Impacts of a strong El Niño event on leaf phenology and carbon dioxide exchange in a secondary dry dipterocarp forest

Rungnapa Kaewthongrach[a], Amnat Chidthaisong[a,*], Doojdao Charuchittipan[b], Yann Vitasse[c], Montri Sanwangsri[d], Pariwate Varnakovida[e], Sapit Diloksumpun[f], Samreong Panuthai[g], Tiwa Pakoktom[h], Tanita Suepa[i], Monique Y. LeClerc[j]

[a] The Joint Graduate School of Energy and Environment and Center of Excellence on Energy Technology and Environment, King Mongkut's University of Technology Thonburi (KMUTT), Bangkok, 10140 Thailand
[b] Department of Physics, Faculty of Science, Silpakorn University, Nakorn Pathom 73000, Thailand
[c] WSL Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland
[d] School of Energy and Environment, University of Phayao, Phayao 56000, Thailand
[e] Geospatial Engineering and Innovation Center, Department of Mathematics, Faculty of Science, King Mongkut's University of Technology Thonburi (KMUTT), Bangkok 10140, Thailand
[f] Faculty of Forestry, Kasetsart University, P.O. Box 1054, Bangkok 10900, Thailand
[g] National Park, Wildlife and Plant Conservation Department, Chatuchak, Bangkok 10900, Thailand
[h] Department of Agronomy, Faculty of Agriculture at Kamphaeng Saen, Kasetsart University, Nakorn Pathom 73140, Thailand
[i] Geo-Informatics and Space Technology Development Agency, Bangkok 10900, Thailand
[j] College of Agricultural and Environmental Sciences, The University of Georgia, Griffin Campus, Griffin, GA 30223, United States

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ABSTRACT

This study evaluates the impacts of the 2015/2016 El Niño event on the phenology and carbon dioxide (CO_2) exchange in a secondary dry dipterocarp forest (DDF). In western Thailand, El Niño events significantly reduced rainfall and increased air temperature, leading to prolonged dry season with low soil water content and high vapor pressure deficit (VPD). During 2014–2017, leaf phenology was monitored and CO_2 exchanges in this forest were measured by an eddy covariance method. During El Niño year, dry dipterocarp species were shed their leaves earlier when compared to neutral years (i.e. with no El Niño event). The species *Shorea siamensis* Miq. and *Sindora siamensis* Teijsm.&Miq. showed complete deciduousness during the dry season 2015/2016 as typically observed for these species, but the leafless period was longer than during non-El Niño years. *Shorea roxburghii* G.Don and *Shorea obtusa* Wall. showed untypically complete deciduousness during the El Niño year. For the species *Sindora siamensis*, however, the timing of first leaf expansion was not affected by the strong El Niño. In addition, El Niño resulted in a decline of the annual gross primary productivity (GPP) and evapotranspiration (ET) by 9.6 and 14.1%, respectively. The net ecosystem productivity (NEP) was only affected by El Niño during the dry months, but not during the following wet season therefore the total annual NEP was not significantly affected. Our result demonstrates that El Niño events have a strong impact on canopy duration of DDF ecosystem. However, our study suggests that the carbon loss during this prolonged dry season of 2015/2016 can be compensated in this young secondary DDF during the following wet season, leading to increased NEP on a yearly basis.

1. Introduction

Tropical forests contain about 25% of the carbon in the terrestrial biosphere and account for 34% of Earth's gross primary productivity (U.S. DOE, 2012). Unlike in temperate forests where temperatures fluctuate widely during the course of a year, temperatures in tropical forests (at a given elevation) vary little, and trees are thus adapted to thrive in a relatively narrow thermal range (U.S. DOE, 2012). Consequently, climatic warming is expected to substantially affect tropical vegetation because predicted changes in temperature are large compared to normal interannual variations (IPCC, 2013). In addition, alterations in precipitation patterns such as a shift toward more extreme events and extended droughts under projected climate change could potentially result in a large amount of carbon dioxide (CO_2) released
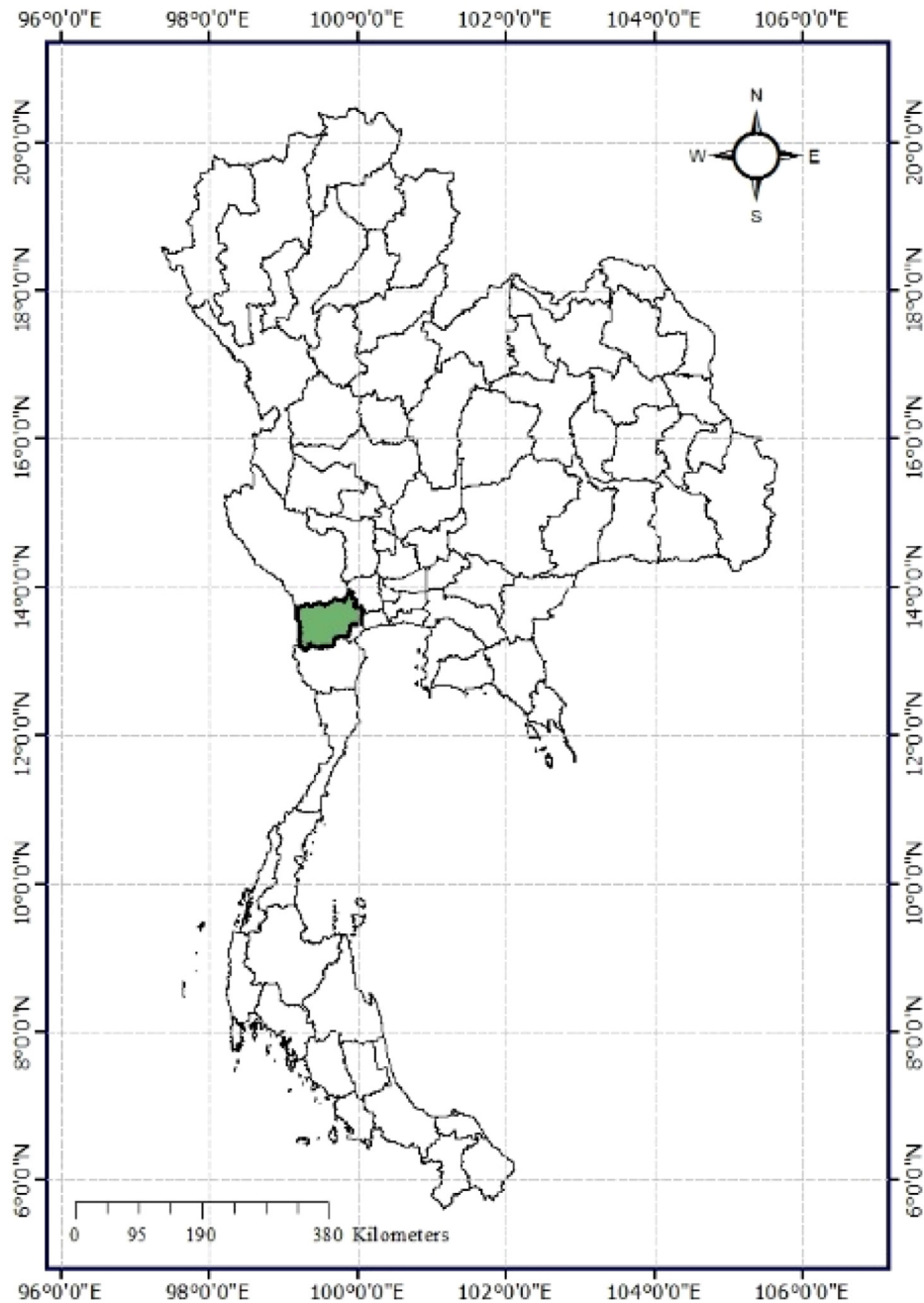

Fig. 1. Site location of a secondary dry dipterocarp forest, located in Ratchaburi province, western Thailand.

into the atmosphere (Betts et al., 2016; IPCC, 2013).

