Paddy and Water Environment (2020) 18:623–636
https://doi.org/10.1007/s10333-020-00806-7

ARTICLE

Partitioning of eddy covariance-measured net ecosystem exchange of CO_2 in tropical lowland paddy

Sumanta Chatterjee[1,2] · Chinmaya Kumar Swain[2] · Amaresh Kumar Nayak[2] · Dibyendu Chatterjee[2] · Pratap Bhattacharyya[2] · Smruthi Sagarika Mahapatra[2,3] · Manish Debnath[2] · Rahul Tripathi[2] · Prabhat Kumar Guru[2] · Biswaranjan Dhal[2]

Received: 7 September 2019 / Revised: 27 February 2020 / Accepted: 17 April 2020 / Published online: 6 May 2020

Abstract

Net ecosystem exchange of CO_2 (NEE) measurement was carried out in tropical lowland paddy at ICAR-National Rice Research Institute, Cuttack, Odisha, India, in 2015 using eddy covariance technique with the objective to assess the variation of NEE of CO_2 in lowland paddy and to find out the most suitable model for better partitioning of net ecosystem exchange of CO_2 in tropical lowland paddy. Paddy is grown twice (dry and wet season) a year in this region in the lowland, and the field is kept fallow during the remainder of the year. Two different flux partitioning models (FPMs)—the rectangular hyperbola (RH) and the Q10, were evaluated to assess NEE of CO_2, and its partitioning components—gross primary production (GPP) and ecosystem respiration (RE), and the resulting flux estimates were compared. The RH method assessed the effects of photosynthetically active radiation on the NEE, whereas the Q10 method utilized the relationship between ecosystem respiration and temperature in lowland paddy. The average NEE during the dry season and wet season was − 1.62 and − 1.83 g C m^{-2} d^{-1}, respectively, whereas it varied from − 5.71 to 2.29 g C m^{-2} d^{-1} during the observation period covering both the cropping seasons and the fallow period. The mean difference between modeled GPP and RE from two FPMs was found significant in both the seasons. The maximum correlation for GPP estimation was found between two FPMs at the panicle initiation stage during both the dry season ($R^2 = 0.767$) and wet season ($R^2 = 0.321$). It was evident from the study that the Q10 method reliably produced the most realistic carbon flux estimates over the RH method, for the lowland paddy. The Q10 model which used nighttime flux and temperature data to estimate RE produced estimates that had lower prediction error (RMSE) as compared to the RH model. It can be concluded that in lowland paddy, the Q10 predicted better estimates of RE and GPP values than the RH method, suggesting that the Q10 model can be used for partitioning of NEE in tropical lowland paddy.

Keywords Eddy covariance · Lowland paddy · Net ecosystem exchange · Flux partitioning · Ecosystem respiration · Gross primary production

✉ Amaresh Kumar Nayak
aknayak20@yahoo.com

Sumanta Chatterjee
schatterje22@wisc.edu

Chinmaya Kumar Swain
chinu.swain@gmail.com

Dibyendu Chatterjee
dibyenducha@gmail.com

Pratap Bhattacharyya
pratap162001@gmail.com

Smruthi Sagarika Mahapatra
sagarika.s22@gmail.com

Manish Debnath
debnathmanish55@gmail.com

Rahul Tripathi
rahulcrri@gmail.com

Prabhat Kumar Guru
prabhatkumarguru@gmail.com

Biswaranjan Dhal
biswadhal@gmail.com

[1] Department of Soil Science, University of Wisconsin-Madison, 1525 Observatory Drive, Madison, WI 53706, USA

[2] Division of Crop Production, ICAR-National Rice Research Institute, Cuttack, Odisha 753006, India

[3] Department of Agricultural Microbiology, Indira Gandhi Krishi Vishwavidyalaya, Raipur, Chhattisgarh 492012, India

Introduction

Net ecosystem exchange (NEE) measurements of carbon dioxide (CO_2) are now playing a crucial role in the progress of climate change science through multiple scales with an increasing number of eddy covariance towers worldwide (Baldocchi 2008). Eddy covariance (EC) measurements of NEE are widely used globally to quantify the role of vegetation in controlling the scale and variability of the global carbon sink (Sarmiento and Wofsy, 1999; Baldocchi 2008).

Globally paddy is cultivated in about 160 M-ha, divulging a vital role in carbon cycle (Pathak et al. 2018; Chatterjee et al. 2019a, b). Paddy is grown in about 43.95 M-ha in India with an annual production of 106.54 Mt (GOI 2014). The NEE of CO_2 of lowland paddy, a semiaquatic crop, can be measured over a large area using the EC technique (Chapin et al. 2006; Swain et al. 2018a, b). For assessment of the processes which control NEE in lowland paddy, EC data mostly depend on models that partition NEE into two components—gross primary production (GPP) and ecosystem respiration (RE). For understanding the partitioning of NEE with more accuracy to interpret its controls, this is imperative as the global budget for GPP is highly uncertain with the values ranging from 110 to 150 Pg-C yr^{-1} (Beer et al. 2010; Jung et al. 2011). Often estimates of GPP and RE data differ depending upon the choice of flux partitioning models. There are several measurements and modeling methodologies which are used for partitioning NEE, each of which has its own advantages and disadvantages (Desai et al. 2008). These flux partitioning models (FPMs) can be very useful for gap filling of missing data, thus allowing estimates of CO_2 flux over long time periods (Falge et al. 2002). Hence, FPMs are important tools for inferring EC data, yet very few studies so far have critically examined how the choice of a given FPM affects the degree and variability of C-flux estimates in tropical lowland paddy.

Yearlong EC time series data from the lowland paddy in eastern India were used to generate NEE, GPP and RE estimates using two FPMs that differ significantly in the data source used (i.e., daytime versus nighttime data) and difficulty of the modeling procedure. These estimates from two models were then compared against each other to assess the magnitude and seasonal variability of NEE, RE and GPP. While doing the inter-comparison of data, it is imperative to note that model-based estimates are generally liable to various random and systematic errors and may not always denote the unknown "true" flux value. There is a substantial interest in partitioning the measured NEE of CO_2 to find better perceptions into the process-level controls over NEE. During the nighttime, partitioning is simple, as RE becomes equal to NEE, whereas, during the daytime, the partitioning depends on the model used. Hence, there are considerable uncertainties related to the estimates of GPP and RE (Hagen et al. 2006; Richardson et al. 2006). The daytime RE can be extrapolated from the nighttime flux measurements using some temperature response function, but this approach does not account for daytime inhibition of foliar respiration, which is estimated to be 11–17% of GPP (Wohlfahrt et al. 2005). There is another method by which daytime RE is estimated from the y-axis intercept from a light response curve (Lasslop et al. 2010). Desai et al. (2008) reported that most of the partitioning methods varied by less than 10% in terms of yearly integrals and more variability among the methods was observed when extra gaps were included in the data. It was apparent that patterns of GPP across the locations tended to be consistent when a single partitioning algorithm was applied which indicates that choice of algorithm mostly results in asystematic bias of unknown magnitude since the "true" GPP is not known. In the case of the partitioning of RE, more variability within algorithms was observed at shorter timescales (e.g., with regard to diurnal cycles) (Lasslop et al. 2010). Soil also plays an important role in ecosystem respiration by sequestering C in labile and non-labile pools and subsequent release as CO_2 which get altered with different agronomic management practices such as mulching, irrigation and fertilizer management (Chatterjee 2014; Chatterjee et al. 2016, 2017, 2018) and other organic input managements. Hence, estimates of the RE in large scale often contain errors in the data.

