

Net ecosystem CO₂ exchange from jute crop (*Corchorus olitorius* L.) and its environmental drivers in tropical Indo-Gangetic plain using open-path eddy covariance technique

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Abstract Present study is a maiden attempt to assess net ecosystem exchange (NEE) of carbon dioxide (CO₂) flux from jute crop (*Corchorus olitorius L.*) in the Indo-Gangetic plain by using open-path eddy covariance (EC) technique. Diurnal variations of NEE were strongly influenced by growth stages of jute crop. Daytime peak NEE varied from $-5 \mu mol m^{-2} s^{-1}$ (in germination stage) to $-23 \mu mol m^{-2} s^{-1}$ (in fibre development stage). The ecosystem was net CO₂ source during nighttime with an average NEE value of 5–8 µmol m⁻² s⁻¹. Combining both daytime and nighttime CO₂ fluxes, jute ecosystem was found to be a net CO₂ sink on a daily basis except the initial 9 days from date of sowing. Seasonal and growth stage-wise NEEs were computed, and the seasonal total NEE over

Highlights

- Diurnal, daily, and seasonal variations of net ecosystem exchange of CO₂ from jute fibre crop were assessed by using open-path eddy covariance technique.
- Daytime peak net CO_2 influx reached $-23 \ \mu mol \ m^{-2} \ s^{-1}$ during fibre development stage of jute crop.
- Jute ecosystem was a net CO_2 sink with seasonal net ecosystem CO_2 exchange of 268.5 gC m⁻² (i.e. 10.3 t CO_2 ha⁻¹).
- Maximum photosynthetic capacity of jute crop was 63.3 μmol CO₂ m⁻² s⁻¹ in the active vegetative stage and maximum apparent quantum yield was 0.072 μmol CO₂ μmol photon⁻¹ in the fibre development stage.

the jute season was found to be – 268.5 gC m⁻² (i.e. 10.3 t CO₂ ha⁻¹). In different jute growth stages, diurnal variations of NEE were strongly correlated ($R^2 > 0.9$) with photosynthetic photon flux density (PPFD). Ecosystem level photosynthetic efficiency parameters were estimated at each growth stage of jute crop using the Michaelis–Menten equation. The maximum values of photosynthetic capacity (P_{max} , 63.3 ± 1.15 µmol CO₂ m⁻² s⁻¹) and apparent quantum yield (α , 0.072±0.0045 µmol CO₂ µmol photon⁻¹) were observed during the active vegetative stage, and the fibre development stage, respectively. Results of the present study would significantly contribute to understanding of the carbon flux from the Indian agroecosystems, which otherwise are very sparse.

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Introduction

Steady increases in concentrations of greenhouse gases notably CO₂ in the atmosphere, particularly during the time frame of post-industrial revolution period, are considered to be the major drivers of global warming and climate change (Datta et al., 2011; Field et al., 2014). Assessment of various sources and sinks of atmospheric CO₂ and its dynamics is essential to mitigate the menace of climate change. Terrestrial ecosystem has been considered as a large sink of atmospheric CO_2 (3.1±0.9 Gt C year⁻¹), but disturbed heavily by land use change and unsustainable agricultural practices (Le Quere et al., 2016). Long-term monitoring of ecosystem-atmosphere carbon exchanges by eddy covariance (EC) flux towers is routinely being used for accurate quantification of the carbon budget of any ecosystem (Baldocchi et al., 2001). A global network of more than eight-hundred active EC stations, called FLUXNET, exists across the North, Central, and South America, Europe, Asia, Africa, and Australia (http:// fluxnet.fluxdata.org). The Indian subcontinent is underrepresented in this network and thus has a lot of uncertainty in carbon budgeting (Chakraborty et al., 2021; Deb Burman et al., 2020; Patra et al., 2013). India has diverse agro-ecosystems with nearly 198 M ha of gross cropped area (Agricultural Statistics at a Glance, 2018). Hence, the Indian agricultural systems play a very vital role in ecosystem-atmosphere carbon exchanges and global carbon budget as a whole. However, such EC measurements over agricultural ecosystems are still limited in number and also insufficient for representing the diverse agricultural landscapes of the country (Bhattacharyya et al., 2013a, b; Chakraborty et al., 2021; Chatterjee et al., 2020; Deb Burman et al., 2020; Patel et al., 2011, 2021). Hence, there is an urgent need for measurements and reporting of carbon fluxes data of various agricultural ecosystems including the jute ecosystem.

Jute crop (*Corchorus* spp.) provides an eco-friendly (Hoque et al., 2018) natural 'bast fibre' (Summerscales et al., 2010; Kundu et al., 2012) popularly known as 'golden fibre'. The fibres are long, lustrous, strong, and also economical, and therefore used to make diversified household goods and various industrial products

(Shahinur et al., 2015). The worldwide menace of plastics especially of single use plastics can be prevented by replacing them with jute fibre products. Jute holds second position after cotton as the textile fibre production in the world. Globally, jute crop is mainly grown in India, Bangladesh, China, Uzbekistan, Nepal, Myanmar, and Thailand (FAOSTAT, 2018). The crop is cultivated over an area of 1.54 M ha with production of 3.6 M tonnes across the globe (FAOSTAT, 2018). India has the highest jute growing area of 0.76 M ha with average fibre yield of 2.55 tonnes per ha and total production of 1.9 M tonnes. Among the major jute producing countries, India ranks first and followed by Bangladesh and China (FAOSTAT., 2018). India and Bangladesh together contribute more than 95% of the global jute fibre production, and therefore jute plays an important role in the economies of India (Mahapatra et al., 2009) and Bangladesh (Islam & Ali, 2017). In India, it is predominantly grown over the Gangetic delta in the eastern part of the country covering the states of West Bengal, Assam, Bihar, and Odisha (Mahapatra et al., 2009).