Tropical dry forests (TDFs) cover 42% of the tropical forest area and are typically characterized by the alternation of a dry and a wet season (Olson et al., 2001). Phenology of the trees growing in such biomes is adapted to undergo the dry season, with a reduction of leaf canopy, with some species being semi-deciduous and other completely deciduous during this period (Borchert, 1994; Borchert et al., 2002; Sobrado, 1997; Valdez-Hernández et al., 2010). In the continental Southeast Asia (SEA), dry dipterocarp forests (DDF) are the most common type of the TDFs (Nguyen and Baker, 2016). The DDF is dominated by tree species of the Dipterocarpaceae family that is absent from Neotropic and Afrotropic forests (U.S. DOE, 2012). Since study on DDF responses to climatic factors such as climate extreme events is still lacking, little is known about how this forest and its individual species

will adapt to future warmer and drier expected conditions (Allen et al., 2017; Castro et al., 2018).

A distinct seasonality is a dominant characteristic of DDF. As of other tree species growing in TDFs, DDF avoids the costs of maintaining leaves during the unfavorable dry season by shedding their leaves and carrying the costs of constructing new leaves during the onset of growing season (February and Higgins, 2016). The growing season, defined here as the time window between leaf-out and leaf senescence, affects various ecosystem function including biogeochemical cycles and interspecific interactions (Richardson et al., 2013; Zohner and Renner, 2017). In southeast Asia, TDFs are regularly experiencing El Niño events that lead to severed and prolonged drought particular in DDF (Bunyavejchewin et al., 2011). However, our understanding on the responses of leaf phenology of DDF to such El Niño events are still

limited.

Recent studies indicate that secondary forests are increasing worldwide including in SEA (Estoque et al., 2019; Chazdon et al., 2016) due to the promotion of reforestation and afforestation. In 2015, secondary forests in SEA have expanded its covers to an approximately 65% of total forests (206.5 M ha), of this 45.1% is considered as young secondary forest of ≤ 20 years old (Estoque et al., 2019). The secondary forests are important terrestrial carbon sinks as they can actively take up atmospheric CO_2 during their growth (Chazdon et al., 2016). However, investigations on the effects of climatic extreme events on CO_2 exchanges and tree seasonality in the secondary DDF are still rare, despite the high potential to disrupt plant productivity through phenological disturbances. In the Borneoand Sarawak tropical forests, for example, the 1997/1998 strong El Niño caused 12–30 times higher tree mortality than during non El Niño years especially in small sized trees (Itoh et al., 2012; Nakagawa et al., 2000). In fact, decreased rainfall in 2010 due to El Niño event was reported to significantly reduce gross primary productivity (GPP) and evapotranspiration (ET) of DDF (Sanwangsri, 2017; Sanwangsri et al., 2017). In secondary TDF of Costa Rica, the annual precipitation was reduced by 30% and 63% during El Niño in 2014 and 2015 compared to 2013, while the GPP was reduced by 13% and 42%, respectively. The severe El Niño-induced drought in 2015 resulted in shorter canopy duration leading to reduction of carbon uptake (Castro et al., 2018). El Niño events also have important impacts on water cycle. A study conducted in semi-deciduous forests in Amazon showed that ET declined significantly during the El Niño 2002 event as a consequence of the lower rainfall and warming (Vourlitis et al., 2015).

Linking phenology and climate information across spatial scales is necessary for laying the groundwork for predicting the sensitivity, adaptive capacity, and vulnerability of species as well as ecosystems to future climate change (Enquist et al., 2014; Vose et al., 2012). The information on species level functioning can also provide insights for forest management (Brearley et al., 2016). Here we investigated the relationship between the climate extremes due to the strong 2015/2016 El Niño on leaf phenology and exchanges of carbon and water in a secondary DDF. The objectives of the study were to evaluate; (i) the impacts of drought induced by El Niño on the leaf phenology of the dominant tree species of the DDF, (ii) the impacts of the El Niño-induced drought on carbon and water exchanges of the DDF, both at seasonal and interannual scales.

2. Data and methods

2.1. Site description

This study was conducted in a secondary dry dipterocarp forest, located in Ratchaburi province, western Thailand (13° 35′ 13.3″ N: 99° 30′ 3.9″ E, 110 m a.s.l.) (Fig. 1). The total forest area was 88.9 ha. Meteorological and eddy covariance measurements tower have continued since 2008 (more details in Sanwangsri et al., 2017). Annual averages of temperature and precipitation (2009–2018) were 27.0 ± 1.6 °C and 946.7 ± 364.3 mm, respectively. Previously, this forest was exploited by nearby communities for timber, charcoal or other products. Since 2005, this forest has been protected and trees have naturally regenerated (Hanpattanakit et al., 2015). In 2015, the re-generated trees were about 10 years old. The dominant species in the forest were determined by laying out a fixed plot of 10×10 m^2 for 4 plots, covering 448 individual trees with average tree height and diameter tree breast height (DBH) of 7.0 m and 6.8 cm, respectively. The importance value index (IVI) of each species with a DBH equal to or greater than 0.5 cm was evaluated following the method described by Phillips (1959). About 20 species were found in this secondary DDF. The top five dominant tree species were *Dipterocarpus obtusifolius* Teijsm. Ex Miq, *Shorea siamensis* Miq., *Shorea obtusa* Wall., *Shorea roxburghii* G. Don, and *Sindora siamensis* Teijsm. & Miq. Their

importance value index (IVI) were 50.6, 44.7, 37.3, 31.1 and 21.2, respectively. These five species accounted for 61.7% of total IVI in this forest. The number of individual trees of these five dominant species and their characteristic as tree height and DBH were presented in Table S1.

2.2. Microclimate and eddy covariance flux measurements

At the site, microclimate variables consisting of air temperature, rainfall, relative humidity and net radiation were measured by sensors mounted on the tower at 10 m above the ground. Soil water content and soil temperature were measured at 5 cm soil depth. Detailed microclimate measurements were described by Sanwangsri et al. (2017). This study covers the period between November 2014 and October 2017.

The CO_2 fluxes were measured by eddy covariance (EC) technique which utilizes the fast response fluxes (10 Hz) of an open-path infrared CO_2/H_2O analyzer (LI-7500, LI-COR, Lincoln, NE, USA) and three-dimensional sonic anemometer-thermometer (CSAT3, Campbell Scientific, Inc., Logan, Utah, USA) as described in the previous study (Sanwangsri et al., 2017). The main flux data processing and correction were analyzed by EddyPro software version 6.0.0 (LI-COR, Lincoln, NE, USA). A half-hourly net ecosystem exchange (NEE) values outside the range of -50 to 50 µmol $m^{-2} s^{-1}$, and the statistical outliers outside the $\pm$ 3 SD range of two week window were removed (Wolf et al., 2011). 48% of flux data were removed and these together with missing data were gap-filled. Small data gaps were filled by linear interpolation and by mean diurnal variation (MDV) as described by Sanwangsri et al. (2017). Large gaps during daytime (when photosynthetically active radiation (PAR) was greater than 10 µmol $m^{-2} s^{-1}$) were rebuilt by non-linear light response curves (Michaelis and Menten, 1913) with a moving window for two weeks. The night time data were filled using linear interpolation based on the relationship between night time fluxes and night temperature. The GPP is expressed as GPP = -NEE + RE = NEP + RE, where the RE is an ecosystem respiration calculated by sum of the NEE during the night time and NEP is the net ecosystem productivity which is equal to negative NEE (-NEE). A positive NEP indicates net carbon uptake by forest ecosystem from the atmosphere (Reichstein et al., 2002; Yu et al., 2008). The ET (evapotranspiration) was calculated by dividing the latent heat (LE) by the specific heat of vaporization (Stull et al. 1998). The small missing data gap of ET was filled in a similar manner as that of the NEE. The large gaps were filled by fitting the relationship between LE and available energy flux as net radiation (Rn) minus by ground heat flux (G) with moving window for two weeks as described by Gong et al. (2017).