The current study focused on two different FPMs that have a strong basis in ecosystem physiology, particularly those that parameterize well-known relationships between respiration and temperature or between NEE and photosynthetically active radiation (PAR). The rectangular hyperbola (RH) is an established method to assess the effects of PAR on NEE. It has been reported that the flux data from the EC system at nighttime and temperature are significantly related to each other (Lee et al. 1999). On the other hand the Q10 method is very useful to model RE using temperature as a dominant factor. The Q10 method is also used for gap filling of missing flux data collected during nighttime conditions having sufficient turbulence (e.g., $u^* > 0.2$ m s^{-1}) by using air temperature as a key physical driver of RE (Stoy et al. 2005). These methodologies engage the simple equations used by many ecosystem models and, therefore, can produce transferable information for future studies of C-dynamics both across time and space at the lowland paddy ecosystem and other ecosystems relating with similar characteristics. Thus, it was hypothesized that NEE of CO_2 varies with paddy-growing season, and there is a significant difference in estimates of GPP and RE partitioned by two different FPMs and choices of the model may influence the

partitioning of NEE in tropical lowland paddy. To investigate this hypothesis, the current study was carried out with the following objectives (1) to study the variation of the net ecosystem exchange of CO_2 in lowland paddy and (2) to find out the best-suited model for better partitioning of net ecosystem exchange of CO_2 in lowland paddy.

Materials and methods

Study site and establishment of crop

The field experiment was conducted at the eddy covariance site of ICAR-National Rice Research Institute (20°26′ 60.0″N, 85°56′ 10.9″E, 24 m above average sea level) in Cuttack, Odisha, India, during the paddy-growing season of 2015. The climate of Cuttack is tropical humid, with wet hot summers (March to June) and brief mild winters (December to February). The annual average maximum and minimum temperatures in 2015 were 39.2 and 22.5 °C, respectively, whereas the annual average temperature was 27.7 °C. The PAR in this site varied from 112.70 to 1101.32 µmol m^{-2} s^{-1}. Average annual rainfall was 1500 mm. The soil texture of the experimental site was sandy clay loam (25.9% clay, 21.6% silt and 52.5% sand) and categorized as Aeric Endoaquept in soil taxonomic classification system (Chatterjee et al. 2019a, b). The average bulk density of the study site was 1.42 Mg m^{-3}. The measured pH (1:2.5 soil: water suspension) varied from 6.20 to 6.32, and a low average electrical conductivity (0.44 dS m^{-1}) was recorded. Total carbon and total nitrogen of the study area varied from 11.2 to 11.4 g kg^{-1} and 0.78 to 0.9 g kg^{-1}, respectively.

Paddy crop was grown in two seasons, i.e., dry season (DS) and wet seasons (WS) of 123 and 131 days, respectively, including two fallow periods, i.e., dry fallow (DF) and wet fallow (WF) of 64 and 47 days, respectively. Four crop growth stages were mostly identified which are vegetative (Veg), panicle initiation (PI), flowering (FL) and harvesting or maturity (H). Twenty-one-day-old seedlings of paddy (cultivar *Naveen* in DS cultivar *Swarna Sub-1* in WS) were transplanted to a puddled soil with a spacing of 20 cm × 15 cm. Transplanting was done on the 2nd week of July in WS and 1st week of January in DS and harvested in November and last week of May, respectively. Nitrogen fertilizer was applied in three equal splits at basal, vegetative and panicle initiation stages. The rate of N application was 80 kg ha^{-1} in WS and 100 kg ha^{-1} in DS. Phosphorus (P) and potassium (K) were added at the rate 40 kg ha^{-1} each at basal during land preparation in both the seasons. During the fallow period, there was no crop left and the water was drained out before 15 days of the harvest. There was 8 cm standing water during the paddy-growing period, and before harvesting, it was drained out.

Eddy covariance instrumentation setup

The eddy covariance instrument was fitted in the lowland paddy field at its middle position covering a fetch area of 2.25 hectares. To assure a uniform height of paddy crop year-long uniform breeder paddy variety was grown within the fetch area of the EC system. The components that comprised the eddy system were (1) a three-dimensional sonic anemometer (CSAT3, M/s Campbell Scientific Corp., Logan, Utah, USA) which measures wind speed along with three non-orthogonal sonic axes in the real time, (2) open path infrared gas analyzer (LI-7500A, M/s LICOR Inc., Canada) measuring fluctuations in CO_2 and water vapor densities, (3) a temperature-humidity sensor (HMP45C, Campbell Scientific Corp., Logan, Utah, USA) measuring air temperature (Ta), relative humidity (RH), (4) a 4-component radiation sensor (CNR4, KIPP and ZONEN, Netherlands) measuring net radiation, (5) a soil temperature probe (107 B, Campbell Scientific Corp., Logan, Utah, USA) which measures soil temperature and (vi) a PAR sensor (LI190SB) which measures PAR. Both the sonic anemometer and infrared gas analyzer were mounted on a tripod aluminum mast at 1.5 m height. All the signals from different sensors were logged and stored in a data logger (CR3000, Campbell Scientific Corp., Logan, Utah, USA) at a sampling frequency of 10 Hz.

The NEE was calculated to sum up the half hourly daily CO_2 flux and CO_2 storage change. As paddy canopy height was relatively low, hence the storage term was neglected for the NEE calculation. The average vertical CO_2 flux density (g C m^{-2} d^{-1}) was calculated by the following formula (Webb et al. 1980; Baldocchi 2003):

$$F_c = \rho_a \overline{\omega' C'} \quad (1)$$

where ρ_a is dry air density (kg m^{-3}), C' is CO_2 mixing ratio, ω' is the 30-min covariance between vertical fluctuations of wind speed (m s^{-1}), time averaging was denoted by over bar, whereas the primes denote fluctuations of the average value. The flux symbol is negative when CO_2 is assimilation by the vegetation from the atmosphere, and positive, otherwise. Average of NEE was used to compute daily and seasonal net exchange by the 30-min data representation (Massman and Lee 2002).

