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Environmental controls on net CO_2 exchange over a young rubber plantation in Northeastern Thailand

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ABSTRACT: Net ecosystem CO_2 exchange (NEE) over a 5-year-old rubber plantation was measured, using Eddy Covariance technique in 2014 to (1) quantify the seasonal distribution of NEE and its partitioning into daily gross primary production (GPP) and ecosystem respiration (R_d) and (2) examine how key environmental factors influence those carbon fluxes. We found that the daily amplitude of carbon fluxes varied substantially within the growing season, with the largest daily changes occurring in July. The daily maximum NEE generally occurred before noon, while maximum R_d occurred around sunset. The NEE peak of each growth stage was different. The seasonal variations of NEE, GPP and R_d, all of which were closely related to the rubber phenology, reached the peak value in July. Annual NEE, Reco and GPP were 715.21, 591.98, and 1298.93 g C m^{-2} y^{-1}, respectively. The 5-year-old rubber plantation behaved as a carbon sink from the end of refoliation stage to the beginning of defoliation period, while it acted as a carbon source within 1–2 weeks. The response of daytime NEE to light (PAR, photosynthetic active radiation) showed that 37–69% of the variation in NEE was explained by the change in net solar radiation. The effect of PAR was dependent on growth stage of rubber plantation. The 3-light response parameters, maximum photosynthetic capacity (P_{max}), ecosystem apparent quantum yield (α) and ecosystem respiration (R_d), varied with the growth stage, i.e., initial stage, refoliation, fully expanded leaf and defoliation. Range of P_{max}, α, and R_d were −9.44 to −46.61 µmol CO_2 $m^{-2}\,s^{-1}$, −0.0041 to −0.0428 µmol CO_2 µmol^{-1} photon, and 1.06–4.91 µmol CO_2 $m^{-2}\,s^{-1}$, respectively. The highest values of P_{max} occurred in defoliation stage. Both of α and R_d were highest in fully expanded leaf stage. The impact of air temperature (Ta) and vapour pressure deficit (VPD) on NEE light response was studied. The magnitude of P_{max} , α, and R_d decreased with increasing of Ta. P_{max} increased with the increase in VPD, the maximum value of P_{max} occurred at low level of VPD (VPD $\leqslant$ 1 kPa). Values of α and R_d at medium level of VPD ($1 < \text{VPD} < 2$) were the highest. Multiple linear regression and correlation methods were used to assess the relationship between NEE and environmental factors. The environmental factors controlling NEE were different depending on growth stage.

KEYWORDS: net ecosystem CO_2 exchange, light response, Eddy covariance, rubber

INTRODUCTION

Changes in the global climate system due to increased levels of CO_2 and other greenhouse gases are predicted to significantly impact the Earth's terrestrial ecosystems. Current climatic changes induce not only increase in mean air and soil temperatures, but also alter distributions of rainfall such as drought and intense storms[1,2]. Such climatic variations affect the canopy structure and the carbon flux in total ecosystem respiration and gross productivity, the two components of net ecosystem productivity, thus leading to contrasting seasonal variations in the carbon balance in regions[3]. Exchange of CO_2 between terrestrial ecosystems and the atmosphere is controlled by the balance between CO_2 uptake during photosynthesis (gross primary production, GPP) and CO_2 emission via plant and soil respiration (ecosystem respiration, R_d). Photosynthetic uptake and respiratory release are separated processes, with different responses to environmental change. GPP depends on temperature, radiation and moisture during the growing season if temperature is adequate for growth[4–6], whereas Reco is mainly regulated by temperature and moisture[7,8]. Although recent studies also suggested a tight coupling between those processes, light, temperature, and moisture are out of phase over the course of the year. The photosynthetic uptake and respiratory release may have dissimilar periods of activity. Hence, it is necessary to understand the biological and physical controls on photosynthesis and respiration in order to estimate how net ecosystem exchange of CO_2 will respond to the ongoing climate change.

Recently, Eddy covariance (EC) technique became one of the best micrometeorological methods for estimating the CO_2, water vapor, and energy exchange between the atmosphere and terrestrial ecosystems. The EC technique is now widely used to measure the vertical turbulent CO_2 flux between the atmosphere and biosphere as it provides continuous flux information integrated at the ecosystem scale, and annual carbon sink or source strength for a wide variety of ecosystems[9,10]. In recent years, many studies have used EC technique to measure immediately net ecosystem exchange of CO_2 (NEE) or net flux of photosynthetic carbon uptake and respiratory release, regardless of plant growth, allocation, and other biological processes. Thus, EC data provides a valuable tool for studying variability in carbon fluxes related to photosynthesis period, gross primary production and respiration of ecosystems[11,12]. The strength of this method is able to measure over short and long time scales (hour, days, seasons, and years), providing high temporal resolution flux data with a possess longitudinal dimension ranging between a hundred meters to several kilometers under small or no disturbance when compared with traditional biometric method.

