

# Net ecosystem production of a tropical secondary forest in Jengka, Pahang, Malaysia

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Secondary tropical forests are important contributors to atmospheric carbon exchanges in tropical regions. However, our understanding of how secondary succession affects carbon cycling and carbon sequestration in these ecosystems is limited. We studied carbon cycling and net ecosystem production (NEP) in a secondary lowland forest using a full biometric-based flux measurement (2018-2019) and a partial biometric-based measurement (2017). Net primary production ranged from 6.01 to 8.37 Mg C ha<sup>-1</sup> year<sup>-1</sup> (2018-2019). This was partitioned in changes in aboveground biomass (0.98-3.66 Mg C ha<sup>-1</sup> year<sup>-1</sup>), coarse roots (0.23-0.88 Mg C ha<sup>-1</sup> year<sup>-1</sup>), litterfall (2.74-3.94 Mg C ha<sup>-1</sup> year<sup>-1</sup>) and fine roots (0.86-1.09 Mg C ha<sup>-1</sup> year<sup>-1</sup>). The total annual soil surface CO<sub>2</sub> efflux was 10.56, 8.90, and 12.23 Mg C ha<sup>-1</sup> year<sup>-1</sup> for 2017, 2018, and 2019. The net ecosystem production of the forest was -2.89 and -3.86 Mg C ha<sup>-1</sup> year<sup>-1</sup> for the years 2018 and 2019. Litterfall exhibited the highest percentage of change (32%-58%) followed by aboveground biomass (14%-44%) and fine roots (13%-14%). The negative NEP values showed that the site is a C source and may be partially influenced by forest fragmentation. Seasonal variations also influence the dynamics of NPP and NEP.

**Keywords:** Carbon Cycling, Net Primary Production, Seasonal Variations, Tropical Secondary Forest, Soil Efflux

## Introduction

Secondary forests are defined as forests essentially regenerating through natural processes after significant human and/or natural disturbance of the original forest vegetation at a single point in time or over an extended period. They can display a major difference in forest structure and/or canopy species composition with respect to nearby primary forests on similar sites (Chokkalingam & Jong 2001). Carbon cycling in a forest varies during stand development, and the carbon sequestration rate is influenced by the forest's age and successional stage (Ohtsuka et al. 2010). Woody biomass increments of stems and branches in secondary forests are essential components of carbon sequestration in forest ecosystems, and their functions as sinks/sources are gravely underestimated in the carbon cycle. Moreover, there is uncertainty about how carbon is partitioned and accumulates in forest ecosystems. Net

Ecosystem Production and/or carbon accumulation (NEP) is a fundamental property of ecosystems. It was originally defined by Woodwell & Whittaker (1968) as the difference between the amount of organic carbon fixed by photosynthesis (gross primary production, GPP) in an ecosystem, and total ecosystem respiration (ER). Ecosystem respiration encompasses the total respiration in an ecosystem, including both autotrophic respiration (by plants) and heterotrophic respiration (by decomposers and other organisms). Thus, NEP essentially represents the net amount of carbon that is either accumulated in or lost from it by export or non-biological oxidation (NEP = GPP-ER – Randerson et al. 2002).

Net Primary Production (NPP) is the amount of organic carbon that remains after accounting for the carbon respired by plants (autotrophic respiration, AR). Thus, NPP = GPP - AR. This study used the biometric method to measure the yearly

changes in NPP and carbon sequestration. Alternatively, the eddy covariance (EC) method is widely used for estimating CO<sub>2</sub> fluxes and other gases between the atmosphere and forest ecosystems. This technique provides continuous data on the exchange of gases and is particularly useful for estimating GPP and ER over time. However, EC is known to be expensive, requires periodic visits to field sites and may underestimate nighttime respirations; also, ways to remove this bias remains controversial (Black et al. 1996, Aubinet et al. 2000). Compared with chronosequence studies of net CO exchange using the eddy covariance method (Rodda et al. 2021, Kiew et al. 2018), there have been few studies on ecological inventories of carbon cycling and biometrically based flux measurements in the secondary forests (Yoneda et al. 2016).

Nevertheless, both methods of eddy covariance and biometric-based NEP provide process-level information on forest C-dynamics, in addition to validating localized data and regional estimates. Net ecosystem production of a forest can vary due to seasonal variations in gross primary production or unexpected defoliation (Ito et al. 2005, Luyssaert et al. 2007, Saigusa et al. 2008), and this can concurrently impact the global carbon cycle. Despite the literature on inter-annual variations captured by long-term flux measurements is substantial (Yasuda et al. 2003, Kosugi et al. 2008), data on biometric-based NEP needs to be explored, as both techniques may expose different factors that control C dynamics.