Processing, quality control and gap filling eddy covariance data

Raw eddy covariance flux data set has been processed for quality control and flux corrections (Mauder et al. 2006; Mauder and Foken 2011). The other corrections included are: the planar fit coordinate rotation correction (Wilczak et al. 2001), coordinate rotation (Kaimal and Finnigan

1994), translation of buoyancy into sensible heat flux (Liu et al. 2001); density fluctuations correction ("WPL" correction) (Tanner and Thurtell 1969; Webb et al. 1980). The u* filtering (Reichstein et al. 2005; Papale et al. 2006) and spike removal with linear interpolation for the detected spikes were performed (Vickers and Mahrt 1997). The threshold of frictional velocity (u*) for data during the nighttime was filtered as 0.1 m s^{-1} in this lowland paddy (Bhattacharyya et al. 2014). Gap filling of lost and discarded data was completed by the "look-up" table method (Falge et al. 2002).

Flux partitioning methods

Two different methods of varying complexity were explored for NEE partitioning into its components, i.e., GPP and RE. The study is mainly based on the methods that parameterize known relationships between driving meteorological parameters and NEE. One method, namely Q10 method, uses measured nighttime fluxes to predict RE as a function of air temperature. The second one is based on the rectangular hyperbolic fit (RH) which uses the intercept of the relationship between PAR and NEE of daytime to model RE. GPP was then calculated from the definition:

$$\mathrm{GPP} = \mathrm{NEE} - \mathrm{RE} \tag{2}$$

The units of NEE, GPP and RE is in μmol m^{-2} s^{-1}

Rectangular hyperbola (RH)

The rectangular hyperbola is an established method to assess the effects of PAR on NEE. It has been reported that the flux data from the EC system at nighttime and temperature are significantly related to each other although it is largely scattered (Lee et al. 1999). They used an intercept parameter (γ) of the RH model (i.e., the Michaelis–Menten model) to examine the seasonal dynamics of RE in a way that was less bound by the limitations of nighttime EC data quality, and finally the NEE is written as (Ruimy et al. 1995):

$$\mathrm{NEE}_{\mathrm{RH}} = -\left[\frac{\alpha \cdot \beta \cdot Q}{\alpha \cdot Q + \beta}\right] + \gamma \tag{3}$$

where α denotes apparent ecosystem considerable yield, β is light saturation determined CO_2 uptake rate (μmol m^{-2} s^{-1}), γ signifies estimate of RE (μmol m^{-2} s^{-1}), and Q denotes PAR (μmol m^{-2} s^{-1}). In this study, the parameters of Eq. (3) were determined crop growth stage-wise and daily γ value was used as an estimate of RE (Table 1). Instantaneous data sets, β, γ and Q, are in μmol m^{-2} $s^{-}1$.

Q10 approach

One of the most popular approaches to model RE using temperature as a dominant factor is the so-called $Q10$ equation:

$$\mathrm{RE}_{\mathrm{Q10}} = R_{10} Q_{10}^{\frac{(T_a - 10)}{10}} \tag{4}$$

where R_{10} denotes ecosystem base respiration at 10 °C, T_a is air temperature (°C), and Q_{10} describes the temperature sensitivity parameter, here delineating the amount of change in RE for a 10 °C change in temperature. This method is very useful for gap filling of missing flux data collected during nighttime conditions having sufficient turbulence (e.g., $u^* > 0.2$ m s^{-1}) by using air temperature as a key physical driver of RE (Stoy et al. 2005). The parameter values of R_{10} and Q_{10} were determined for each growth stage of paddy crop and season-wise for the whole year of study. It was noted that while parameterizing Eq. (4) seasonal variations in u^* impact the eddy data set which is biased toward colder seasons (Gu et al. 2005; Reichstein et al. 2005).

For Q10 we built regression relationship of day-time NEE versus day-time air temperature. We considered that

Table 1 Parameters for rectangular hyperbola model for lowland paddy

Description	Growth stages	α	β	Q	γ
Dry season (cv. *Naveen*)	Vegetative	1.04	9	594.46	7.12
	Panicle initiation	0.38	10	704.32	7.94
	Flowering	0.17	20	810.02	12.37
	Harvesting	0.20	24	849.60	15.19
Dry fallow	–	0.53	20	803.56	15.49
Wet season (cv. *Swarna Sub-1*)	Vegetative	0.70	10	580.33	7.60
	Panicle initiation	0.29	20	681.49	13.86
	Flowering	0.84	22	657.28	16.17
	Harvesting	1.38	22	643.50	15.38
Wet fallow	–	1.24	20	495.06	11.89

α denotes apparent ecosystem considerable yield, β is light saturation determined CO_2 uptake rate, γ signifies estimate of ecosystem respiration (RE), and Q denotes photosynthetically active radiation (PAR). Instantaneous data sets, β, γ and Q are in μmol m^{-2} s^{-1}. Stage-wise and seasonal data sets, β, γ and Q, are in g C m^{-2} d^{-1}

nighttime NEE is mostly contributed by RE in the absence of photosynthesis (GPP) during that period. Thus, we used this relationship to model day-time RE and day-time GPP as NEE = GPP − RE. The regression equations which were used for building the Q10 model are shown in Table 2.

For model validation and comparison we did an extensive literature survey for GPP and RE estimates in paddy in similar climatic conditions in different part of the world and assumed that our estimates of GPP and RE would follow similar trend. We did not have direct measurements of GPP and RE; hence, we compared with estimates of previous researchers (Ruimy et al. 1995; Bhattacharyya et al. 2013, 2014; Stoy et al. 2006; Desai et al. 2008; Wohlfahrt and Galvagno 2017; Oikawa et al. 2014, 2017; Wehr et al. 2016; Wohlfahrt and Gu 2015; Swain et al. 2016, 2018a; Vargas et al. 2011) for similar edaphoclimatic conditions.

Statistical analysis

Paired sample *t* test statistics for both the models of NEE partitioning was done by using statistical analyses software SPSS (version 20.0). Model root-mean-squared error (RMSE), standard deviation (SD) and coefficient of determination (R^2) values were obtained from MS-Excel 2010 software.

Table 2 Regression equations for Q10 models

Growth stages	Equations	R^2
Dry season	$y = 0.0007x^2 - 0.018x + 0.0883$	0.44
Dry fallow	$y = -0.0023x^2 + 0.1917x - 3.5202$	0.41
Wet season	$y = -0.0005x^2 + 0.0742x - 1.6777$	0.32
Wet fallow	$y = 0.007x^2 - 0.2944x + 3.0663$	0.36

y denotes nighttime instantaneous NEE (μmol m^{-2} s^{-1}), *x* is nighttime air temperature (°C), R^2 is coefficient of determination

Results

Daily, seasonal and annual variations in NEE

The average NEE of the lowland paddy field varied from − 5.71 to 2.29 g C m^{-2} d^{-1} during the observation period covering both the cropping seasons and the fallow period (Fig. 1). The average NEE during the DS and WS was − 1.62 and − 1.83 g C m^{-2} d^{-1}, respectively. The average NEE during the fallow period after harvest of the dry season and wet season crop was − 1.49 and − 0.29 g C m^{-2} d^{-1}, respectively. The average and cumulative NEE for the year 2015 was − 5.23 and − 542.47 g C m^{-2} d^{-1}, respectively. Cumulative NEE for DF and WF was − 95.37 and − 14.81 g C m^{-2}, whereas cumulative NEE values during DS and WS were − 199.73, − 232.55 g C m^{-2}, respectively.