2.3. Phenological observations

Leaf phenology of all individual trees of the top-five dominant species (total of 294 individual trees, see Table S1) was monitored by using crown density scores between March 2015 and October 2017. Leaf phenology was visually estimated every 30th day of the month during March 2015-April 2017 using a scoring method from 0–4 scores for each of the four phenophases including young leaves, mature leaves, senescence leaves and leafless. Young leaves are defined as newly flushed leaves. Mature leaves are referred to expanded leaves with a dense green color. Senescence leaves are leaves that start to turn yellowish-brown and wilt. Leafless period is the period of time when no leaves remain on the branch. The full mature leaves phenophase for a given individual tree corresponds to a score value of the mature leave phenophase of 4 whereas all the other three phenophases (young leaves, senescence leaves and leafless) are scored as 0. The scores of 3, 2, 1 for the mature leave phenophase represent three quarters, half and one quarter of mature leaves in the canopy, respectively. The total composite score of 4 is the sum of scores from these all four phenophases. When all the four phenophases of an individual tree were found in a

similar fraction on the observation day, each phenophase is scored as 1, so that the total scores never exceed 4 (Kuaraksa et al., 2012). The current study presented only the average score of mature leave that is assumed to be the active photosynthetic leaves of five dominant species. In addition to mature leaf phenology, during the first leaf expansion of deciduous dominant species, observations were also made twice a week for three months between March and May of 2016 and 2017. Furthermore, the leaf symptom damages such as burning spot was also noted.

The litterfall was collected from $1 \times 1 \ m^2$ litter trap every month during November 2014 – October 2017. These litter traps were distributed randomly inside the plots. Three litter traps were installed per plot, for a total of 12 litter traps. The litterfall was then dried at 80 °C and weighed. In addition, the carbon stock in litterfall was calculated by multiplying the biomass of litterfall with the carbon fraction (0.50, Hanpattanakit and Chidthaisong, 2012).

2.4. Data analyses and statistics

The correlations between climate variables and either leaf phenology or gasses exchanges were presented using linear regressions, and significance was determined at 95% confidence level. We also estimated their sensitivities by reporting the slopes of these relationships. In addition, the timing comparison of first leaf expansion between El niño and non-El niño was analyzed by Student's t-test at 95% confidence level. All statistical analyses were carried out by using R software (R Core Team, 2017).

3. Results and discussion

3.1. Microclimate at the secondary dry dipterocarp forest site

In this study, we distinct two seasons: the dry and the wet season, following the description by Tanaka et al. (2008). The wet season starts in May and ends in October and the dry season begins in November and ends in April of the following year. During this study period, there were three dry seasons in 2014/2015, 2015/2016 and 2016/2017, and three wet seasons in 2015, 2016 and 2017. Climate variables indicated severe and extended drought during the dry season 2015/2016. During the study period, the mean temperatures in each month during dry and wet season were in the range between 24.6–29.5 and 25.9–29.9 °C, respectively. The highest maximum temperatures and VPD were found in April each year with the highest temperature and VPD recorded at the end of the dry season 2015/2016, i.e. during the strong El Niño event (41.7 °C and 6.7 kPa). The soil temperature showed similar trend as maximum air temperature and reached the highest value in April 2016 (Fig. 2a and Table S2). During the study period, unusual long period of drought was found in 2015/2016 with very low rainfall (Fig. 2b). The annual total rainfall for three years (November of preceding year - October) during the study period were 777.2, 769.4, 1000.3 mm respectively. The rainfall during the dry season 2015/2016 accounted for only 9.3% of the annual rainfall, whereas the dry season 2014/2015 and dry season 2016/2017 accounted for 35.9 and 22% of the annual rainfall. The soil water content (SWC) was consistent with the amount of rainfall. The SWC dropped and remained at lower level than 5%VWC for five months in the dry season 2015/2016, while the rainfall was lower than 25 mm. The number of days with low SWC condition ($\leq 5\%$ VWC) during this drought period was more than 20 days month^{-1}. The average net radiation was $131.5 \pm 16.8 \ Wm^{-2}$. The radiation was higher during the wet season between May and June (Fig. 2b and Table S1). From these observations, it can be summarized that various climate variables especially rainfall and soil moisture indicated severe and extended drought during the dry season 2015/2016. This was consistent with the strong El Niño 2015/2016 as reported by many studies (Betts et al., 2016; Jiménez-Muñoz et al., 2016; Santoso et al., 2017; Wen-Juan et al., 2016). In fact, the signals for this strong El Niño was

already reported during the wet season 2015 (NOAA, 2019). This was reflected in the amount of rainfall during the wet season 2015 that was 200 mm lower than during the other wet seasons (Table S2).

3.2. Leaf phenology of the secondary dry dipterocarp forest and the effects of 2015/2016 El Niño

The leaf phenology of the five dominant species was presented in Fig. 3. Most dominant trees shed and emerged their new leaves during the dry season. Overall, longer and greater deciduousness was found during the 2015/2016 El Niño. During this period, the leafless period extended to five months compared to two months in other years due to earlier end and delay onset of growing season (Fig. 3). In typical dry season, leaf emergence of the five dominant species occurred in March-April and leaves reached their maturity in May but during the dry season 2015/2016 leaf emergence was delayed to May-June with the highest peak of leaf maturity reached much later (Fig. 3). Although El Niño induced the earlier leaf shedding and delay of leaf production, but the trees could keep their leaves for 7–9 months (depending on species) both in El Niño and non-El Niño years. Therefore, it seems that the leaf lifespan of DDF trees was not different between El Niño and non- El Niño.

Responses to drought at species level were also observed. *Shorea siamensis* and *Sindora siamensis* always showed a complete deciduousness period for each dry season, but this leafless period was extended during the El Niño dry season 2015/2016. *S. roxburghii* and *S. obtusa* showed complete deciduousness only during the dry season 2015/2016. *D. obtusifolius* always showed incomplete deciduousness during dry seasons but we observed higher amount of burning spots on leaves during the dry season 2015/2016 compared to other dry seasons. We noticed that the mature leaf emergence in April 2015 was shifted to emerge on June 2016 during El Niño and shifted to emerge on April again in 2017 (non-El Niño). This indicates somehow the relatively high plasticity of the dipterocarp species in spite of having be strongly affected by the 2015/2016 El Niño.

The monthly accumulation of litterfall was consistent with leaf phenology, which indicates that trees shed their leaves earlier between December and February during the El Niño dry season 2015/2016 compared to February and March for other seasons (Fig. 3). Approximately 72–83% of the annual total litterfall was produced during the dry season. After the prolonged period of drought, the litterfall in dry season continued to increase from 5.64, 5.90 to 7.82 Mg ha^{-1} from the dry season 2014/2015, 2015/2016 to 2016/2017, respectively (Table S3). The annual litterfall slightly declined during the El Niño in 2015/2016 (7.64 Mg ha^{-1}) compared to preceding year in 2014/2015 (7.79 Mg ha^{-1}), and the year after that (9.44 Mg ha^{-1}). This was caused by a relatively low litterfall amount in the wet season 2016 compared to the wet season 2015, indicating the effects of severe drought in the previous dry season 2015/2016.

