the eddy covariance method. Agric For Meteorol 218:25–36
- Wang Y, Zhou G, Wang Y (2008) Environmental effects on net ecosystem CO₂ exchange at half-hour and month scales over *Stipa krylovii* steppe in northern China. Agric For Meteorol 148:714–722
- Wang Y, Hu C, Dong W, Li X, Zhang Y, Qin S, Oenema O (2015) Carbon budget of a winter-wheat and summer-maize rotation cropland in the North China Plain. Agric Ecosyst Environ 206:33–45
- Willianms WE, Gorton HL (1998) Circadian rhythms have insignificant effects on plant gas exchange under field conditions. Physiol Plant 103:247–256
- Wilson KB, Baldocchi DD, Hanson PJ (2001) Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest. Plant Cell Environ 24:571–583
- Wilson K, Goldstein A, Falge E, Aubinet M, Baldocchi D, Berbigier P et al (2002) Energy balance closure at FLUXNET sites. Agric For Meteorol 113:223–243
- Wright IJ, Cannon K (2001) Relationship between leaf lifespan and structural defenses in a low nutrient, sclerophyll flora. Funct Ecol 15:351–359
- Xu L, Baldocchi DD (2004) Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agric For Meteorol 123:79–96
- Xu ZZ, Zhou GS (2008) Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. J Exp Bot 59:3317–3325
- Xu ZZ, Zhou GS, Wang YL, Han GX, Li YJ (2008) Changes in chlorophyll fluorescence in maize plants with imposed rapid dehydration at different leaf ages. J Plant Growth Regul 27:83–92
- Xu ZZ, Zhou GS, Han GX, Li YJ (2011) Photosynthetic potential and its association with lipid peroxidation in response to high temperature at different leaf ages in maize. J Plant Growth Regul 30:41–50
- Xu ZZ, Jiang YL, Jia BR, Zhou GS (2016) Elevated-CO₂ response of stomata and its dependence on environmental factors. Front Plant Sci 7:657. https://doi.org/10.3389/fpls.2016.00657
- Yamori W, Kondo E, Sugiura D, Terashima I, Suzuki Y, Makino A (2016) Enhanced leaf photosynthesis as a target to increase grain yield: insights from transgenic rice lines with variable Rieske FeS protein content in the cytochrome b6/f complex. Plant Cell Environ 39:80–87
- Yang JC, Zhang JH (2010) Crop management techniques to enhance harvest index in rice. J Exp Bot 61:3177–3189
- Yin X, Struik PC (2017) Can increased leaf photosynthesis be converted into higher crop mass production? A simulation study for rice using the crop model GECROS. J Exp Bot 68:2345–2360
- Yuan W, Liu S, Zhou G, Zhou G, Tieszen LL, Baldocchi D et al (2007) Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. Agric For Meteorol 143:189–207
- Zelitch I (1982) The close relationship between net photosynthesis and crop yield. Bioscience 32:796–802
- Zha TS, Kellomäki S, Wang KY, Rouvinen I (2004) Carbon sequestration and ecosystem respiration for 4 years in a Scot pine forest. Glob Change Biol 10:1492–1503
- Zhang F, Zhou GS (2017) Deriving a light use efficiency estimation algorithm using in situ hyperspectral and eddy covariance measurements for a maize canopy in Northeast China. Ecol Evol 7:4735–4744
- Zhang L, Sun R, Xu Z, Qiao C, Jiang G (2015) Diurnal and seasonal variations in carbon dioxide exchange in ecosystems in the Zhangye oasis area, Northwest China. PLoS One 10:e0120660
- Zhu XG, Long SP, Ort DR (2010) Improving photosynthetic efficiency for greater yield. Annu Rev Plant Biol 61:235–261