Daily, seasonal and yearlong variations in GPP in two FPM

Throughout the entire cropping seasons (DS and WS) and fallow periods (DF and WF), the daily variation of average GPP varied from − 7.25 to − 20.80 μmol m^{-2} s^{-1} and from − 0.025 to − 22.68 μmol m^{-2} s^{-1}, obtained from RH and Q10 method, respectively. The annual average values of GPP obtained from RH and Q10 method are − 16.02 and − 10.46 μmol m^{-2} s^{-1}, respectively, and the statistical mean difference between GPP values estimated by these two different FPMs is significant (Table 3). During the DS the average GPP values (modeled by RH method) were − 8.20, − 10.28, − 15.81 and − 18.55 μmol m^{-2} s^{-1} in Veg, PI, FL and H stages, respectively, with a seasonal average value of − 13.37 μmol m^{-2} s^{-1}. The average GPP values during DS (modeled by Q10 method) were − 1.76, − 5.12, − 10.77 and − 17.16 μmol m^{-2} s^{-1} estimated in Veg, PI, FL and H stages, respectively, with a seasonal average

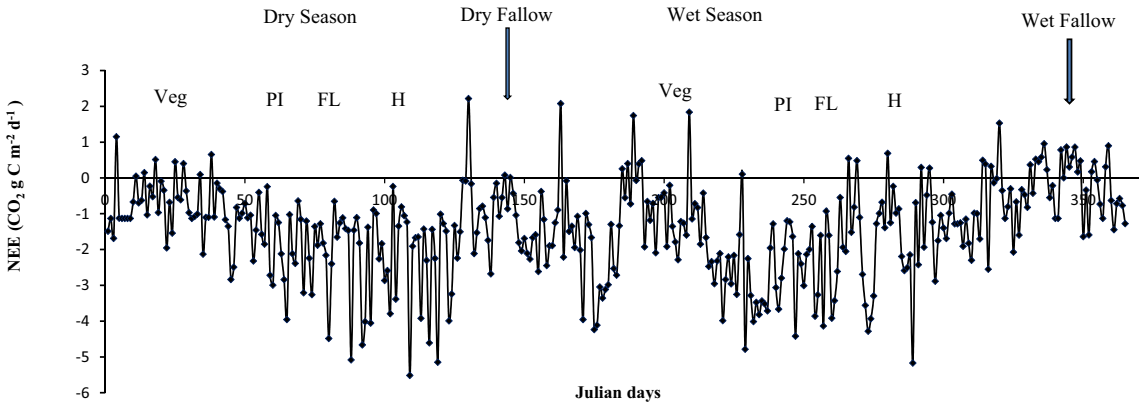

Fig. 1 Variation of daily average net ecosystem exchange of CO_2 during the dry and wet season (*Veg* vegetative, *PI* panicle initiation, *FL* flowering and *H* harvesting stages) and the fallow period of lowland paddy

Table 3 Paired samples t test for gross primary production (CO_2 g C m^{-2} d^{-1}) estimated from two flux partitioning models

	Crop stages	Mean ± SEM		R^2	Mean difference	Degrees of freedom
		RH	Q10			
Dry season	Vegetative (Veg)	8.20 ± 0.035	1.76 ± 0.137	0.007	6.44	34
	Panicle initiation (PI)	10.28 ± 0.347	5.12 ± 0.38	0.767	5.15*	24
	Flowering (FL)	15.81 ± 0.150	10.77 ± 0.54	0.415	5.04*	24
	Harvesting (H)	18.55 ± 0.205	17.16 ± 0.50	0.125	1.38*	37
Dry season total		13.37 ± 0.40	9.03 ± 0.60	0.889	4.33*	122
Dry season fallow		18.07 ± 0.009	12.36 ± 0.34	0.081	5.71*	63
Wet season	Vegetative (Veg)	10.20 ± 0.42	6.91 ± 0.53	0.077	3.28	26
	Panicle Initiation (PI)	18.24 ± 0.31	12.57 ± 0.59	0.321	5.66*	27
	Flowering (FL)	19.55 ± 0.13	15.19 ± 0.53	0.132	4.35*	37
	Harvesting (H)	18.41 ± 0.11	10.08 ± 0.84	0.001	9.32	37
Wet season total		17.30 ± 0.34	11.44 ± 0.42	0.262	5.85*	130
Wet season Fallow		16.58 ± 0.170	8.89 ± 0.65	0.417	7.68*	46
Total (365)		16.02 ± 0.211	10.46 ± 0.28	0.526	5.55*	364

SEM standard error of the mean, *RH* rectangular hyperbola, R^2 coefficient of determination

*Mean difference is significant at the 0.05 level ($p < 0.05$)

value of − 9.03 µmol m^{-2} s^{-1}. During the DS it was observed that GPP values gradually increased as the cropping season progressed from Veg to H stage irrespective of any FPM. During the WS the average GPP values (modeled by RH method) were − 10.20, − 18.24, − 19.55 and − 18.41 µmol m^{-2} s^{-1} estimated in Veg, PI, FL and H stages, respectively, with a seasonal average value of − 17.30 µmol m^{-2} s^{-1}, whereas the average GPP values in WS (modeled by Q10 method) were − 6.91, − 12.57, − 15.19 and − 10.08 µmol m^{-2} s^{-1} during Veg, PI, FL and H stages, respectively, with a seasonal average value of − 11.44 µmol m^{-2} s^{-1}. The highest GPP was estimated during FL stage by both the FPM. It was observed that in both the seasons (DS and WS) the statistical mean difference between the GPP values estimated from RH and Q10 was significant although it was not found significant during Veg stages of both the cropping season in both the FPM. During the DF period the average GPP values, estimated from RH and Q10 method, were − 18.07 and − 12.36 µmol m^{-2} s^{-1}, respectively, whereas during wet fallow (WF) the estimated average GPP values were − 16.58 and − 8.90 µmol m^{-2} s^{-1}, respectively. The statistical mean difference between the GPP values estimated from both the FPM was also found to be significant in both the fallow period (Table 3). The seasonal and stage-wise variations of GPP in both the FPM are shown in Figs. 2 and 3, respectively.