Rubber (*Hevea brasiliensis* Müll. Arg.) is among the major economic tree crops of tropical areas throughout the world, especially in Southeast Asia. In Thailand, the rubber plantation area is much larger than the area of forest plantations. In 2015, the total area of rubber plantation was 3.73 million ha, more than 2 million ha plantation is mainly grown in southern part of Thailand because the climatic condition in this area is similar to that in area of origin in the Amazon, where rainfall is 2000 mm without dry season, and a mean annual temperature is $28 \pm 2\,°C$[13]. Due to the increase of world natural rubber demand, rubber is currently expanding rapidly in non-traditional areas of Thailand, especially in the north and north-east. These areas, however, are marginal for rubber cultivation, having about half of the year with near-ideal conditions, while other months with stressful conditions including low or high temperature or near-drought conditions with the annual rainfall of less than optimal level for rubber plantation. Several reports have shown that unsuitable environmental conditions would significantly affect the latex productivity, the timber production of rubber, decreasing of biodiversity, reduction of total carbon biomass, alteration of the hydrological regime, and acceleration of erosion[14–16]. In traditional area of rubber plantation, the rubber trees are grown under rained condition, water availability is highly unpredictable over the course of the year. Moreover, the extreme weather is expected to occur. Rainfall variability and subsequent dry periods may have different impact on the plants and soil microbe activities and the ecosystem carbon exchange in rubber plantation such as lack of water during very long dry period, it could be the cause of NEE reduction through a decrease of photosynthesis from partial stomatal closure. Further, a previous study found that ecosystem respiration suddenly increased following rainfall due to the quick activation of soil microbial with the consequent mineralization of organic matter and nutrient and activation of plant growth[10], thus it would be expected that the increase in rainfall variability can increase carbon cycling in an ecosystem. Information about ecosystem exchange of CO_2 is more available in forest and grassland but it is still scarce for rubber ecosystem. If we have more information about CO_2 exchange in rubber plantation, which is important for understanding the response to climate change and predicting the rubber ecosystem, this will help to improve rubber productivity under global climate change. In addition, to investigate and quantify the strength of the carbon sink or source of the rubber plantation and its sensitivity to seasonal and annual climate variability, this will help politicians and economists to make policies that coordinate harmonize interactive relations among land use, economic growth and climate change.

The main objective of this experiment is to continuously measure and understand the net ecosystem exchange of CO_2 and its variation characteristics as well as the controlling environment factors over young rubber ecosystem in Northeastern Thailand. These information were used to (1) quantify the seasonal distribution of GPP and its partitioning into NEE and Reco and (2) examine how key environmental controls influence those carbon exchanges.

MATERIALS AND METHODS

The experimental site was located at Pak Khat district, Bueng Kan province (18°13′22.77″N, 103°18′59.46″E and elevation 186 m asl), north-eastern Thailand. The plantation was a monoclonal stand of rubber trees (*Hevea brasiliensis* Müll. Arg.) planted with the clone RRIM 600 in 2009, with a tree spacing of 7×3 m^2. The clone RRIM 600 is the most extensively planted in Thailand (78% of the planted area). In 2014, the mean annual temperature and precipitation were 27 °C and 1816 mm, respectively. Soil is a sandy clay loam and has a bulk density of 1.41 ± 0.07 g cm^{-3} (mean ± SD, n = 6) in the upper 10 cm of the soil profile.

Eddy flux measurements

The Eddy covariance (EC) instruments were mounted at a height of 11.5 m on a tower. EC system consisting of a three-dimensional ultrasonic anemometer (CSAT-3, Campbell Scientific Inc., USA) and the open-path infrared gas analyser (IRGA) (LI-7500, LI-COR Inc., USA) which were used to measure speed and direction of the wind, and concentration of CO_2 and water vapour, respectively. The sensor head of IRGA was tilted 15 South and 20 cm horizontally from the CSAT-3 in order to avoid direct sunlight contamination in the optical path and to facilitate the draining of rain water from the lower lens surface. The EC technique applied here is based on the assumption that the flux of a given scalar parameter can be measured as an average of the covariance between the 20-Hz fluctuations in the vertical wind speed and the 20-Hz fluctuations of the scalar parameters. CO_2 flux was calculated as the mean covariance of vertical wind velocity and scalar fluctuations, with the appropriate corrections applied[17]. The following equation presents the calculation of CO_2 flux[18], $F_{CO_2} = \overline{\rho_a w'c'}$, where ρ_a is density of the air, w' and c' are vertical wind speed and CO_2 concentration fluctuations from the means, respectively, and the bar indicates the time averaging. All raw data were collected at a rate of 20 Hz by a data logger (CR5000, Campbell Scientific Inc., USA). The 30-min mean CO_2 fluxes were calculated by using all raw data. Before covariance calculation these time series data were de-spiking and linearly detrended. The fluxes were three-dimensional coordinate rotations[19] to align the sonic anemometer axis along the long-term streamlines and WPL-correction[20]. Following the sign convention in the atmospheric flux community, positive flux covariance represents net carbon gain by the atmosphere and loss from the ecosystem. In contrast, negative flux covariance indicates the loss of carbon from the atmosphere and gain by the ecosystem. Continuous measurements of CO_2 flux data were started in January 2014 and continued through the end of the growing season in December 2014.