When analyzing the relationships between mature leave phenology and precipitation or soil moisture, we found that low precipitation and soil moisture resulted in lower leaf production both first leaf expansion and mature leaf stages especially during the El Niño dry season 2015/2016 (Fig. 4). More than a month in onset delay for *Shorea siamensis, S. obtusa* and *S. roxburghii* during the El Niño dry season was observed, except for *Sindora siamensis* that the timing of first leaf expansion did not change between the two years (Fig. 5a and Table 1). *D. obtusifolius* was not presented in Fig. 5a because of its incomplete deciduousness, so the timing of its the first leaf expansion cannot be precisely defined. Increases in accumulative rainfall in March induced the first leaf expansion during usual dry season in 2016/2017. However, first leaf expansion was delayed from March to May during the El Niño (Fig. 5a-5b). The first leaf expansion during the El Niño of three species including *Shorea siamensis, S.obtusa, S. roxbughii* was significantly delayed by 42, 33 and 35 days, respectively (Table 1). In addition, during the El Niño dry season, lower amount of rainfall was needed to induce the first
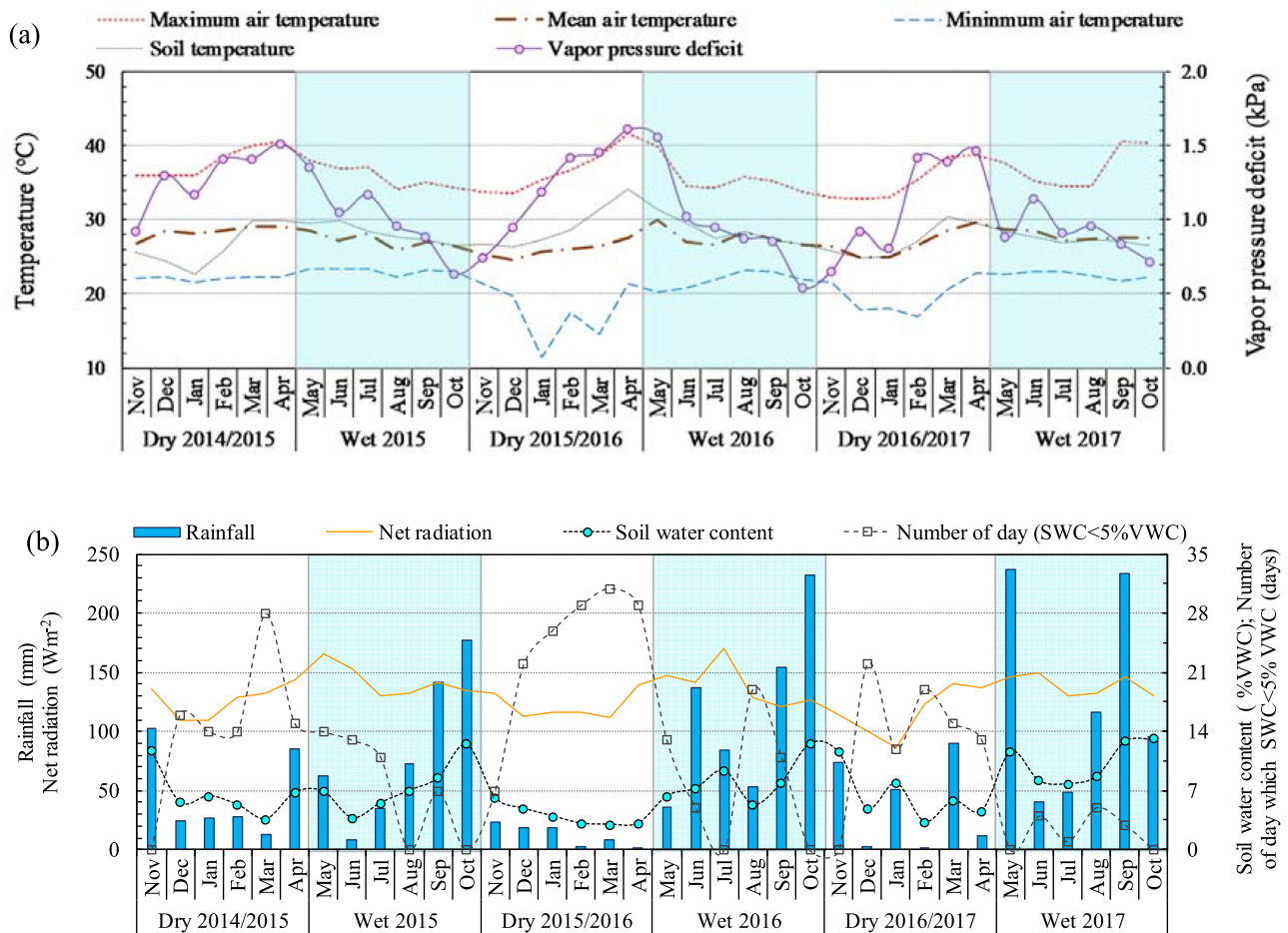
Fig. 2. Climatic characteristics of the sites on a monthly basis from November 2014 to October 2017, consisting of (a) air temperature, soil temperature, and vapor pressure deficit, (b) rainfall, net radiation, soil water content (SWC) and number of day during which SWC was lower than 5%VWC.
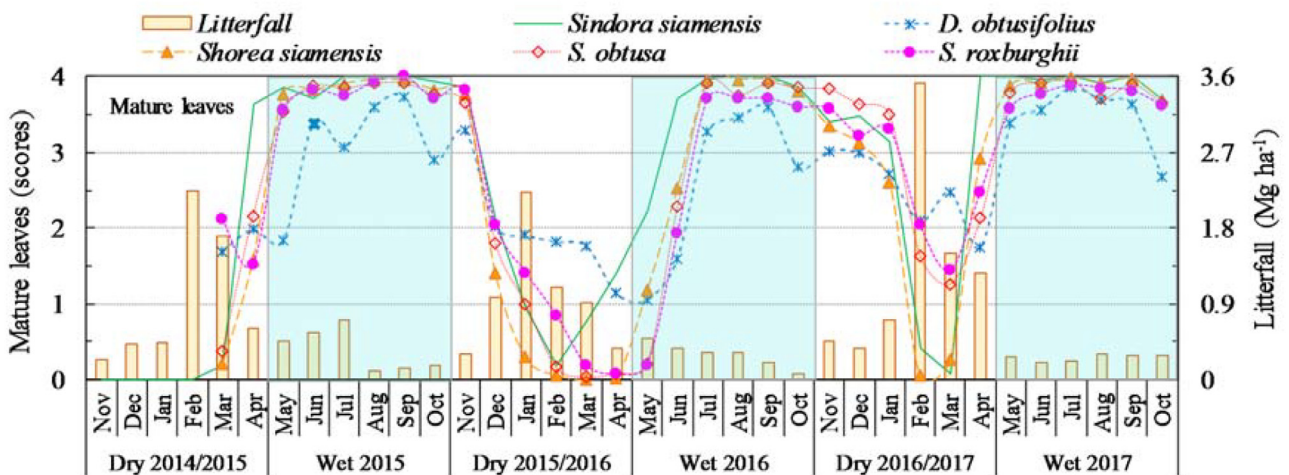

Fig. 3. Average score of mature leaves of five dominant species in each month was shown in line whereas total litterfall production in each month was shown in brown bar. The wet season was highlighted in blue in this figure.

leave expansion compared to during the non-El Nino years (Table 1). *Sindora siamensis* required much smaller accumulative rainfall (2.8 mm) than other species (11–12 mm) to induce its first leaf expansion. These three species (*Shorea siamensis, S.obtusa, S. roxbughii*) flushed within 4 days when the rainfall accumulated around 11 mm or greater (Table 1).