Being a high biomass producing crop, jute has the potential to be a good carbon sink by absorbing a substantial amount of CO_2 from the atmosphere during its growing season. Further, jute fibres and its by-products remain in use for years before naturally degrading into the ecosystem (Banerjee & Mathew, 1985; Mohanty et al., 2000; Chander et al., 2002; Saha et al., 2012). Hence, jute crop plays an important role in carbon sequestration by removing carbon from the atmosphere as well as by longer residency in the ecosystem as fibre products. The eddy covariance (EC) measurement of carbon flux during jute production can give a clear picture about carbon sequestration in the jute ecosystem. However, EC measurements of fluxes of CO₂ and/ or water vapour have mainly been done either in grain producing agricultural crops viz., paddy rice (Alberto et al., 2009; Bhattacharyya et al., 2013a; Saito et al., 2005; Zheng et al., 2008), wheat (Moureaux et al., 2008; Zheng et al., 2008; Aubinet et al., 2009), barley (Lohila et al., 2004), grain sorghum (Wagle et al., 2018), maize (Dold et al., 2019; Suyker & Verma, 2010; Wagle et al., 2018), pulse and oil seed (Chakraborty et al., 2021; Dold et al., 2019; Suyker & Verma, 2010; Wagle et al., 2017) or in pasture (Wagle et al., 2014), and forest ecosystems (Babst et al., 2013; Jha et al., 2013; Rodda et al., 2016). EC-based measurements of CO_2 and moisture fluxes from fibre crops like cotton were also reported (Alferi et al., 2012; Fong et al., 2020). However, to

the best of our knowledge, such high-frequency precise EC-based measurement of carbon flux for 'bast fibre' crop of jute had not been reported till date.

To address the knowledge gap as mentioned above, present study was carried out to quantify the net ecosystem exchange (NEE) of CO_2 fluxes from irrigated jute crop along with related meteorological variables using an open-path eddy covariance system. This is the first EC-based study on assessment of NEE from jute crop at diurnal, daily, phenological, and seasonal scales along with its relationship with environmental drivers in tropical climate. The response of CO_2 flux to PPFD at different growth stages of the jute crop was also quantified and ecosystem level photosynthetic parameters were retrieved.

Materials and methods

Study site

The study site (22°45'30.64" N, 88°25'40.83" E; 9 m above msl) is located in the experimental farm of Indian Council of Agricultural Research-Central Research Institute for Jute & Allied Fibres (ICAR-CRIJAF), Barrackpore, Kolkata, India. EC flux tower along with biometeorological sensors was installed in the centre of the experimental field in such a way that its fetch covers only jute crop (Fig. 1). The climate is tropical hot and moist sub-humid (NBSS & LUP, 1990). The average annual rainfall is 1552 mm of which about 73.3%

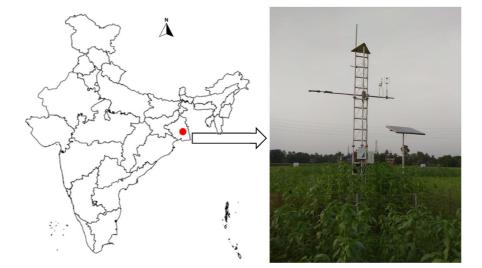
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is received during monsoon season (June to September) and 14.3% during pre-monsoon season (March to May), and the mean annual maximum and minimum temperatures are 31.1 °C and 20.8 °C, respectively (Barman et al., 2017). Soil temperature regime of the study site is classified as hyperthermic, which means that the mean annual soil temperature remained more than 22 °C (NBSS&LUP, 1994). Soil type is well drained, moderately deep, sandy clay loam (Anthropic Irragic Anthrosols (Stagnic, Dystic)) (Mazumdar et al., 2018).

Crop growth and input management

The field experiment was conducted for irrigated jute crop during April to August of 2018. The jute crop was sown on 17th April, 2018 and harvested after 111 days on 5th August, 2018. Standard agronomic practices were followed to raise the crop (Mitra et al., 2006). Sowing was done by maintaining row to row spacing of 25 cm and plant to plant spacing of 5 to 7 cm. Recommended doses of nitrogen (N), phosphorus (P), and potassium (K) fertilisers (per ha 80 kg N, 40 kg P and 40 kg K) were applied. The total amount of P and K, and one-third of N dose were applied as basal dose at the time of land preparation. First top dressing of N (1/3rd of N dose) was applied 30 days after sowing and after weeding operation. The second top dressing of N (1/3rd of N dose) was applied 60 days after sowing. Each top dressing was followed by irrigation. The harvested jute crop was bundled

Fig. 1 Open-path eddy covariance flux tower over jute crop at Indian Council of Agricultural Research-Central Research Institute for Jute & Allied Fibres (ICAR-CRIJAF), Barrackpore, West Bengal, India



and kept in the field for 2 to 3 days to shed the leaves, later taken for retting and then extraction of fibres.