Partitioning of NEE into GPP and Reco

To separate NEE into photosynthetic and respiration fluxes, NEE were divided into day and night period to develop non-linear regressions for evaluating environmental effects on NEE. GPP is the difference between the estimated Reco and observed NEE. GPP was partitioned into its components using the equation[21], GPP = Reco − NEE, where GPP represents CO_2 assimilation by photosynthesis of and Reco consists of respiratory CO_2 released from soil and vegetation, respectively. During the nighttime (incoming solar radiation < 10 W/m^2), nighttime NEE values are equal to Reco because the GPP equals zero at night. To estimate day-time ecosystem respiration, daytime estimated of Reco were obtained from the nighttime NEE-temperature relationship. The relationship between nighttime NEE and air temperature can be described by Van't Hoff equation[22], $\mathrm{Reco} = a\,e^{bT}$, where a and b are regression parameters and T is the air temperature (°C). Daily and monthly values of GPP and Reco were summed from the half-hourly data

Meteorological measurements

Along with the EC measurements, standard meteorological data and soil parameters were measured continuously with an array of sensor. These sensors included Quantum sensor (LI-190SB, LI-COR Inc., USA) for Photosynthetically active radiation (PAR) measurement. Solar radiation and net radiation were measured by using net radiometers (CNR-1 and NR-Lite, Kipp & Zonen, The Netherlands). Rainfall was measured by using the tipping bucket rain gauge (TE525, Campbell Scientific Inc., USA). Air temperature and relative humidity were measured by the temperature and relative humidity probe (HMP45C, Vaisala, Finlamd). Belowground parameters were measured at 3 locations in rubber plantation. Soil temperature at depths of 0.02, 0.04, 0.06, 0.32, 0.64, and 1 m from soil surface were measured with a custom built chromel-constantan thermocouple. Soil volumetric water content at depths of 0.10, 0.30, 0.50, 0.70, 1, and 1.5 m. from soil surface was measured with Water Content Reflectometer (CS616, Campbell Scientific Inc., USA). All parameters were measured every 10 s and stored the 30 min average data with data logger (CR1000, Campbell, Scientific Inc., USA). Leaf Area Index (LAI) was estimated by using the litter collection method. 20 litter traps were randomly placed across the plantation at a height of 1 m above ground level. The traps were square with 1 m^2 area. The litters were collected twice a month and separated to leaves, branches, seeds and fruits. All parts of litters were weighed after drying at 60 °C for 48 h.

Statistical analysis

Multiple regressions analysis was used to assess the relationship of NEE with concurrent changes in the environmental variables, PAR, Ta, VPD, and volumetric soil water content (SWC). For daytime data based (incoming solar radiation > 10 W/m^2), variation of NEE was also correlated with PAR by using the Michaelis-Menten hyperbolic rectangular equation[23],

$$\mathrm{NEE} = \frac{\alpha P_{\max} \mathrm{PAR}}{P_{\max} + \alpha \mathrm{PAR}} + R_d, \qquad (1)$$

where α (μmol CO_2 μmol^{-1} PAR) is the ecosystem apparent quantum yield (initial light use efficiency), $P_{\max}$ (μmol CO_2 $m^{-2}\,s^{-1}$) is the maximum photosynthetic capacity and R_d (μmol CO_2 $m^{-2}\,s^{-1}$) is the average daytime ecosystem respiration.

RESULTS AND DISCUSSION

Seasonal variation in environmental conditions

In order to study the carbon exchange between the rubber plantation and the atmosphere, it is necessary to first understand the seasonality of key environmental variables. In 2014, the daily mean PAR ranged from 74.16 (30 Oct) to 556.9 (1 Jun) μmol $m^{-2}\,s^{-1}$ (Fig. 1a). The daily mean air temperature (Ta) and soil temperature at 6 cm below soil surface (Ts) values showed the same pattern, ranging from 15.8–30.8 °C and 17.3–29.5 °C, respectively (Fig. 1b). The distribution of relative humidity (RH) showed a large variation and mean RH was 74.2% with a daily maximum at 96.3% in June (Fig. 1b). Rainfall peak was in September. The total rainfall was 1545 mm, with the largest daily rainfall occurred on 16 September (83.6 mm) (Fig. 1c). The variation of SWC at 10 cm depth has a similar pattern with rainfall, ranging from 0.081–0.344 $m^3 \cdot m^{-3}$. In rainy season (Apr–Sep), SWC at 10 and 30 cm-depths closely followed the changes in rainfall. But in dry season (Oct–Dec, Jan–Apr), SWC at both depths declined slowly and remained relatively constant as a season progressed. In rainy season (Apr–Sep), SWC at both depths was similar. But in dry season, SWC at 10 cm-depth was lower than the other one and were below 0.1 $m^3 \cdot m^{-3}$ for 174 days, suggesting severe drought in the ecosystem (Fig. 1c. Otherwise, SWC at 30 cm-depth was less responsive and generally lagged rainfall.