The results presented above clearly indicate that longer period and greater degree of deciduousness of DDF were induced by the 2015/

2016 El Niño compared to non-El Niño years, though with substantial differences among tree species (Fig. 3). Leaf shedding is a strategy to avoid water loss during the unfavorable, i.e. during the dry period here. Such variations in degree and duration of deciduousness can be discussed in regards to lifespan of mature leaves. Shorter leaf lifespan generally means longer deciduous period. To illustrate this and in relation to the observed different leaf phenology of dominant species, we
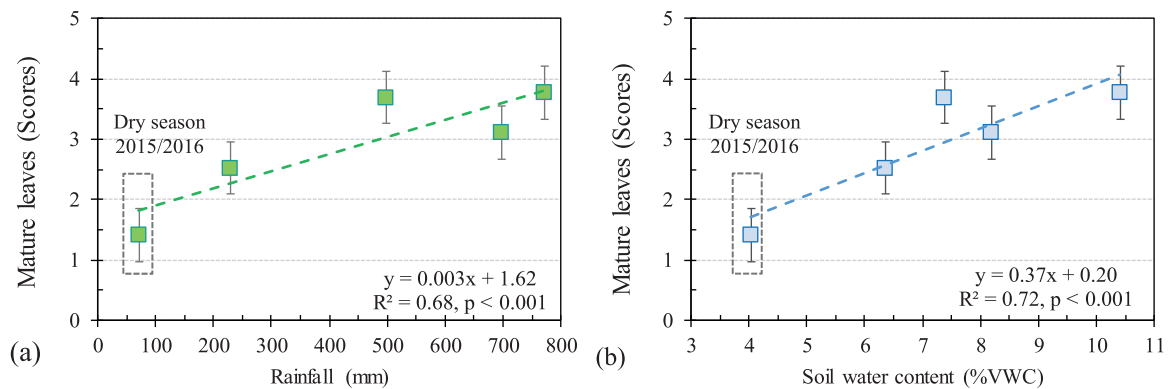
Fig. 4. Relationships between seasonal mature leaf phenology score and rainfall (a), or soil water content (b) recorded between dry season 2014/2015 and wet season 2017 of all five- dominant species (the error bar presents the standard error (SE) and the dashed grey rectangles presents the data during the El Niño dry season 2015/2016).

have approximated leaf lifespan based on the score of mature leaves of greater than 2. We found that the leaf lifespan of *Sindora siamensis* was markedly longer (~9 months) than that of *Shorea siamensis, S. obtusa* and *S. roxburghii* (7–8 months). Rundel et al. (2017) also reported that *Sindora siamensis* had a long leaf lifespan up to 11 ± 0.14 months in Northeast Thailand. Leaf lifespan is related to leaf area, transpirational cooling and photoprotective mechanisms (Ishida et al., 2014; Rundel et al., 2017). In DDF forest, species such as *Shorea siamensis* and *S. obtusa* (Dipterocarpaceae family) have a leaflet area of 47.7 and 17.8 cm^2, respectively (Rundel et al., 2017). They required two times higher transpiration rates to prevent heating above ambient temperature compared to the small legume leaves of *Dalbergia oliveri* (Fabaceae family) with leaflet area of 3.9 cm^2 (Rundel et al., 2017). In our study, *Sindora siamesis* (Fabaceae family), which has a long lifespan, might need less transpirational cooling during the drought because of its small leaflet area of 1.7 cm^2 (Rundel et al., 2017). Thus, this may be one of the reasons that makes *Sindora siamesis* less responsive to El Niño-induced drought (and high temperature) as observed in this study. In contrast, the leaf size of *D. obtusifolius* (Dipterocarpaceae family) was twice larger than leaves of *S. siamesis*, explaining why *D. obtusifolius* would need a larger amount of water to cool down during the El Niño and why we observed substantial amount of burning leaves for this species. A study by Cha-Um et al. (2018) indicated that *Dipterocarpus tuberculatus* (Dipterocarpaceae family) which has a large leaf area also exhibited the visual symptoms of leaf chlorosis in responses to water deficit. Our observations in the shift of leave phenology are in line with the adaptation of secondary DDF species to drought. In our case, the

leaf phenology of DDF species responses readily to prolonged drought by shedding their leaves earlier than usual. After the prolonged drought, much lesser amount of accumulative rainfall compared to the usual dry season was required to initiate leave emergence.

3.3. Carbon dioxide exchange and evapotranspiration over the forest canopy

The CO_2 exchanges were active between the time window from 7 am to 6 pm as shown in Fig. 6a. During the study period, negative NEP reflecting carbon release to the atmosphere occurred during March-April over the dry season 2014/2015 and 2016/2017 at a rate of -29.27 and -19.23 gC m^{-2} month^{-1} or total the carbon loss on a year basis were -58.54 and -38.45 gC m^{-2}, respectively. This period of carbon loss during the El Niño year was extended by 3 months from March to May, resulting in the total carbon loss of -152.29 gC m^{-2}. The highest rate of carbon loss was found in May 2016 with -83.27 gC m^{-2} month^{-1} (Fig. 7a and Table S3). Although the carbon loss during the end of the dry season 2015/2016 was more pronounced than during the dry season 2014/2015, the accumulated NEP over the dry season was similar during these two years (dry season 2014/2015: 244.60 gC m^{-2}; dry season 2015/2016: 234.88 gC m^{-2}), but higher in 2016/2017 (344.36 gC m^{-2}). In this study, the annual NEP for three years between 2015 and 2017 (November of preceding year to October) has increased from 527.26 to 1039.97 (Table S3). The annual NEP increased by 26.87% in 2016 compared to 2015, whereas it increased by 44.24% in 2017 compared to 2016. These NEP increasing trends
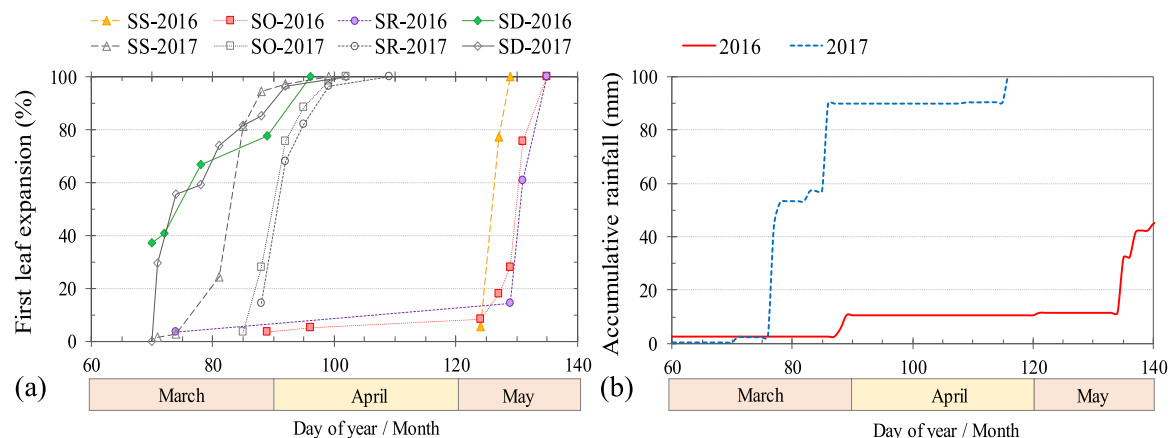

Fig. 5. (a) Timing of first leaf expansion of *Shorea siamensis* (SS), *S. obtusa* (SO), *S. roxburghii* (SR) and *Sindora siamensis* (SD) between March and May in 2016 (dry season 2015/2016) during El Niño and 2017 (dry season 2016/2017) during non-El Niño years, (b) accumulative rainfall during March-May of 2016 (El Niño) and 2017 (non-El Niño).