Daily, seasonal and yearlong variations in RE in two FPM

During the two cropping seasons (DS and WS) and fallow periods (DF and WF), the daily variation of average RE varied from 6.80 to 20.15 µmol m^{-2} s^{-1} and from 0.77 to 10.61 µmol m^{-2} s^{-1} obtained from RH and Q10 method, respectively. The annual average values of RE obtained from RH and Q10 method are 13.44 and 4.62 µmol m^{-2} s^{-1}, respectively and the statistical mean difference between RE values estimated by the two FPM is significant (Table 4). During the DS the average RE values (modeled by RH method) were 7.78, 8.67, 12.65 and 15.17 µmol m^{-2} s^{-1} during Veg, PI, FL and H stages, respectively, with a seasonal average value of 11.24 µmol m^{-2} s^{-1}. The average RE values (modeled by Q10 method) were 2.10, 2.63, 3.75 and 5.01 µmol m^{-2} s^{-1} during Veg, PI, FL and H stages, respectively, with a seasonal average value of 3.42 µmol m^{-2} s^{-1}. During the DS it was observed that magnitude of RE gradually increased as the growing season progressed from Veg to H stage of paddy and estimated the highest at H stage. During the WS the average RE values (modeled by RH method) were 8.72, 15.39, 16.65 and 16.11 µmol m^{-2} s^{-1} during Veg, PI, FL and H stages, respectively, with a seasonal average value of 14.59 µmol m^{-2} s^{-1}, whereas the average RE values (modeled by Q10 method) were 3.72, 4.53, 4.98 and 4.33 µmol m^{-2} s^{-1} during Veg, PI, FL and H stages of paddy, respectively, with a seasonal average value of 4.43 µmol m^{-2} s^{-1}. The highest RE in the WS was estimated during FL stage in both the FPM (Table 4). It was observed that in both the season (DS and WS) the statistical mean difference between the RE values estimated from both the FPM was significant though it was not found significant during Veg stage of WS paddy (Table 3). During the DF period the average RE values, estimated from RH and Q10 method, were 15.85 and 6.55 µmol m^{-2} s^{-1}, respectively, whereas during the WF the estimated average RE values were 12.67 and 5.70 µmol m^{-2} s^{-1}, respectively. The

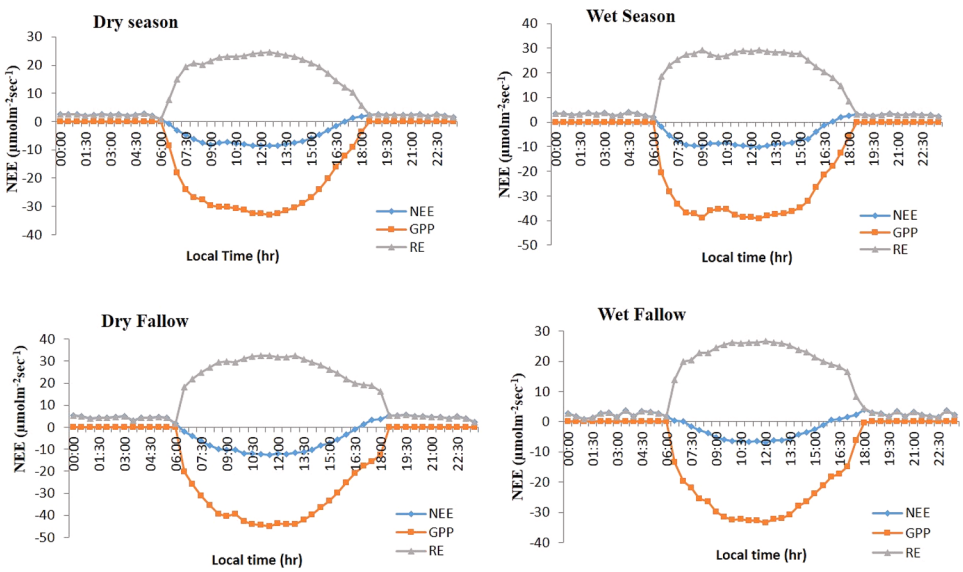

Fig. 2 Partitioning of net ecosystem exchange rectangular hyperbola into gross primary production and ecosystem respiration and diurnal variation (IST, Indian Standard Time) by method during the dry and wet seasons and fallow period of lowland paddy

statistical mean difference between the RE values estimated from both the FPM was also found to be significant in both the fallow period (Table 4). The seasonal and stage-wise variation of RE partitioned by both the FPM is shown in Figs. 4 and 5, respectively.

Discussion

Variation of NEE in lowland paddy

Positive and negative sign of NEE denoted net CO_2 emission into the atmosphere and net CO_2 assimilation by lowland rice, respectively. The lowland paddy field acted as net CO_2 sink throughout the entire growing season except for few days at the maturity and fallow period. The NEE in lowland paddy is mainly controlled by several factors and environmental variables such as latent heat, heat stress, vapor pressure deficit, canopy irradiance, stomatal response, circadian rhythm, growth stages of rice crop, leaf area index, biomass, high evaporative demand (Nair et al. 2011). Net ecosystem exchange also depends water management and the particular stages of the crop (Saito et al. 2005). It was observed that the amplitude of the daily variation in NEE increased with the progress of growing season and reached its maxima around the PI to FL stage and, then, decreased progressively till the maturity. It might be due to the reduction in leaf chlorophyll content or leaf senescence. These findings are in agreements with the findings of (Pakoktom et al. 2009) and (Bhattacharyya et al. 2013). Net ecosystem exchange becomes more negative during the day due to increasing CO_2 assimilation by photosynthesis (increase in GPP) as air temperature and PAR increased (Figs. 6a, b, and 7). Similar results were reported by (Alberto et al. 2009) and (Nair et al. 2011). The presence of aquatic plants and algae in the floodwater may also affect the NEE (Miyata et al. 2000; Bhattacharyya et al. 2013).

Variations in GPP in two FPM

It is evident from the results that the GPP estimated by the two different FPM (RH and Q10) significantly differed with each other and it is supported by their mean difference, RMSE and SD values (Tables 3 and 5). For DS, DF, WS and WF, the model RMSE values for RH method were 41.77, 21.40, 43.71 and 19.24% higher respectively, than Q10 method for the same following time frame, whereas the SD values were more in case of Q10 than RH method. Based on this observation it is obvious that RH method may be overestimating the GPP values as compared to the Q10 model in the lowland paddy field. The RH model used PAR data to partition NEE, and in wet season, PAR data (Fig. 7) are impacted due to cloud cover which may be attributed to error in the RH model while analyzing the data for WS period. The Q10 lacks this deficiency as it depends on temperature for partitioning NEE. While fitting the regression equation (for Q10) between nighttime air temperature and nighttime NEE we achieved a significant positive correlation ($r^2 \approx 0.4$–0.5) in both the season. Similar findings in this regard were reported by Stoy et al. (2006), Wohlfahrt and Galvagno (2017) and Oikawa et al. (2017).