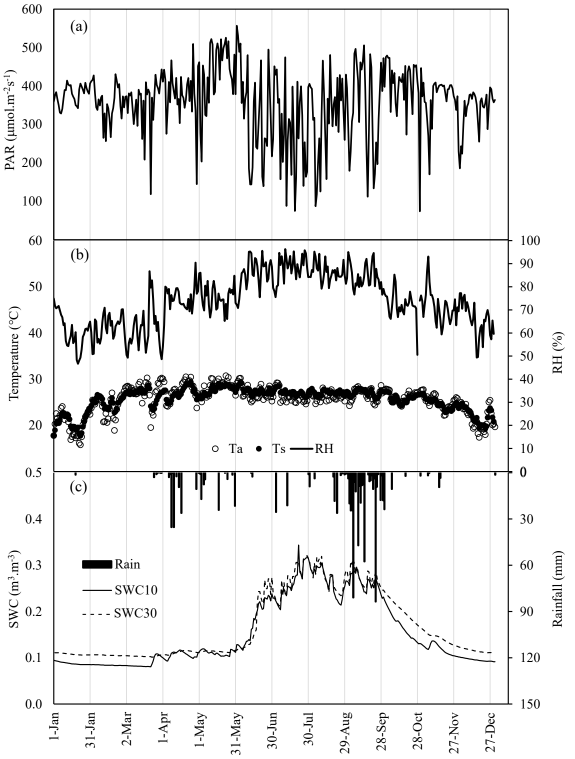

Fig. 1 Seasonal variations of (a) photosynthetic available radiation (PAR), (b) air temperature (Ta, opened circle), soil temperature at 6 cm below soil surface (Ts, closed circle) and relative humidity (RH), and (c) soil water content at 10 (SWC10) and 30 (SWC30) cm below soil surface and rainfall. Daily means were shown for PAR, Ta, Ts, RH, and SWC. Daily sum was shown for rainfall.

Diurnal and seasonal variation of NEE

The diurnal variation of NEE was calculated for different growth stages of young rubber plantation in 2014 (Fig. 2). The growing season could be divided into 4 phenological stages: No leaf (Dry season, 1–23 Jan), Refoliation stage (24 Jan–14 Mar), Fully expanded leaf stage (15 Mar–30 Sep), and Defoliation stage (1 Oct–31 Dec). Diurnal

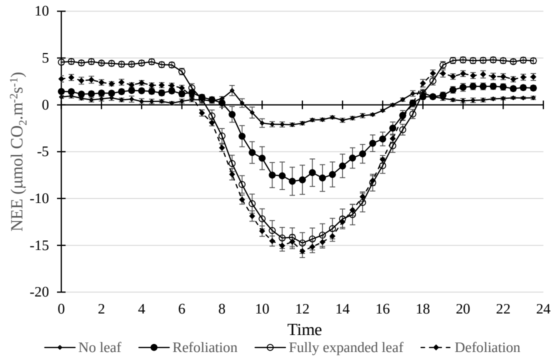

Fig. 2 Diurnal variations of net ecosystem exchange (NEE) in the different growth stage of rubber plantation. Bars represent standard errors of means.

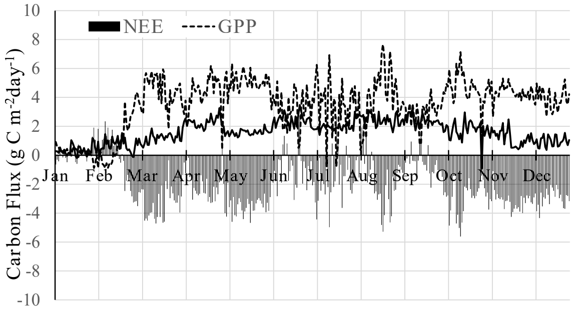

Fig. 3 Seasonal variations of net ecosystem CO_2 exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (Reco) over rubber plantation in 2014.

variation of NEE has the same and obvious pattern for all growth stages. The NEE peak of each growth stage was different. NEE values were negative in day-time and positive in night-time. The minimum of NEE appeared around noon. The negative NEE represents that CO_2 was absorbed by rubber tree and was used in photosynthesis.

The average diurnal variations of NEE for each half hour showed obvious pattern. From 0–7 a.m., the NEE was positive and moves to negative value around 7 a.m. The daytime uptake rate is highest around noon, and afterwards it begins to decrease. Night time NEE showed nearly constant release of CO_2 over the whole period.