Table 1
Comparison between the median of day of year (DOY) during the first leaf expansion and accumulative rainfall and number of rainy day from the 1st of February (DOY = 32) to the timing of leaf expansion during El Niño in early 2016 and non-El Niño in early 2017 (Significant differences with Student's t-test at 95% confidence level are indicated by p value).

Species	No. of sample	First leaf expansion (median of DOY)			Accumulative rainfall before first expansion was detected (mm)		Number of rainy day before first expansion was detected (days)	
		dry season 2016	dry season 2017	p value	dry season 2016	dry season 2017	dry season 2016	dry season 2017
Shorea siamensis	77	127	85	<0.001	11.7	57.3	4	6
Shorea obtusa	72	127	94	<0.001	11.7	90.0	4	7
Shorea roxburghii	28	130	95	<0.001	11.7	90.0	4	7
Sindora siamensis	28	75	83	>0.050	2.8	57.3	1	6

suggest that this DDF, though affected by El Niño during the dry season 2015/2016, could recover rapidly after the El Niño event, likely because the study trees were very young (< 10 years old). Sanwangsri (2017) reported that the average annual NEP in this secondary forest during 2009–2011 was 798 gC m^{-2} yr^{-1}.

It was reported that during the dry season, the maximum stomatal conductance, maximum carbon assimilation rates, quantum yield of photosystem II and electron flow through photosynthesis of deciduous species normally remain high until the leaves abscised (Ishida et al., 2006). In addition, the short leaf lifespan of drought avoiding deciduous species including *Shorea siamensis*, has a high nitrogen content in their leaves and thus could maintain relatively high photosynthesis rate (Ishida et al., 2006). These might also be the reasons why deciduous trees in secondary DDF are able to compensate for the carbon loss and continue to grow after severe drought.

The ET was active during the same time window with NEP (Fig. 6b). The ET during non-El Niño dry seasons and wet seasons were in a range of 476.40–478.84 mm and 701.56–838.46 mm, respectively (Table S3). The ET was significantly lower during the El Niño dry season 2015/2016 especially from January to April (Fig. 6b and Fig. 7b); approximately 37.88% lower compared to the average ET during non-El Niño dry seasons. The annual total ET in 2016 (November 2015 to October 2016) was 14.10% lower than that of in 2015 (November 2014 to October 2015).

The GPP during the wet seasons was much higher than during the dry seasons, and within the range of 1451.96–1886.11 gC m^{-2}. During the El Niño dry season 2015/2016, the GPP was 799.06 gC m^{-2}, accounting for 72.68% of the average GPP for non-El Niño dry seasons (1099.41 gC m^{-2}) (Fig. 7a and Table S3). The annual total GPP during strong El Niño in 2016 (November 2015-October 2016) was about 9.64% lower than the annual total GPP in 2015 (November 2014-October 2015). The GPP was 28.59% higher during the following year in 2017 when compared to that in 2016 (Table S3). These variations were consistent with the lack of rainfall and soil water content and the long leafless period during dry season 2015/2016. The ratio of GPP to RE indicated that RE had taken over GPP for one extra month during El Niño year, and this explains the extra carbon loss during that period (Fig. 7a). The RE during the El Niño dry season 2015/2016 was accounted for 70.09% of that of the usual dry season. At the same site during the previous El Niño, the RE in El Niño dry season 2009/2010 was about 57.84% of that of the non- El Niño dry season 2010/2011 (Sanwangsri, 2017). During such period soil respiration is the key source of RE in this forest (Hanpattanakit et al., 2015).

The link between mature leaves and carbon exchange was illustrated in Fig. 8a-8d. It is clear that mature leave score decreased more rapidly at the end of wet season during the El Niño year and this score remained longer at a low level during the dry season of El Niño year (i.e. leaf production was delayed) compared to non-El Niño years (Fig. 8a). On the other hand, during typical drought in 2014/2015 and 2016/2017, the accumulative NEP increased slightly between November and January, after that it remained at fairly constant level and increased again in April until the end of wet season in October. During

El Niño 2015/2016, the accumulative NEP dropped profoundly between April and May 2016 compared to non-El Niño. However, the accumulative NEP then sharply increased in June. This accumulative NEP increased shortly after leaves emergence in May during the El Niño year, instead of April following leaf emergence in March during typical years (Fig. 8b).

The reduced carbon exchange due to greater deciduousness during the dry season 2015/2016 was also indicated by the constant level of accumulative GPP between January to May, instead of a slight increase during typical dry seasons (Fig. 8c). Thus, our results clearly demonstrate that the El Niño-induced drought affected on leaf phenology following by carbon exchange in this secondary DDF.

Regression analysis illustrated the responses of the carbon exchanges to drought-related climatic factors such as rainfall, SWC and water demand in the air as VPD. From the slopes of these relationships, we found that GPP seems more sensitive to drought than RE (Fig. 9a-l). Thus, the low NEP found during the strong El Niño may be the consequence of a greater decline in the GPP than RE. This was consistent with the greater deciduousness that indicates less carbon uptake in DDF (Fig. 8a, c). The decline in carbon release through ecosystem respiration during El Niño was followed by active carbon uptake after leaf flushing during the subsequent wet season. This could stimulate carbon compensation as indicated by increase in annual NEP during these three consecutive years. However, our results suggest that even though climate extremes such as El Niño could be dramatically reduced carbon uptake of DDF during the dry season, these forests can still be a net atmospheric carbon sink on the annual basis. This indicates the capacity of young secondary forests to extreme events, which may be able to absorb atmospheric carbon under the projected high variability of the climate in the future. This feature of flexibility is different from that in the old forest. For example, Wharton and Falk (2016) reported that the old forest turns from a small sink to a net source of atmospheric CO_2 when facing with ENSO.

Relationships between ET and climate variables were analyzed. The low rainfall and SWC significantly induced the declined ET, and vice versa for VPD (Fig. 8i-8l). Thus, the lowest rainfall and soil moisture during dry season 2015/2016 were resulted in the declined activities of carbon and water exchanges in the secondary DDF.