The crop biophysical parameters such as plant height, basal diameter, leaf area index (LAI), and total chlorophyll content of leaf were measured at different jute growth stages. Plant height and basal diameter were measured using a measuring scale, and a vernier calliper, respectively. Leaf area index (LAI) was measured using a canopy analyser (LI 2200, LICOR Inc., USA). Total leaf chlorophyll content was measured using the dimethyl sulfoxide (DMSO) method (Lichtenthaler, 1987). In this method, 50 mg fresh leaf tissue was taken in a test tube containing 10 ml of DMSO and incubated at 60 °C for 4 h, and then the absorbances were recorded at 663 and 645 nm. Total chlorophyll was calculated using the formula, total chlorophyll (mg g⁻¹ fresh weight) = $[20.2 \times A645 + 8]$ $.02 \times A663 \times (V/W) \times 1000$; where, A645 and A663 are absorbance at 645 at 663 nm, respectively, V is volume of extract, W is weight of fresh leaf tissue.

Flux data and meteorological measurements

The eddy covariance (EC) technique has extensively been employed as the state-of-the-art micrometeorological method for monitoring fluxes of CO₂, water vapour, and heat, which are necessary to determine carbon and energy balances of the land surfaces (Foken, 2008; Aubinet et al., 1999, 2012; Burba, 2013). The exchanges of trace gases between terrestrial ecosystems and the atmosphere are measured by the widely adapted EC technique because of its large coverage of the extent of an ecosystem along with shortand long-term data collection (Baldocchi et al., 2003). By this technique, continental level of carbon balance is estimated through a 'bottom-up' approach using subhourly to inter-annual timescales data (Takata et al., 2017). The EC technique is fundamentally based on high-frequency (10 Hz) measurements of wind speed and direction using a three-axis sonic anemometer as well as the CO₂ and H₂O concentrations by a fastresponse infrared gas analyser (IRGA) at a certain height above the crop canopy (Foken, 2008; Aubinet et al., 2012; Burba, 2013). In the present study, the CO₂ and H₂O fluxes over the canopy were measured using an open-path IRGA (LI-7500A, LICOR Inc., USA). Three-dimensional wind speeds and sonic temperature were measured using a 3-D sonic anemometer (GILL WINDMASTER-PRO). Both the sensors were installed at 4.8-m height above the ground considering the maximum height of the full-grown jute crop to be nearly 3 m. Generally, it is recommended to maintain minimum of 1.5- to 2-m distance between the top of the canopy and the sensors. These two sensors were separated by a distance of 20 cm and such separation was adjusted statistically during data processing. The LI-7500A set back to sonic anemometer considering the predominant wind direction to minimise flow distortion. The head of the LI-7500A sensor was tilted about 10° from the vertical line for minimising accumulation of precipitation in the window. Data were collected by the Sutron (Xlite 9210) data logger.

Concurrent measurements of different meteorological variables were also carried out continuously with a suite of sensors placed with the flux tower. Downward/ upward short- and long-wave radiation components were measured using four components net radiometer (CNR4, Kipp & Zonen) whereas photosynthetic photon flux density (PPFD) was measured using LICOR (LI-190R) quantum sensor. Air temperature (T_a) and relative humidity (RH) were measured using temperature and humidity sensors (HMP155, Vaisala, Helsinki, Finland). Soil temperature (T_s) and soil water content (SWC) were measured at 5-cm depth by temperature and moisture sensors (Hydra Probe II, Stevens, Portland, Oregon), and soil heat flux (SHF) was also measured at 5-cm depth by self-calibrating soil heat flux plate (HFP01SC-15, Hukseflux Thermal Sensors B.V., Delft-The Netherlands). Rainfall was recorded using tipping and bucket type rain gauge (Texas Electronic). These micrometeorological observations and air pressure were recorded in 1 Hz, and averaged over a 30-min time interval.

Flux calculation and correction

The EC system recorded CO₂ fluxes and other meteorological variables as (.ghg) raw data file format. These raw data files (.ghg) were processed by using the Eddy-Pro® 6.2 software (LI-COR, Inc., 2016), and the CO₂ fluxes were obtained as half-hourly data. The eddy flux of CO₂ (F_c) is computed as the mean covariance between deviations in instantaneous vertical wind speed (w') and density of CO₂ in air (c') using the following equation given by Baldocchi et al. (1988).

$$F_c = \overline{w'c'} \tag{1}$$

The standard flux correction measures (Mauder et al., 2013) were applied for the flux data. It is important to note that the height of the jute crop increased very fast and attained 2.75 m within 111 days. The increase of height causes changes in the displacement height and roughness length that are crucial for canopy level mass and energy exchanges (Jacob & Boxel, 1988). Height of the jute crop, therefore, was adjusted by processing the raw data in weekly time windows as per the field condition using the dynamic metadata file in the EddyPro® software. The primary processing includes different statistical corrections such as angle of attack correction (Nakai & Shimoyama, 2012), tilt correction (Wilczak et al., 2001), time lag compensation by covariance maximisation and frequency response correction (Moncrieff et al., 1997, 2004), and Web-Pearson-Leuing (WPL) correction for density fluctuations of CO₂/water vapour due to thermal expansion and dilution (Webb et al., 1980). Further, the secondary processing includes spike removal (Thomas et al., 2011), frictional velocity correction (Zhu et al., 2006), and uncertainty analysis. The inherent gaps or low-quality EC data were corrected by gap filling method as employed by the CarboEurope (http://www. bgc-jena.mpg.de/bgc-mdi/html/eddyproc/, Reichstein et al., 2005), which is an improved technique of the look up table method (Falge et al., 2001). It considers both the covariations of fluxes with meteorological variables and the temporal autocorrelation of the fluxes. These gap-filled data were used to derive seamless half-hourly time series data of NEE.