There was large seasonal variation in ecosystem photosynthetic and respiration activity as illustrated in the average diurnal patterns of NEE during rubber growing season (Fig. 2). The half hour data were averaged from 0:00 to 23:00 periods. The diel amplitude of carbon fluxes varied substantially within the different growth stages. During the no leaf, Dry season, NEE fluctuated within ±3 μmol $m^{-2}\,s^{-1}$. Then as LAI and day length increased during refoliation stage, NEE exhibited a rapidly rising trend. The amplitude of the diurnal variation in NEE increased with the growth of rubber and the daily maximum CO_2 uptake values occurred during the peak growing seasons. The maximum uptake rate was -15.26 ± 1.22 μmol $m^{-2}\,s^{-1}$, occurring in the fully expanded leaf stage. With the decrease of air temperature and the defoliation of rubber ecosystem, the decline in ecosystem CO_2 exchange began in October and very little diurnal variation was evident in NEE at the end of the dry season. The greater reduction in NEE was observed during severe dry periods. The reduction of NEE under dry conditions is usually caused by reduction of both ecosystem photosynthesis and respiration. The reduction of photosynthesis under dry conditions could be partially attributed to stomatal closure, while the latter could be the decrease of leaf photosynthetic activity which can lead to irreversible reduction of plant photosynthesis[24, 25].

Fig. 3 shows the daily average of the NEE, GPP and Reco. Daily of NEE over 2014 ranged from −5.12 to 2.35 g C $m^{-2}\,day^{-1}$, with average values of −1.96 g C $m^{-2}\,day^{-1}$. The highest value of NEE was found during the short, dry period in January (2.35 g C $m^{-2}\,day^{-1}$) and the lowest during the rainy season in August (−5.12 g C $m^{-2}\,day^{-1}$). The mean value of NEE was positive and reached its peak in mid-January near the period when Reco was at the peak, so the ecosystem acted as a carbon source during the early growing season and immature leaves. After the leaf was large enough to provide canopy closure, GPP increased quickly than Reco, thus NEE became negative following increase in LAI during refoliation period. The maximum net CO_2 uptake period occurred in the fully expanded leaf period (mid-April to October), associated with highest crop growth and more optimal growing conditions. When dry season starts in mid-October, NEE increased and turned the ecosystem into a weak carbon sink in January. Daily GPP in the growing season ranged from −0.88 to 7.66 g C $m^{-2}\,day^{-1}$, with average value of 3.56 g C $m^{-2}\,day^{-1}$. GPP reached a maximum of 7.66 g C $m^{-2}\,day^{-1}$ on 21 August as a result of the highest LAI. Maximum Reco was 3.48 g C $m^{-2}\,day^{-1}$ on 23 June. Annual NEE was −715.21 g C $m^{-2}\,day^{-1}$. Annual Reco contributed 591.98 g C $m^{-2}\,day^{-1}$, leading to an annual GPP of 1,298.93 g C $m^{-2}\,day^{-1}$. These results are consistent with previous studies because few studies also found that the rubber ecosystem is a carbon sink.

For example, Annamalainathan et al[26] measured the 4–5 year old rubber ecosystem in India and found that it was a CO_2 sink, taking up −33.5 t CO_2 $ha^{-1}\,y^{-1}$ in 2010. Song et al[27] found that the 33-year-old rubber plantation in southwestern China is a carbon sink and the values of NEE was −2.69 t C $m^{-2}\,y^{-1}$. NEE value observed in this study is lower than that obtained by Tan et al[28] in tropical rain forests using eddy covariance technique (−1.19 Mg C $ha^{-1}\,y^{-1}$), and biometric method (−3.59 t C $ha^{-1}\,y^{-1}$) and also lower than that in subalpine coniferous forest[29] (-4.05 ± 0.41 t C $ha^{-1}\,y^{-1}$) in southwest China. This is possibly related to tree age which may be one reason for difference in carbon uptake. The rubber ecosystem we studied was a young tree, and it thus represents a huge C fixation potential. Hence, more age of rubber ecosystem in the future may lead to substantially increase carbon sequestration capacity in Southeast Asia. At our site, precipitation in 2014 was at least 1545 mm which was higher than the long-term mean (1467 mm), future studies that assess how rubber ecosystems respond to inter-annual variability in water availability are expected.

Response of daytime NEE to PAR

Photosynthesis is driven by light but there were marked differences in the light response curve among seasons for the evolution of the rubber canopy. To assess the response of daytime NEE to net solar radiation, Fig. 4 shows the light-response curve for short periods of the main stage of plant growth. It is widely acknowledged that photosynthetically active radiation (PAR) is the most significant environmental factor for variation in NEE[30,31]. In general, photosynthetic activity and carbon uptake by the ecosystem increase as PAR levels increase. As a result, 37–69% of the variation in NEE was explained by the change in net solar radiation. The effect of PAR was dependent on growth stage of rubber plantation. This Fig. 4 shows that daytime NEE decreased with increases in PAR but increased as LAI increases when compared with the same values of PAR. The low NEE at the early season (DOY (day of year) 1–14) was most likely due to small canopy size, low temperature, and immature leaves. The light saturation point varies with different growth stage. The NEE reached saturation at values ranging between −15 and −25 μmol $m^{-2}\,s^{-1}$ when PAR was greater than 700 W m^{-2} in the period of DOY 85–98 associated with the highest LAI.