Variations in RE in two FPM

The RE estimated by the two models significantly differed with each other which is supported by their mean difference, RMSE and SD values (Tables 4 and 5). For DS, DF, WS and WF, the model RMSE values for RH method were 86.81,

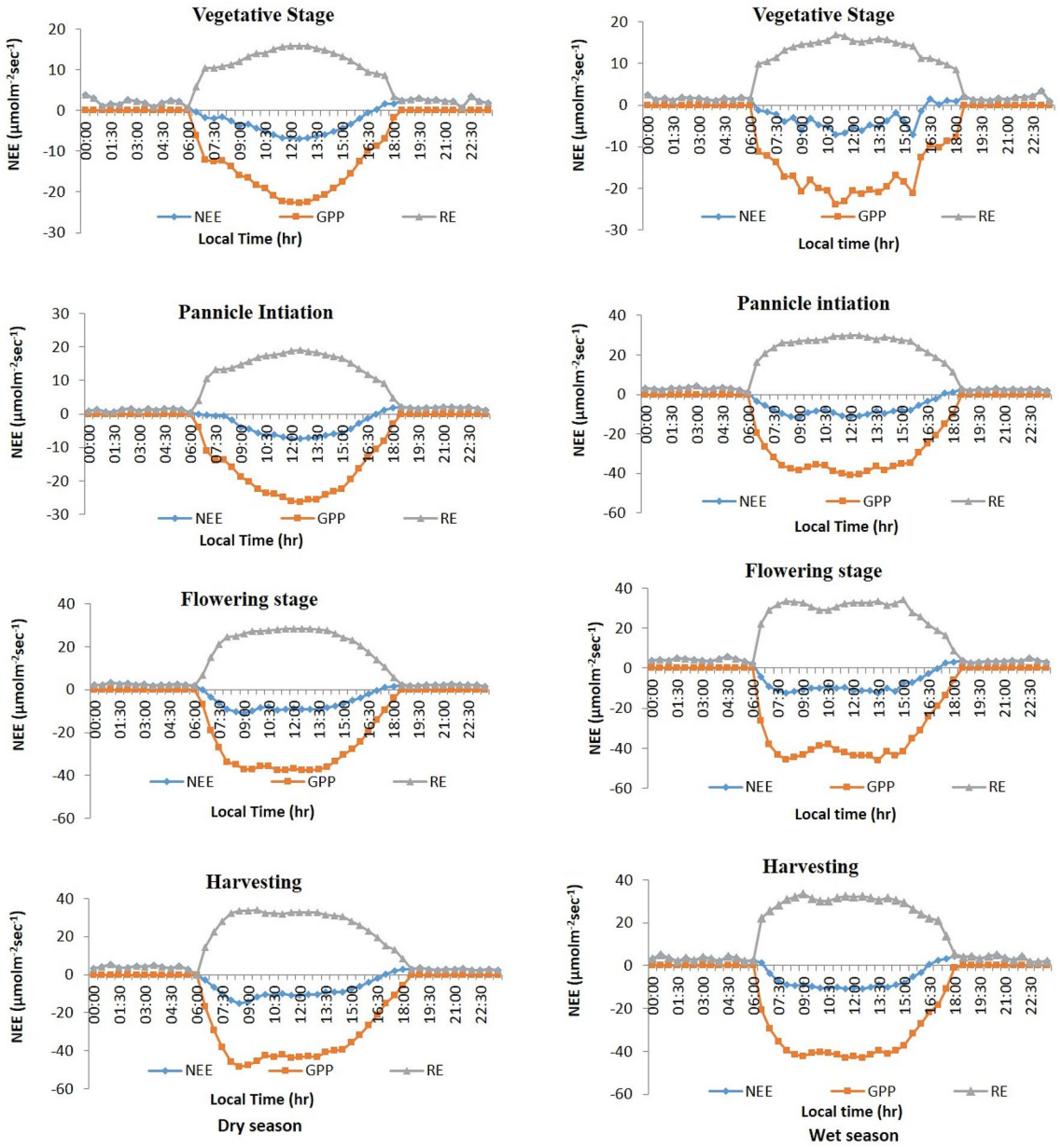

Fig. 3 Partitioning of net ecosystem exchange by rectangular hyperbola method into gross primary production and ecosystem respiration and diurnal variation (*IST* Indian Standard Time) in different crop growth stages of lowland paddy during dry and wet season

87.02, 84.22 and 77.30% higher, respectively, than Q10 method for the same time period. Similarly, the SD values were also more in case of RH as compared to Q10 method. From these observations it can be anticipated that the RH model was overestimating RE values much more than Q10 model; hence, Q10 was found best fit for this lowland paddy fields. However, Q10 approach may lead to systematic biases while partitioning as nighttime data were used to model daytime ecosystem respiration (RE), assuming that respiration processes did not cease in daytime and that the temperature responses of RE behaved similarly throughout the day and night. However, Reichstein et al. (2005) reported that these two assumptions are often violated. Nighttime plant respiration is often higher than daytime respiration which leads to an overestimation of daytime RE and GPP (Amthor 1995; Heskel et al. 2013; Kok 1949; Wehr et al. 2016; Wohlfahrt and Gu 2015). In the agricultural field, it is often difficult to predict daytime soil respiration from nighttime soil respiration rates due to the changing availability of substrate in soil (Oikawa et al. 2014; Tang et al. 2003; Vargas et al. 2011).

The model comparison and validation could have been more robust if we have had true ground measurements of

Table 4 Paired samples t test for ecosystem respiration (CO_2 g C m^{-2} d^{-1}) estimated from two flux partitioning models

	Crop stages	Mean ± SEM		R^2	Mean difference	Degrees of freedom
		RH	Q10			
Dry season	Vegetative (Veg)	7.78 ± 0.10	2.01 ± 0.09	0.157	5.77*	34
	Panicle initiation (PI)	8.67 ± 0.30	2.63 ± 0.15	0.170	6.03*	24
	Flowering (FL)	12.65 ± 0.27	3.75 ± 0.15	0.254	8.90*	24
	Harvesting (H)	15.17 ± 0.34	5.01 ± 0.12	0.278	10.15*	37
Dry season total		11.24 ± 0.31	3.42 ± 0.12	0.766	7.81*	122
Dry season fallow		15.85 ± 0.22	6.55 ± 0.18	0.552	9.30*	63
Wet season	Vegetative (Veg)	8.72 ± 0.24	3.72 ± 0.18	0.007	5.00	26
	Panicle initiation (PI)	15.39 ± 0.32	4.53 ± 0.10	0.271	10.86*	27
	Flowering (FL)	16.65 ± 0.24	4.98 ± 0.16	0.196	11.67*	37
	Harvesting (H)	16.11 ± 0.26	4.33 ± 0.34	0.049	11.78	37
Wet season total		14.59 ± 0.29	4.43 ± 0.124	0.118	10.15*	130
Wet season Fallow		12.67 ± 0.25	5.70 ± 0.33	0.471	6.97*	46
Total (365)		13.43 ± 0.18	4.62 ± 0.10	0.392	8.81	364

SEM standard error of the mean, *RH* rectangular hyperbola, R^2 coefficient of determination

*Mean difference is significant at the 0.05 level ($p < 0.05$)