Correlation analysis between NEE and environmental factors

Correlation analysis was done between NEE (µmol $CO_2 m^{-2} s^{-1}$) and related environmental variables such as net radiation (R_n , $W m^{-2}$), photosynthetic photon flux density (PPFD, µmol $CO_2 m^{-2} s^{-1}$), relative humidity (RH, %), vapour pressure deficit (VPD, kPa), air temperature (T_a , °C), and soil heat flux (SHF, $W m^{-2}$) and soil water content (SWC, %) at 5-cm depth. The correlations were statistically tested with 1% (p<0.01) and 5% (p<0.05) levels of significance. Further, responses of NEE to the light intensity (PPFD) at different growth stages were assessed by regression analysis.

Estimation of photosynthetic parameters for jute ecosystem

The Michaelis–Menten equation as described by Ruimy et al. (1995) was used in the current study to estimate the ecosystem level photosynthetic efficiency parameters and the equation is given below:

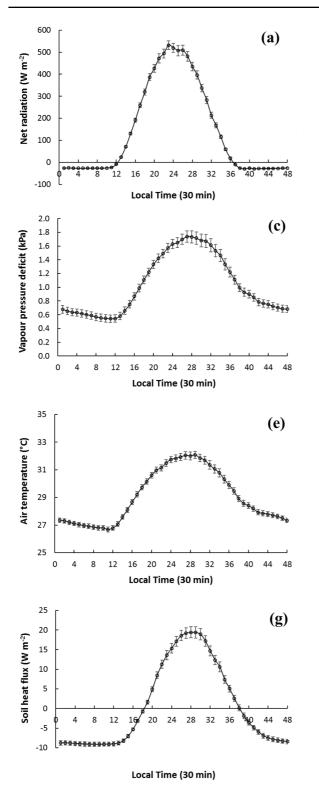
$$NEE = \frac{\alpha \times \text{PPFD} \times \text{P}_{\text{max}}}{\alpha \times \text{PPFD} + \text{P}_{\text{max}}} - R_e$$
(2)

where α (µmol CO₂ µmol photon⁻¹) denotes apparent quantum yield of the ecosystem, PPFD (µmol m⁻² s⁻¹) denotes photosynthetic photon flux density, P_{max} (µmol CO₂ m⁻² s⁻¹) denotes maximum photosynthetic capacity, and R_{e} (µmol CO₂ m⁻² s⁻¹) denotes ecosystem respiration in daytime.

Results and discussions

Meteorological condition

Diurnal variations of the seasonal average meteorological conditions of the present study site during jute growing season are presented in Fig. 2. The diurnal mean net radiation (R_n) ranged from – 29.09 (19.00 h) to+505.17 W m⁻² (12.30 h) with mean value of 134.63 W m⁻² (Fig. 2a). The R_n remained positive from sunrise to sunset (daytime), and it became negative during nighttime due to absence of incoming solar radiation. During the diurnal period, R_n became positive at 6.00 h in the morning immediately after sunrise and it gradually increased with the increasing sun elevation and reached its peak at 12.30 h. Further, it gradually declined due to inclined radiation (Bhattacharyya et al., 2013a) and started to become negative at 18.00 h and reached its lowest negative value at 19.00 h. The PPFD is an inherent part of incoming solar radiation, which is utilised for photosynthetic activities. Hence, it followed a similar diurnal pattern as that of R_n. The PPFD was zero during nighttime and reached its peak of 1200 μ mol m⁻² s⁻¹ in mid-day. The seasonal average air temperature (T_a) was 26 to 27 °C during nighttime, whereas it ranged from 32 to 33 °C in mid-day. At 5-cm depth, diurnal mean soil temperature mainly varied from 30 to 31 °C during the crop season. Soil



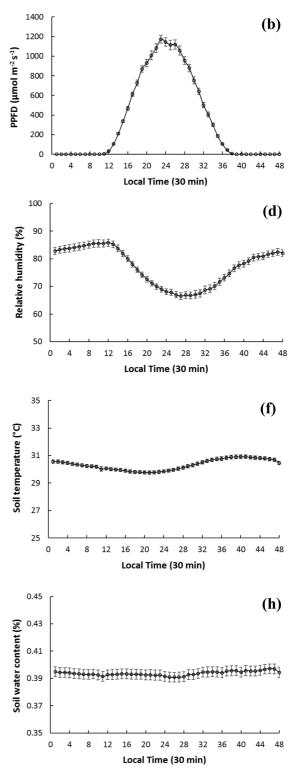


Fig. 2 Diurnal pattern of half-hourly seasonal mean of (a) Net radiation, (b) Photosynthetic Photon Flux Density (PPFD), (c) Vapour Pressure Deficit, (d) Relative Humidity, (e) Air tem-

perature, (**f**) Soil temperature at 5 cm depth , (**g**) Soil heat flux, and (**h**) soil water content over the jute growth period $(17^{th}$ April to 5th August, 2018)

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heat flux at 5-cm depth ranged from -5 to -10 W m⁻² during nighttime, and reached up to 20 W m⁻² during mid-day. Soil moisture at 5-cm depth remained nearly constant with little variations between 38 and 42% that is well within the available range to the jute crop. Relative humidity varied between 80 to 90% during night-time and from 65 to 70% during daytime. Similarly, vapour pressure deficit ranged from 0.5 to 0.7 kPa during nighttime and reached up to 1.8 kPa during mid-day. In nutshell, weather condition during the jute growing season was hot and humid with bright sunshine, which is typically ideal and favourable for crop growth.