Seasonal dynamics of coefficient of light response curve parameter at different growing stages are summarized in Table 1. The R^2 between NEE and PAR were significant in all growth stages. This means that the PAR and NEE fit well. In general, the P_{max}, α, and R_d changes with the growth stage. Previous studies found that all values first increased, then decreased following the processes of crop growth, development and senescence[32,33]. We find similar results in our experiment. The P_{max}, and R_d values varied from −9.44 to −46.61 μmol CO_2 $m^{-2}\,s^{-1}$, 1.06–4.91 μmol CO_2 $m^{-2}\,s^{-1}$, respectively. The absolute values of P_{max} was highest in defoliation stage. Both of α and R_d were highest in fully expanded leaf stage. The α is a basic parameter of photosynthetic CO_2 absorption, light utilization and material productiovity and absolute value in our study was 0.0041–0.0428 μmol CO_2 μmol^{-1} photons, within the range of published data for forest ecosystem (0.044 μmol CO_2 μmol^{-1} photons)[4] and was lower than intensively managed grasslands and agricultural crops (0.05–0.075 μmol CO_2 μmol^{-1} photons)[34,35]. The R^2 for No leaf stage was much smaller than the for fully expanded leaf stage and defoliation stage, which may be caused by low LAI and low soil water content which limited rubber carbon metabolism rate and rubber growth[36].

In order to further investigate the influences of Ta, and VPD on the response of daytime NEE to PAR, daytime NEE data were separated into two Ta classes (low Ta < 30 °C, and high Ta ⩾ 30 °C), and three VPD classes (low VPD ⩽ 1 kPa, medium 1 kPa < VPD ⩽ 2 kPa, and high VPD > 2 kPa). The effect of PAR was modified by other environmental factors (Fig. 5). The results show that the magnitude of P_{max}, α, and R_d decreased with increasing of Ta. At Ta < 30 °C, P_{max}, α, and R_d were −45.16 μmol CO_2 $m^{-2}\,s^{-1}$, −0.0630 μmol CO_2 μmol^{-1} photons, 9.62 μmol CO_2 $m^{-2}\,s^{-1}$, respectively. The absolute values of P_{max}, α, and R_d when the Ta ⩾ 30 °C were −30.56 μmol CO_2 $m^{-2}\,s^{-1}$, −0.0601 μmol CO_2 μmol^{-1} photons, and 8.95 μmol CO_2 $m^{-2}\,s^{-1}$, respectively (Table 2).

The absolute values of P_{max} decreased as the VPD increased and were highest when VPD ⩽ 1 kPa. The highest P_{max} occurred when Ta < 30 °C and VPD ⩽ 1 kPa. These results are in general agreement with previous findings demonstrating that net CO_2 uptake decreased with the increase in Ta and VPD (Fig. 3), indicating that temperature and water stress occurred. Generally, high VPD may decrease CO_2 input through stomatal close, whereas high temperature could cause increasing

Table 1 Main environmental values and the parameters used to describe the hyperbolic rectangular response of daytime NEE to PAR.[†]

Growth stage	Ta	VPD	SWC	LAI	P_{max}	α	R_d	R^2
Initial stage	19.8	1.03	0.089	0	-9.44	-0.0041	1.58	0.37*
Refoliation	24.8	1.45	0.084		-14.84	-0.0196	2.70	0.38*
Fully expanded leaf	27.1	0.82	0.190		-30.26	-0.0428	4.91	0.64*
Defoliation	24.1	1.02	0.127		-46.61	-0.0180	1.06	0.69*

[†] (–) before P_{max} value represent CO_2 that is absorbed by plant; *, significance of the regression for $p < 0.001$.