4. Conclusions

The strong El Niño 2015/2016 induced a remarkable prolonged drought in the secondary DDF. This strong El Niño event was not only influencing microclimate variables, but also tree phenology and carbon exchanges. During this El Niño, the earlier end and delayed onset of growing season were observed. This led to a longer leafless period of about five months compared to two months during non-El Niño year. We also found differences in the phenological responses among the dominant DDF species with some species showing strong alteration of their phenology (*Shorea siamensis, S. obtusa and S. roxburghii*) and some less (*Sindora siamensis* and *D. obtusifolius*). The El Niño strongly affected on leaf phenology leading to lower capacity of forest carbon uptake as
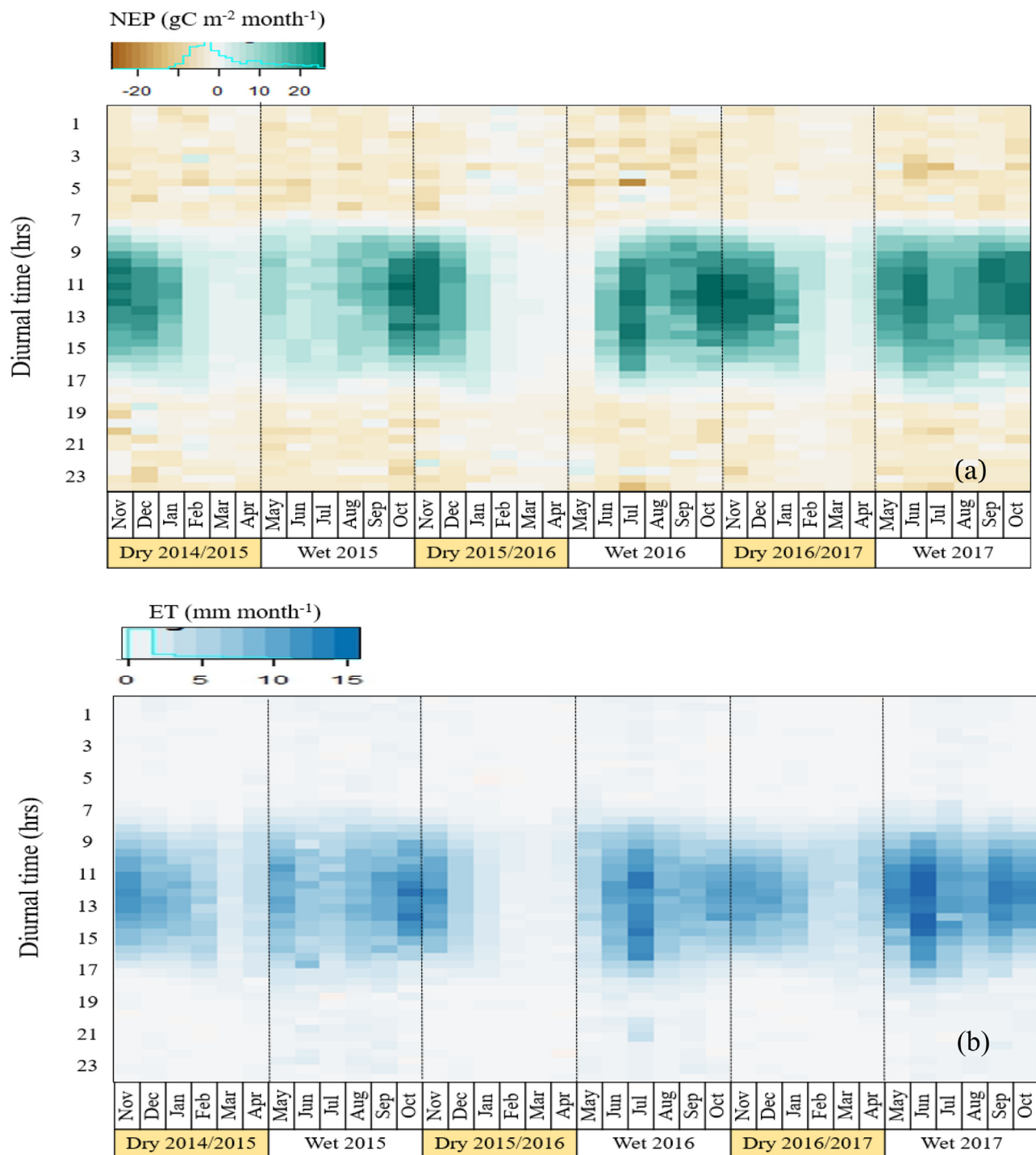
Fig. 6. (a) Monthly net ecosystem productivity (NEP) (dark green color indicates carbon uptake, while the brown color means carbon release), and (b) evapotranspiration (ET) (the blue color means the high ET) between November 2014 and October 2017 in a secondary dry dipterocarp forest.

NEP and GPP particularly in dry season. However, the extra carbon loss during the dry periods that was induced by El Niño was compensated by a high carbon uptake during the following wet season. This may reflect the high capacity of young secondary DDF carbon uptake and its flexibility in coping with climate variability.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
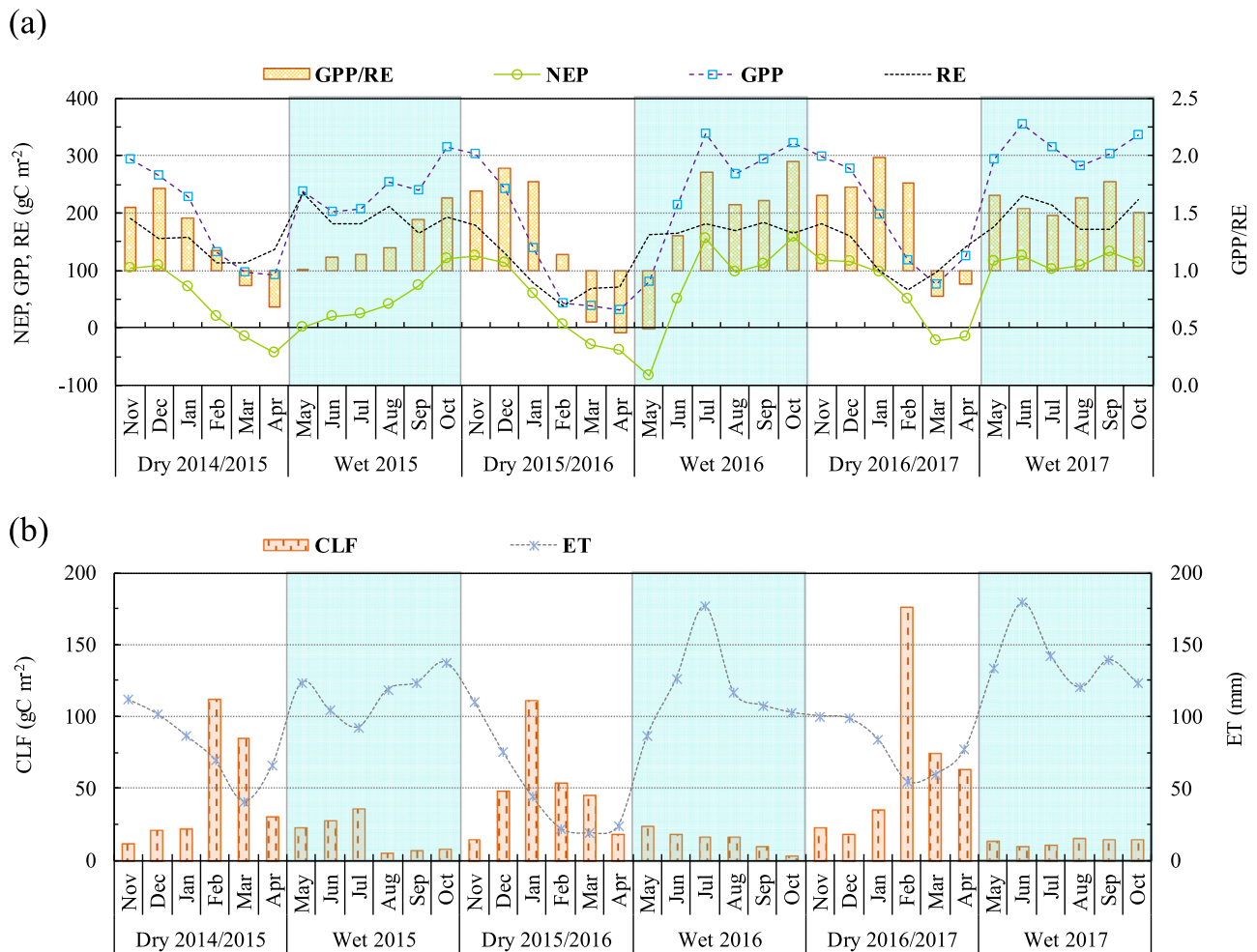
Acknowledgement