Crop growth, biomass, and fibre yield

The germination of jute seeds started 3 days after sowing (DAS), i.e. 109 days of the year (DOY) and completed by 6 DAS i.e. 112 DOY. Growth of the jute plants was initially slow. It took 46 days (153 DOY) to attain 42.4-cm height but thereafter it gained another 92.6-cm height in only 14 days (167 DOY). Plant height in the fetch area increased continuously and reached an average height of 275 cm at harvest by 111 DAS i.e. 217 DOY (Fig. 3). Average basal diameter of the jute plants was 0.92 cm at 46 DAS, 1.27 cm at 60 DAS, and 2.10 cm at harvest (111 DAS). Diameter of the plants reduced from the base towards its tip and formed cylindrical stem slightly tapering towards tip. Leaf Area Index (LAI) of the crop was found to be nearly 1.0, 2.0, 3.0, 4.0, and 4.6 m² m⁻² at 30 (137 DOY), 50 (157 DOY), 65 (172 DOY), 85 (192 DOY), and 111 (217 DOY) DAS, respectively (Fig. 3). Chlorophyll content of leaf varied between 1.5 and 2.5 mg g⁻¹ on fresh weight basis.

Diurnal variations of NEE at different growth stages of jute crop

Jute crop season was divided into different growth stages based on different phenological/developmental phases viz. germination stage [1 to 6 DAS i.e. 107 to 112 DOY], seedling stage (7 to 36 DAS i.e. 113 to 143 DOY), active vegetative stage (37 to 66 DAS i.e.

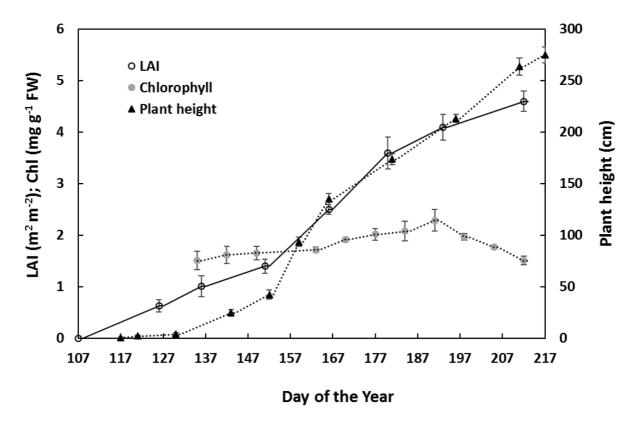


Fig. 3 Leaf area index (LAI), leaf chlorophyll content and plant height of jute crop during its growth period

144 to 173 DOY), fibre development stage (67 to 96 DAS i.e. 174 to 203 DOY), and maturity (97 to 111 DAS i.e. 204 to 218 DOY). Diurnal patterns of the mean NEE of different growth stages of the jute crop are presented in Fig. 4.

NEE was found to be positive in nighttime as photosynthesis process ceased to exist and respiration produced CO_2 from the ecosystem. The nighttime NEE varied between 5 and 8 µmol m⁻² s⁻¹ across different growth stages. The photosynthesis process kicks in after the sunrise and resulted in high influx of CO_2 into the ecosystem, superseding the CO_2 efflux due to ecosystem respiration. Thus, NEE became negative during daytime. Substantial differences were noticed in diurnal variations of NEE across the growth stages. NEE was found to be proportional to the accumulated above-ground biomass except in maturity (Figs. 3 and 4). During the germination stage, photosynthetic activity was minimal but the ecosystem respiration (soil respiration in particular) was high and therefore the NEE was positive. In this stage, the peak influx of CO_2 was $-5 \ \mu$ mol m⁻² s⁻¹

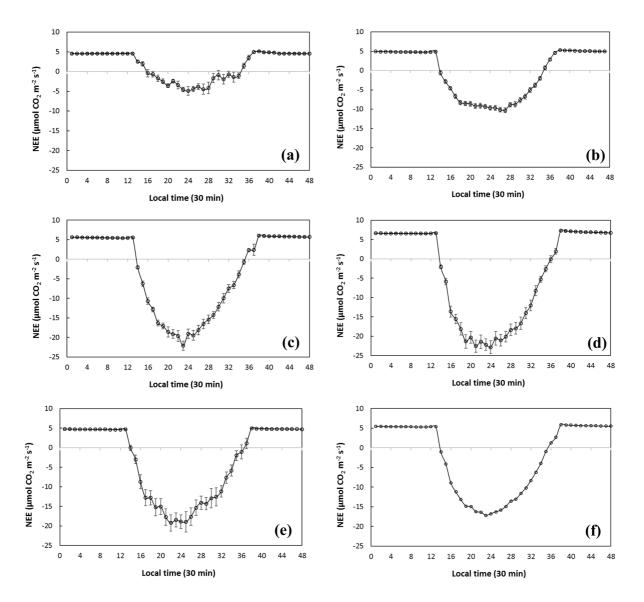
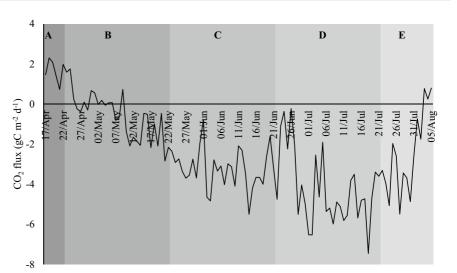


Fig. 4 Net ecosystem exchange of CO_2 (NEE) at different growth stages of jute: (a) germination stage, (b) seedling stage, (c) active vegetative stage, (d) fibre development stage, (e) maturity stage, (f) entire growth period

Fig. 5 Daily net ecosystem CO₂ exchange (NEE) of jute crop during different crop stages. **A**, Germination stage: **B**, Seedling stage: **C**, Active vegetative stage: **D**, Fibre development stage: **E** Maturity stage



during mid-day (Fig. 4a). With progress of the crop season, the ecosystem acted significantly as a net CO_2 sink and the peak CO_2 influx reached – 10, – 20, – 23, and – 20 µmol m⁻² s⁻¹ in seedling, active vegetative, fibre development, and maturity stages, respectively (Fig. 4). It is important to note here that the jute crop was harvested before it produced flowers. Hence, the typical senescence phase was absent and the peak CO_2 influx remained almost the same between active vegetative stage and maturity stage.