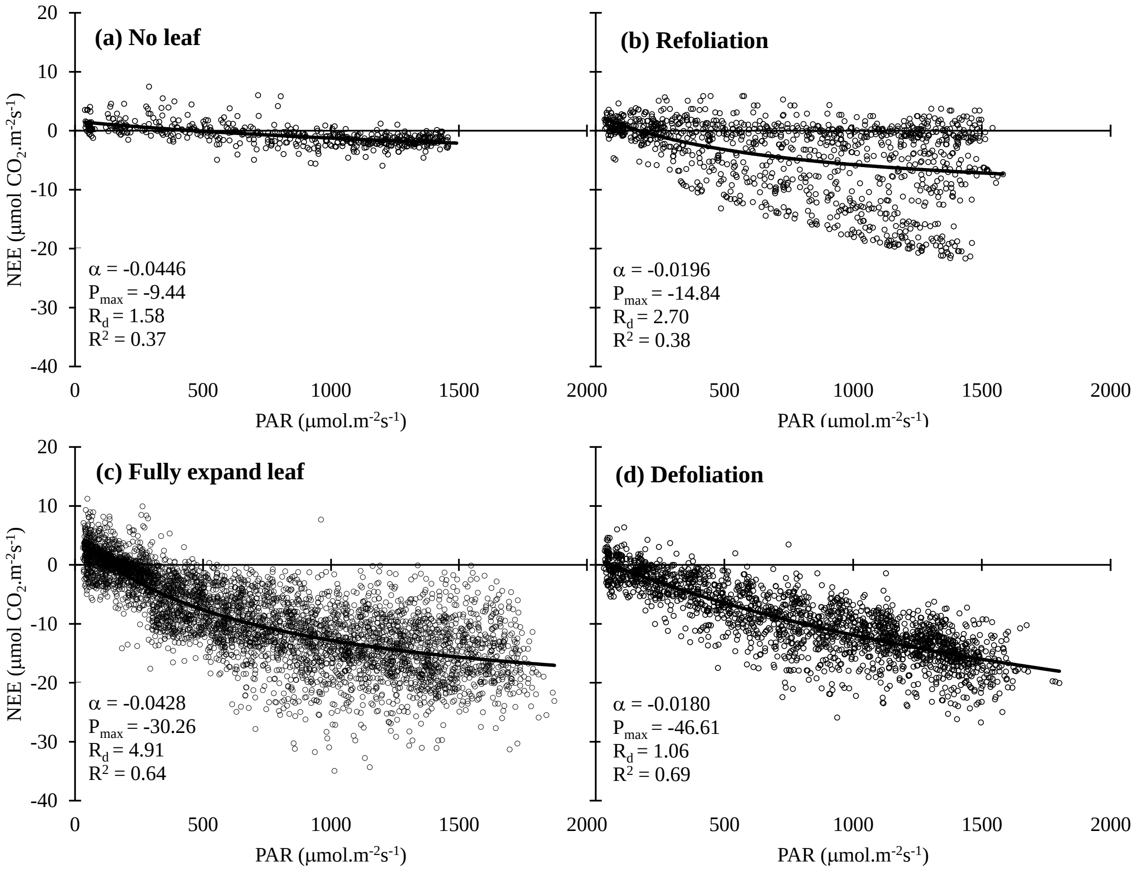

Fig. 4 Examples of light-response curves of CO_2 flux (F_c) at different growth stages. Fitted curves are hyperbolic rectangular as described by Eq. (1). The values of light response parameters were shown in Table 1.

respiration. Under high temperature (Ta ⩾ 30 °C), photosynthesis was prohibited and soil and plant respirations were great, resulting in a lower net CO_2 uptake. On the other hand, VPD controls photosynthetic rate through influencing stomatal closure[37,38]. Fu et al[39] demonstrated that LAI and SWC were the primary factors in inter-annual and inter-site variation in NEE.

Environmental factors of NEE

Multiple linear regression and correlation methods were used to access the relationship between NEE and environmental factors and, further, to identify the prevailing factors and the underlying mechanisms that resulted in the variation in NEE. The multiple regression models are summarized in Table 3. The results showed that the environmental factors of NEE were different in different growth stage. When the interaction terms among Ta, PAR,

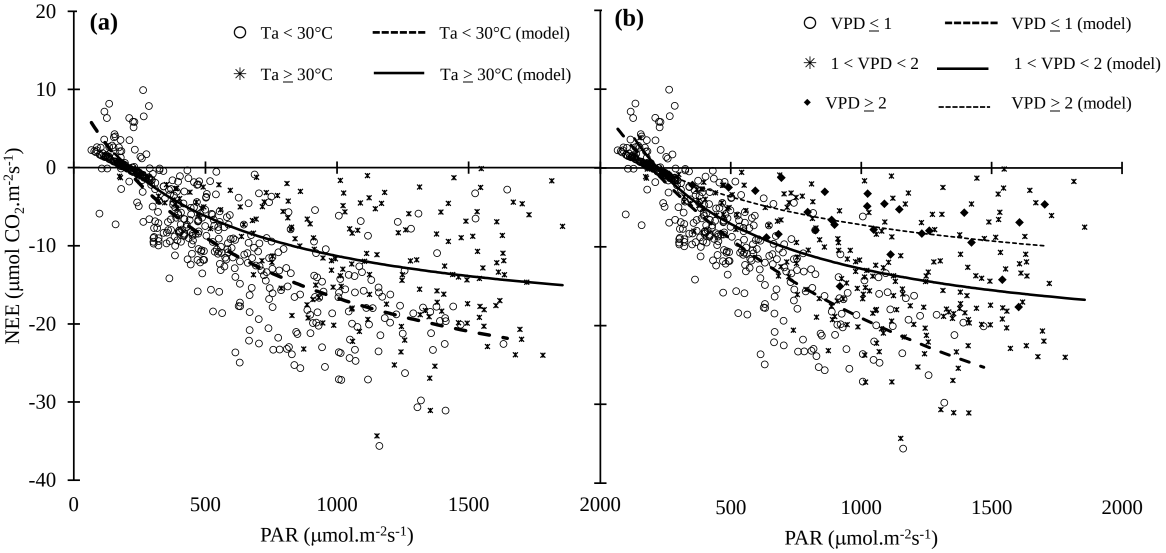

Fig. 5 Daytime net ecosystem CO_2 exchange (NEE) and photosynthetically active radiation (PAR) (a) under different air Temperature (Ta) and (b) under different vapor pressure deficit (VPD). Only data from the growing season (July) was used to minimize the confounding effects of phenology. Fitted curves are hyperbolic rectangular as described by Eq. (1).