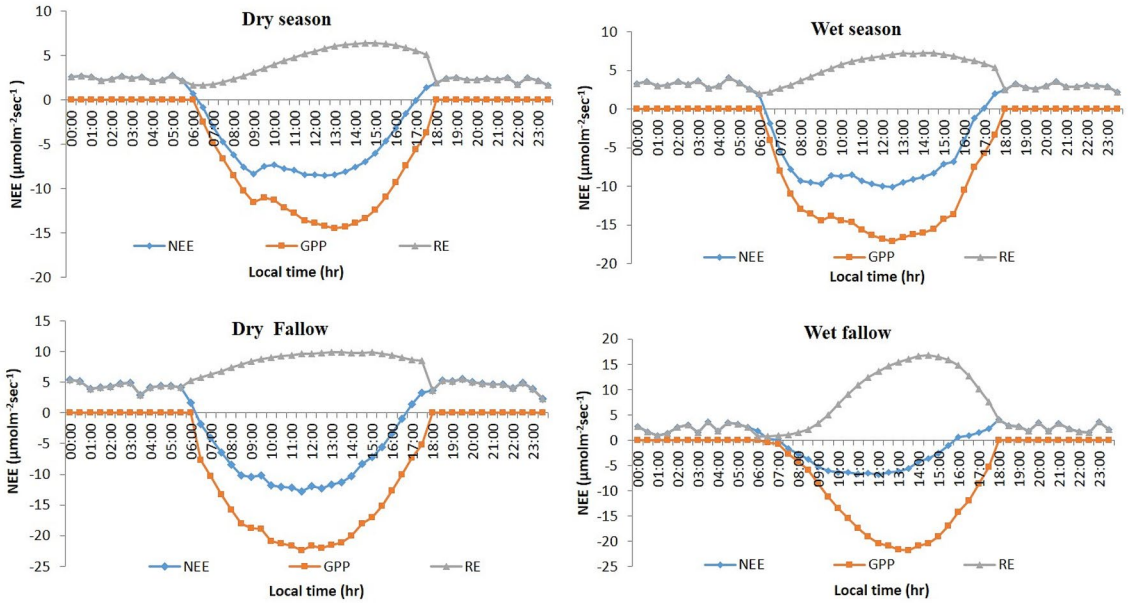

Fig. 4 Partitioning of net ecosystem exchange by Q10 method into gross primary production and ecosystem respiration and diurnal variation (*IST* Indian Standard Time) in different crop growing seasons and fallow periods

the partitioning products (GPP and RE) in this region. Further research is needed for validating the FPM models more accurately and cohesively for a particular edapho-climatic region. This study could be useful in data scarce region of the world.

Conclusions

In this study, the variation of the net ecosystem exchange of CO_2 in lowland seasonal paddy cultivation is assessed

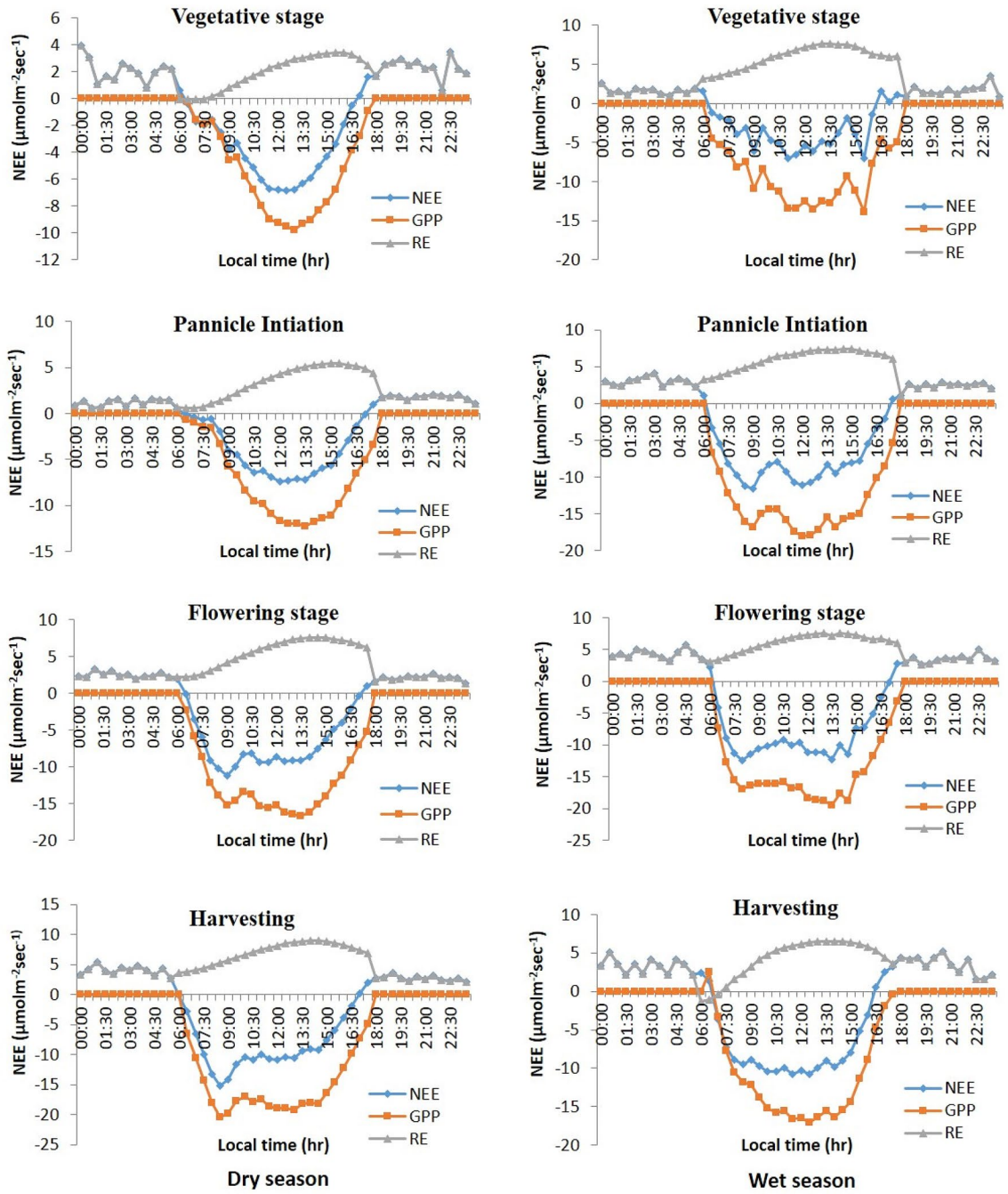

Fig. 5 Partitioning of net ecosystem exchange into gross primary production and ecosystem respiration by Q10 method in different crop growth stages and diurnal variation (*IST* Indian Standard Time) in lowland paddy during dry and wet season

and the best-suited model for partitioning of net ecosystem exchange of CO_2 in lowland paddy is identified. The net ecosystem exchange of CO_2 displayed a distinct daily and seasonal pattern during the paddy-growing season, and it was observed that lowland paddy has the capacity to sequester carbon from the atmosphere in the long run. It is evident from this study that the Q10 model unfailingly produced the most sensible C-flux estimates over rectangular hyperbolic (RH) method in lowland paddy field. The Q10 model that uses nighttime data to estimate RE, produced estimates which have lower RMSE values as compared to the other model. The RH model also requires many parameters, and accurate estimation of these parameters is important for better estimation of the partitioning products. The Q10 model predicted better estimates of RE and GPP values than the RH method that is