Dynamics of daily NEE over the jute growing season

The half-hourly NEEs (including daytime and nighttime observations) were converted to daily time scale for the entire jute season and presented in Fig. 5. Growth stage-wise accounts of mean and cumulative NEE are presented in Table 1. Jute crop acted daily as a net CO_2 sink almost during the entire growing season except initial 9 days from date of sowing to until 25th April, 2018 (115 DOY). In germination stage, the mean NEE was 1.66 gC m^{-2} day⁻¹ with the cumulative NEE of 9.98 gC m^{-2} and the positive values depict that the jute ecosystem acted as a net CO₂ source in this stage. This is because of more soil respiration than photosynthesis due to the much lower value of LAI ($< 0.3 \text{ m}^2 \text{ m}^{-2}$) in this stage. The subsequent negative values of daily NEE signify that the ecosystem acted as a net CO₂ sink until the harvesting of the jute crop. In seedling stage, photosynthetic activities increased as the LAI increased from 0.3 to 1.0 m² m⁻² along with crop height of 30 cm, and the mean NEE reached -0.57 gC m⁻² day⁻¹ with the cumulative value of -17.12 gC m⁻². In the active vegetative stage, crop height and LAI increased rapidly from 30 to 150 cm and 1.0 to 2.6 m² m⁻², respectively. In this stage, the mean and cumulative NEEs were -3.23 gC m⁻² day⁻¹ and -96.87 gC m^{-2} , respectively. The rapid crop growth was also observed in fibre development stage where the crop

Table 1 Net ecosystem CO_2 exchange (NEE) at different growth stages of jute crop and seasonal as a whole

Growth stages	Date	Days after sowing (DAS)	Cumulative NEE (gC m ⁻²)	Mean NEE (gC m ⁻² day ⁻¹)	$\begin{array}{c} \text{LAI} \\ (\text{m}^2 \text{ m}^{-2}) \end{array}$
Sowing to germination	17–22 Apr	1–6	+9.98	+1.66	0.1
Seedling stage	23 Apr-22 May	7–36	-17.12	-0.57	0.8
Active vegetative stage	23 May-21 Jun	37-66	- 96.87	-3.23	2.3
Fibre development	22 Jun–21 Jul	67–96	-126.86	-4.23	4.5
Maturity	22 Jul–5 Aug	97-111	-37.63	-2.51	4.9
Total		111 days	-268.49		

height and LAI increased from 150 to 220 cm and from 2.6 to 4.1 m² m⁻², respectively, and the mean and cumulative NEEs were -4.23 gC m⁻² day⁻¹ and -126.86 gC m⁻², respectively. Among all growth stages, the maximum NEE was observed in the fibre development stage, which might be due to the highest increase in LAI that led to more photosynthetic activities than soil respiration. During maturity stage, crop height and LAI further increased from 220 to 275 cm and 4.1 to 4.6 m² m⁻², respectively, and the mean and cumulative NEEs were -2.51 gC m⁻² day⁻¹ and -37.63 gC m⁻² day⁻¹, respectively. Shedding of lower matured leaves is common during this stage, which might have led to a lower rate of increase

stage, which might have led to a lower rate of increase of LAI. The seasonal cumulative NEE was found to be -268.49 gC m⁻² (i.e. 10.3 t CO₂ ha⁻¹) during 111 days of jute growing season.

Correlation between NEE and major environmental variables

The NEE of the jute agro-ecosystem is governed by multiple environmental variables that mainly influence the biological and physical processes. Therefore, correlation analysis was done between NEE and the related environmental variables such as net radiation (R_n), photosynthetic photon flux density (PPFD), vapour pressure deficit (VPD), air temperature (T_a), soil heat flux (SHF), and soil water content (SWC) and presented in Table 2.

The environmental drivers were found to have collinearity between them. PPFD being a part of R_n was found to be highly correlated. Further, VPD was also highly correlated with T_a and RH. As discussed in the "Meteorological condition" section, the environmental condition was congenial for growth and development of the jute crop. There were no major biotic or abiotic stresses during the growing season. Hence, the crop growth was mainly driven by the available solar radiation. NEE was statistically highly correlated with both PPFD (r = -0.79) and R_n (r = -0.78). Similar results were reported for the rice ecosystem by Bhattacharyya et al. (2013a); Alberto et al. (2009); and Saito et al. (2005). NEE was also statistically significantly correlated with Ta (r = -0.51), SHF (r = -0.44), VPD (r = -0.42), and RH (r = -0.41). Among these correlations, the magnitude of correlation coefficient between NEE and PPFD was found the highest (r = -0.79) which indicates that NEE is highly driven by PPFD.