(a)

(b)

Fig. 7. (a) Monthly net ecosystem productivity (NEP), gross primary productivity (GPP), ecosystem respiration (RE), ratio of GPP to RE (GPP/RE), (b) monthly carbon content in litterfall production (CLF) and evapotranspiration (ET) in the study secondary dry dipterocarp forest.
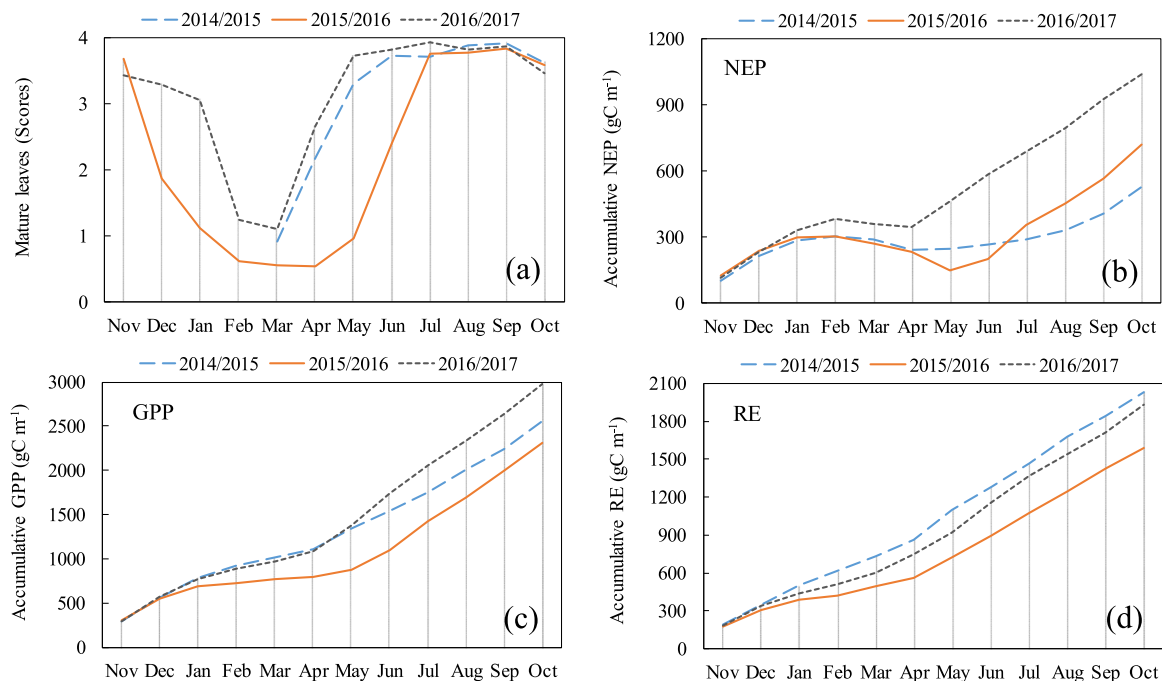

Fig. 8. Effect of the 2015/2016 El Niño on (a) the shift of leaf phenology, (b) accumulative net ecosystem production (NEP), (c) accumulative gross primary productivity (GPP), and (d) accumulative ecosystem respiration (RE).
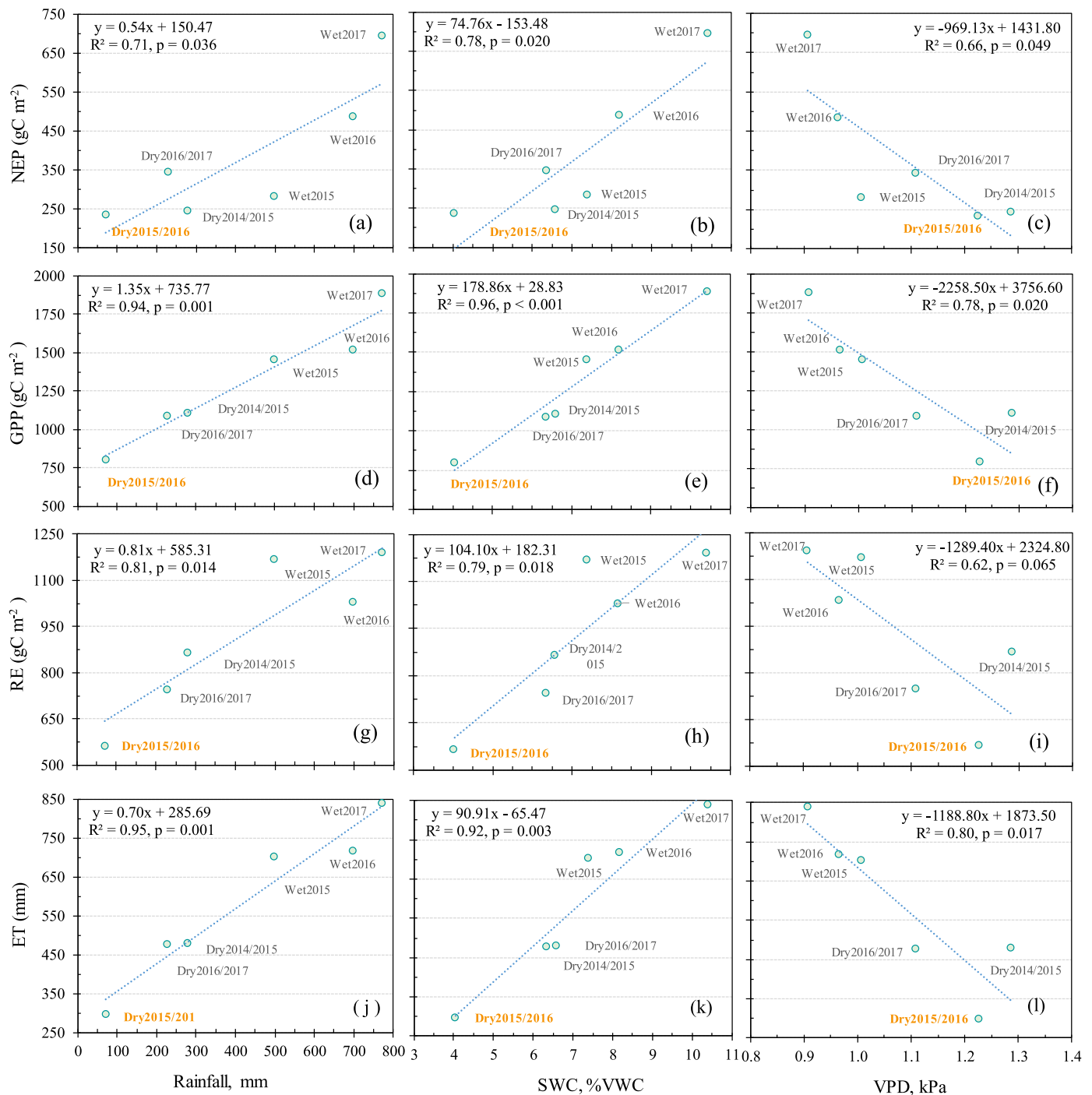
Fig. 9. Relationships between climatic variables including rainfall, soil water content (SWC), vapor pressure deficit (VPD) and (a-c) net ecosystem productivity (NEP), (d-f) gross primary productivity (GPP), (g-i) ecosystem respiration (RE), and (j-l) evapotranspiration (ET).

events".

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.107945.

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