Table 2 Impact of air temperature (Ta) and vapor pressure deficit (VPD) on parameters P_{max}, α, and R_d, derived from the hyperbolic rectangular light-response function.

Ta Condition	P_{max}	α	R_d	R^2
Low (Ta < 30 °C)	-45.16	-0.0630	9.62	0.70*
High (Ta ⩾ 30 °C)	-30.56	-0.0601	8.95	0.29*
VPD Condition	P_{max}	α	R_d	R^2
Low (VPD⩽ 1)	-65.70	-0.0455	7.85	0.76*
Medium (1 < VPD < 2)	-35.41	-0.0844	12.15	0.34*
High (VPD ⩾ 2)	-20.89	-0.0239	3.92	0.30*

*, significance of the regression for $p < 0.001$.

VPD, SWC, and Ts were included in the multiple regression analysis, the variation in NEE could be better explained by the joint effects of two or three variables. At fully expand leaf period, the linear regression

$$\mathrm{NEE} = 5.07 - 0.86\,\mathrm{Ta} - 0.11\,\mathrm{PAR} + 2.54\,\mathrm{VPD} + 39.81\,\mathrm{SWC1} - 33.06\,\mathrm{SWC2} + 3.21\,\mathrm{Ts}_1 - 2.66\,\mathrm{Ts}_2$$

was simple and its coefficient was significant, accounting for 64% of the variations in NEE. The process of carbon exchange is jointly regulated by multiple environmental factors, thus, it is difficult to identify a specific effect on the NEE caused by single factor, especially between air temperature and VPD. Therefore, the understanding of how NEE interacting environmental factors regulate ecophysiological process is needed to develop mechanistic models suitable for rubber ecosystem.

CONCLUSIONS

Net ecosystem CO_2 exchange (NEE) over 5-years old rubber plantation in Thailand was investigated, using Eddy covariance technique in 2014. We found a strong seasonality in NEE and its apparent dependence on environmental factors. During the growing season, the patterns of NEE, GPP, and Reco were found to be closely correlated to LAI, and their peaked daily values mostly occurred in mid-June in the study periods. Daily NEE ranged from -5.12 to 2.35 g C m^{-2} day^{-1}, with average values of -1.96 g C m^{-2} day^{-1}. Daily GPP was from -0.88 to 7.66 g C m^{-2} day^{-1}, with average values of 3.56 g C m^{-2} day^{-1}. PAR was found to be a strong driver for CO_2 sequestration (daytime NEE) with a maximum quantum efficiency of 0.0428 μmol CO_2 μmol^{-1} photon during fully expand leaf stage. Integration of NEE over measured year (715.21 g C m^{-2} y^{-1}) showed that 4-years old rubber plantation was a carbon sink. Reco contributed 591.98 g C m^{-2} y^{-1}, leading to an annual GPP of 1298.93 g C m^{-2} y^{-1}. The flux measurements showed that 4-years old

Table 3 Multiple regression of daytime 30-minute average net ecosystem CO_2 exchange (NEE) and main environmental factors in growing season.

Growth stage	Regression equation[†]	R^2
No leaf	$NEE = 11.99 + 0.65\,Ta - 0.0026\,PAR - 135.23\,SWC1$	0.39*
Refoliation	$NEE = -325.18 - 0.0092\,PAR + 1.63\,VPD + 6656.93\,SWC1 - 4747.84\,SWC2 + 2039.91\,SWC3$	0.74*
Fully expanded leaf	$NEE = 5.07 - 0.86\,Ta - 0.011\,PAR + 2.54\,VPD + 39.81\,SWC1 - 33.06\,SWC2 + 3.21Ts_1 - 2.66Ts_2$	0.62*
Defoliation	$NEE = 13.36 + 0.015\,Ta - 0.012\,PAR + 70.75\,SWC1 - 189.78\,SWC2 + 195.87\,SWC3 + 1.11\,Ts_1 - 2.29\,Ts_2$	0.72*

[†] SWC1, volumetric soil water content at 10 cm depth from soil surface ($m^3 \cdot m^{-3}$); SWC2, at 30 cm depth; SWC3, at 60 cm depth; Ts_1, soil temperature at 16 cm depth from soil surface (°C); Ts_2, at 32 cm depth; *, significance of the regression $p < 0.001$.

rubber plantation was a carbon source during early growing stage with no leaf, but LAI could switch it from a carbon sink to a neutral in C sequestration. This study showed that VPD, SWC, and Ta can have a major influence on carbon balance and must be taken into account when modeling NEE of a young rubber plantation.

The finding from this study can provide quantitative understanding on managing rubber ecosystem at different temporal scale. Carbon sequestration in a rubber ecosystems should be considered high priorities in climate-change adaptation and mitigation strategies throughout the world. The amount of carbon sequestered from the life cycle of rubber plantation need to be done. For a more robust evaluation of C flux in these areas, an intensive, integrated, international program of observational efforts is required.

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