Multiple regression analysis was done by taking halfhourly time series data of the season to develop empirical equation to estimate NEE of jute agro-ecosystem using related environmental drivers and the derived regression model is given below:

NEE =
$$50.01 - 0.02$$
 PFFD + 5.34 VPD - $1.02 \times$ Ta
- $56.71 \times$ SWC (3)

The multiple regression equation between NEE and the environmental predictors explained the variance of the model. The derived model (Eq. 3) can explain the reasons of about 56% variations (R^2 =0.56) of NEE of CO₂ in tropical jute agro-ecosystem using the environmental predictors such as PPFD, VPD, T_a, and SWC.

Table 2 Con	rrelation matrix b	etween net ecosyster	m $\rm CO_2$ exchange	(NEE) and related n	neteorological var	riables $(n=3038)$	3)
	NEE	DDED	n	DII	CHE	T	-

	NEE	PPFD	R _n	RH	SHF	$T_{\rm a}$	VPD
NEE	1.00						
PPFD	-0.79**	1.00					
R _n	-0.78^{**}	0.99**	1.00				
RH	-0.41^{**}	-0.66**	-0.65**	1.00			
SHF	-0.44**	0.68**	0.68**	-0.73**	1.00		
T _a	-0.51**	0.67**	-0.66**	-0.79**	0.81**	1.00	
VPD	-0.42**	0.69**	0.68**	-0.98**	0.76**	0.87**	1.00

NEE net ecosystem CO₂ exchange (µmol m⁻² s⁻¹), *PPFD* photosynthetic photon flux density (µmol m⁻² s⁻¹), R_n net radiation (W m⁻²), *RH* relative humidity (%), *SHF* soil heat flux at 5-cm depth (W m⁻²), T_a air temperature (°C), *VPD* vapour pressure deficit (kPa), *ns* non-significant

**1% level of significance (p < 0.01)

*5% level of significance (p < 0.05)

Relationship of NEE vs PPFD at different growth stages of jute crop

As the photosynthetic activities of jute crop is mainly driven by the radiation factor (availability of photon) with significant correlation between NEE and PPFD, an effort was made to assess the relationship at every growth stages of the crop. The daytime NEE and PPFD were correlated over the different jute growth stages and the season as a whole. For each growth stages, the best-fit logarithmic models and their R^2 values along with corresponding LAI values are presented in Fig. 6. The scatter plot of NEE and PPFD for the entire jute growing season was found to be wide spread with R^2 value of 0.56 (Fig. 6f). The biophysical parameters (LAI/biomass) of jute crop changed very rapidly during the growing season (Fig. 3) and significantly altered the light interception as well as the ecosystem level photosynthetic parameters. Hence, a single fitted equation relating NEE to PPFD ($R^2=0.54$) for the entire growing season could not accommodate the differential light response of jute crop over the season. However, for each of the growth stages, the correlations

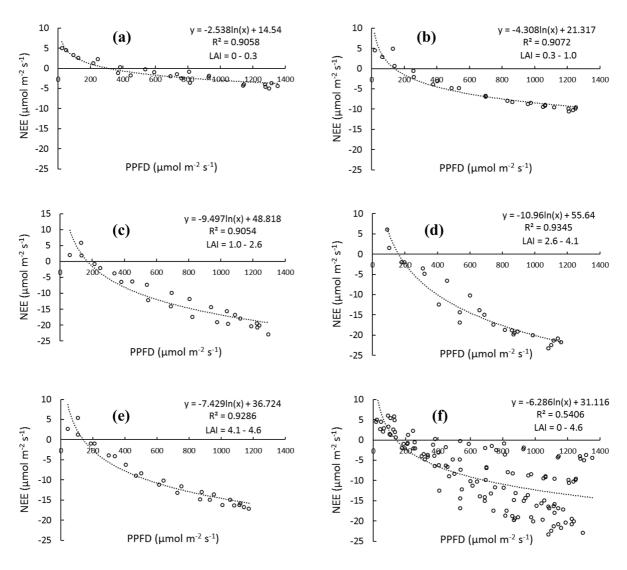


Fig. 6 Relationship between daytime photosynthetic photon flux density (PPFD) and net ecosystem CO_2 exchange (NEE) over jute ecosystem during (a) germination stage, (b) seedling stage,

(c) active vegetative stage, (d) fibre development stage, (e) maturity stage, and (f) entire jute growth period $(17^{th} \text{ April to } 5^{th} \text{ Aug}, 2018)$

Growth stage	$P_{\rm max} \ (\mu { m mol} \ { m CO}_2 \ { m m}^{-2} \ { m s}^{-1})$	α (µmol CO ₂ µmol photon ⁻¹)	$R_{\rm e} (\mu { m mol}{ m CO}_2{ m m}^{-2}{ m s}^{-1})$	R^2
Germination stage	$14.15 \pm (0.45)$	$0.021 \pm (0.0015)$	$5.18 \pm (0.19)$	0.93
Seedling stage	$24.51 \pm (0.78)$	$0.036 \pm (0.0025)$	$5.75 \pm (0.21)$	0.97
Active vegetative stage	$63.30 \pm (1.15)$	$0.039 \pm (0.0031)$	$6.72 \pm (0.24)$	0.95
Fibre development stage	$52.36 \pm (1.12)$	$0.072 \pm (0.0045)$	$9.76 \pm (0.28)$	0.94
Maturity	$41.34 \pm (1.04)$	$0.045 \pm (0.0028)$	$6.45 \pm (0.22)$	0.97

Table 3 Growth stage-wise ecosystem photosynthetic parameters of jute crop with standard error (95% confidence)

 P_{max} maximum photosynthetic capacity, α apparent quantum yield, R_e ecosystem respiration, R^2 coefficient of determination; values in parentheses are standard errors

were found statistically significant with high R² values (> 0.9). But the sensitivity of NEE to PPFD was found to be very low during the germination stage due to low LAI (Fig. 6a). It improved as the jute crop season progressed through the seedling stage (LAI 0.3 to 1.0 m² m⁻²), active vegetative stage (LAI 1.0 to 2.6 m² m⁻²), and fibre development stage (LAI 2.6 to 4.1 m² m⁻²). Sensitivity slightly decreased in the maturity stage (LAI 4.1 to 4.6 m² m⁻²) perhaps due to the reduction of the leaf chlorophyll content (Palit & Meshram, 2004), and yellowing and shedding of lower leaves (Kumar et al., 2016).