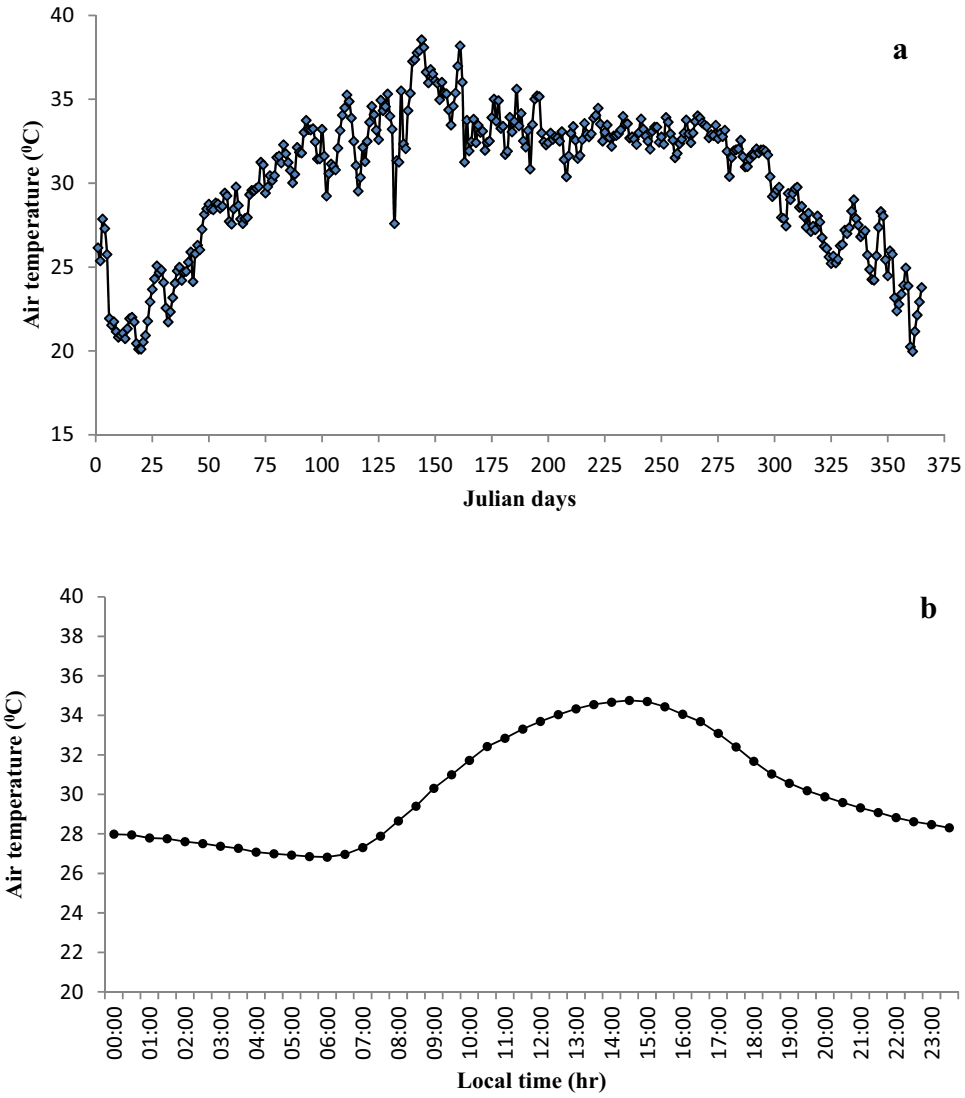

Fig. 6 **a** Mean daily air temperature (in Julian days). **b** Diurnal variation (*IST* Indian Standard Time) of average air temperature throughout the year

seemingly realistic in nature, though further investigations are required to confirm these findings. The major drivers for these models are PAR and air temperature which varied temporally and controlled by many atmospheric and climatic factors. Again NEE is also controlled by many soil–plant-atmospheric factors. So understanding their interrelation is much needed. Partitioning of respiration from soil and biota is also not understood fully by scientific community. Considering these constraints, models are prone to bias and errors are normal. Long-term studies are needed to establish the real truth about efficiency and suitability of a model in a particular ecosystem. The present analysis might be useful for carbon sequestration and emission studies in wetland ecosystem and for partitioning of NEE in data scarce region where true estimates of GPP and RE are lacking

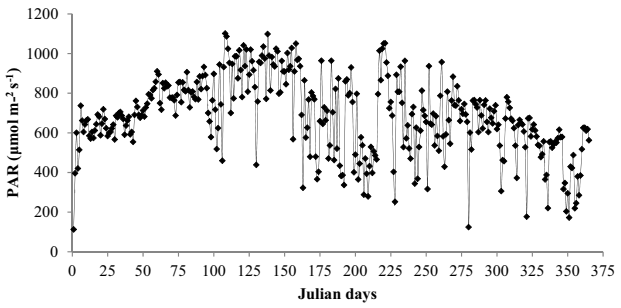

Fig. 7 Variation of daily average photosynthetically active radiation in the year 2015

Table 5 Statistical comparison of modeled gross primary production and ecosystem respiration estimated from two flux partitioning models

Seasons	GPP (CO_2 g C m^{-2} d^{-1})				RE (CO_2 g C m^{-2} d^{-1})			
	RMSE		SD		RMSE		SD	
	RH	Q10	RH	Q10	RH	Q10	RH	Q10
Dry season (DS)	8.93	5.20	5.78	8.59	14.33	1.89	9.03	1.73
Dry fallow (DF)	10.84	8.52	2.53	5.79	18.26	2.37	7.00	1.91
Wet season (WS)	11.62	6.54	5.31	7.49	18.51	2.92	9.62	1.94
Wet fallow (WF)	13.67	11.04	5.10	7.46	13.75	3.12	5.61	2.31

GPP gross primary production, *RE* ecosystem respiration, *RMSE* root-mean-square error, *SD* standard deviation, *RH* rectangular hyperbola

Acknowledgements The authors acknowledge the colleagues and research scholars at ICAR-National Rice Research Institute, Cuttack, India, who have assisted in this study. The first author sincerely acknowledges Dr. Jingyi Huang of University of Wisconsin-Madison, USA, for his suggestions to improve the manuscript. The first author also acknowledges the Indian Council of Agricultural Research for granting study leave and providing financial support.

Funding This study has been supported by the Grant of National Innovations on Climate Resilient Agriculture, Indian Council of Agricultural Research, New Delhi, India.

Compliance with ethical standards

Conflict of interest The authors assert that there is no conflict of interest.

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