Such growth stage-wise relations are also very important to assess the apparent quantum yield (α) of an ecosystem to improve parameterisation for carbon cycle models (Zhang et al., 2006). The apparent quantum yield is described as the fixation of quanta of CO_2 molecules per unit of photon irradiated (Ruimy et al., 1995). It has a key role in understanding the photosynthetic responses of a crop, and also estimating α , which provides important information for large-scale ecosystem models e.g. CASA (Potter et al., 1993), Biome-BGC (Running & Coughlan, 1988), TEM (Raich et al., 1991), TURC (Ruimy et al., 1996), and BIOME3 (Haxeltine & Prentice, 1996). The α is generally computed by fitting a rectangular hyperbolic function between NEE and PPFD (Ruimy et al., 1995; Saito et al., 2005). This function responds to two different light conditions: there is near-linear response during low light conditions, and saturation to maximum productivity response in higher light conditions (Ruimy et al., 1995). Using Eq. (3), growth stage-wise estimated coefficients of photosynthetic efficiency of the jute ecosystem are presented in Table 3.

Substantial differences in photosynthetic efficiency parameters were observed across the jute growth stages. The maximum photosynthetic capacity (P_{max}) was very

low (14.15 μ mol CO₂ m⁻² s⁻¹) in the germination stage due to minimal green biomass. It gradually increased with increase in the above-ground green biomass of the crop and reached 24.51, and 63.3 μ mol CO₂ m⁻² s⁻¹ in seedling stage and active vegetative stage, respectively, but subsequently reduced to 52.36 and 41.34 µmol CO₂ $m^{-2} s^{-1}$ in fibre development stage and maturity stage, respectively. The low value of P_{max} in the maturity stage might be due to cessation of crop growth and shedding of lowers leaves. The apparent quantum yield (α) also followed the similar trend as that of P_{max} . The α -value was found to be maximum in the fibre development stage (0.072 μ mol CO₂ μ mol photon⁻¹). Rapid increase in plant height together with fibre development during this stage necessitates more energy supply and thus well coincided with the maximum value of α . The maximum R_e-value (9.76 μ mol CO₂ m⁻² s⁻¹) was estimated in this stage might be due to high physiological activities in plants. It is apt to note here that jute is a C3 crop and all values of the parameters were well within the ranges of the C3 crops as reported by Ruimy et al. (1995) and Ehleringer and Björkman (1977).

Conclusion

India has very diverse and dynamic agro-ecosystems which play a vital role in ecosystem-atmospheric carbon exchanges and global carbon budget as a whole. The present study could characterise CO_2 fluxes from jute ecosystem using high-frequency measurements by eddy covariance system along with bio-meteorological observations in a hot and sub-humid Indo-Gangetic plain. The study could capture the diurnal, daily, growth stage-wise variations of NEE over the jute crop. It was observed that the diurnal variations of NEE are highly influenced by the different growth stages of the crop and incoming solar radiation (PPFD or R_n). The daytime peak NEE was lowest in the germination stage $(-5 \mu mol CO_2)$ m^{-2} s⁻¹) and highest in the fibre development stage $(-23 \mu mol CO_2 m^{-2} s^{-1})$. At nighttime, the jute ecosystem acted as a net CO₂ source (5 to 8 μ mol CO₂ m⁻² s⁻¹) throughout the jute season. The daily NEE was found to increase (influx) with the progression of crop growth due to accumulation of above-ground biomass or LAI. The daily mean NEEs in germination, seedling, active vegetative, fibre development, and maturity stages of the jute crop were found to be 1.66, -0.57, -3.23, -4.23, and -2.51 gC m⁻² day⁻¹, respectively. The seasonal cumulative NEE was found to be -268.5 gC m⁻² (i.e. 10.3 t CO_2 ha⁻¹) signifying the jute ecosystem as a significant net CO2 sink. The study has also reported the ecosystem level photosynthetic parameters over the different growth stages of jute crop. Maximum photosynthetic capacity was observed during the active vegetative stage $(63.3 \pm 1.15 \text{ }\mu\text{mol CO}_2 \text{ }m^{-2} \text{ }s^{-1})$, whereas peak value of apparent quantum yield was recorded during fibre development stage $(0.072 \pm 0.0045 \,\mu\text{mol CO}_2 \,\mu\text{mol}$ $photon^{-1}$). To the best of our knowledge, such dataset of ecosystem level CO₂ fluxes along with photosynthetic parameters of jute crop is the first report and can be used as a primary data source to develop/validate different jute-specific ecosystem models, crop growth models, satellite-based production estimates, light use efficiencybased productivity models, etc. These models can further be used to upscale the ecosystem CO_2 exchanges at regional level and to assess the response of the jute ecosystem at different climatic scenarios.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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