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**Tab. 1** - Dendromatic statistics of the study site at Jengka Forest Reserve (n = 82). Mean values  $\pm$  standard errors are shown.

| Variable                                            | Values                                          |
|-----------------------------------------------------|-------------------------------------------------|
| Comon tree family                                   | Phyllanthaceae, Dipterocarpaceae, Euphorbiaceae |
| Common genera                                       | <i>Aporosa</i> , <i>Shorea</i> , <i>Croton</i>  |
| Max dbh                                             | 69.8                                            |
| Mean dbh (cm)                                       | 10.27 $\pm$ 1.13                                |
| Max height (m)                                      | 50                                              |
| Mean height estimated (m)                           | 9.2 $\pm$ 0.75                                  |
| Stand basal area (m <sup>2</sup> ha <sup>-1</sup> ) | 22.8 $\pm$ 8.25                                 |
| Trees (trees ha <sup>-1</sup> )                     | 1383                                            |

To our knowledge, there has been no attempt to estimate NEP in Peninsular Malaysia, in contrast to the abundant literature that can be found for Indonesia (Basuki et al. 2021), Vietnam (Van Do et al. 2015), and China (Tan et al. 2010). Thus, understanding the variations in NEP on a larger spatial scale is still limited due to these circumstances. We hypothesize that measurements of NEP in a secondary forest will provide new insights into carbon balance and variables that need to be addressed for national or regional scale carbon modeling initiatives.

Our objectives were to estimate initial two-year measurements of biometric-based NEP in Jengka Forest Reserve and the contribution of different C fractions in a biological ecosystem that influences the C budget.

## Materials and methods

### Site description

The research was conducted in a sec-

ondary lowland forest in Pahang, West Malaysia. This site was chosen as data were available from a previous study (Jeyanny et al. 2015). The experimental site is known as Jengka Virgin Jungle Reserve (Jengka VJR), Jengka 18, Pahang (03° 34.99' N, 102° 34.29' E) located at 50-90 m a.s.l. with slope ranging from 2-8 degrees on a flat terrain. Portions of the Jengka VJR were logged once between 1968 and 1969. It is a secondary forest with minimal disturbances, as selective loggings were done only in the 1960s (Laidlaw 2000). The soil type recorded here is silty clay loam from the Durian Series (Typic Paleudult). The complete description of soil analysis and results can be found in Jeyanny et al. (2013). Six plots measuring 10  $\times$  10 m were set up on site. The major botanical families are Phyllanthaceae, Euphorbiaceae, and Dipterocarpaceae, with trees ranging from 4 to 50 m in height (mean: 9.2 m) and dbh (diameter at breast height) ranging from 5 to 70 cm (mean: 10.2 cm). The common genera are *Shorea*, *Aporosa*, and *Croton* (Tab. 1). Our initial observations showed very little deadwood at the site, which may be a component of flux. The wet season for the experimental site usually occurs from November to March, whereas the dry season occurs from May to September. Distinctive wet periods were recorded from October 2017 to January 2018, September 2018 to December 2018 and October-December 2019 (Fig. 1). In the period between October 2017 to June 2020, rainfall and temperature at Jengka VJR ranged from 20 to 455 mm and 26.0 to 28.5 °C (Fig. 1).

### Experimental design and measurements for NEP

A transect running from North East towards South West was established in the study plot, whereby 60 quadrants measuring 10  $\times$  10 m were established systematically, totaling 0.6 ha over the experimental site (Jeyanny et al. 2021). Out of these 60 quadrants, six falling in the study plot were randomly selected to determine tree species using herbarium specimens and verified by a botanist. All stems with DBH (diameter at breast height) > 5 cm were measured and identified to species level in December 2017 using a diameter tape with the same staff during the research period to avoid human errors. The allometric equations used were described before in Jeyanny et al. (2014). Living biomass was assessed in 2018 and 2019 following the same procedure, and the yearly increments in biomass ( $\Delta M$ ) were thus calculated.

Similarly, the coarse roots increment ( $\Delta Cr$ ) was also estimated for 2018 and 2019. Coarse root increments were determined from the allometric equations developed for tropical ecological conditions by Niiyama et al. (2010).

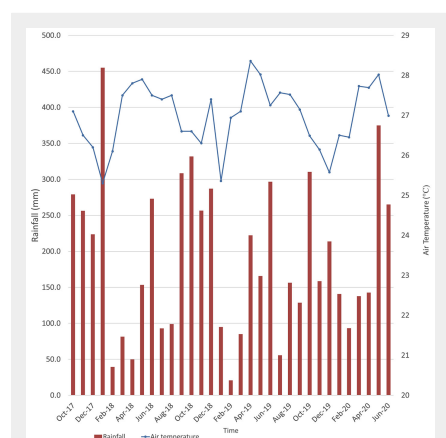
Twenty litter traps, 1  $\times$  1 m in dimension and one meter above the ground, were systematically established within the plots to collect litterfall (Lf) every four months

from 2018 to 2019. Litterfall samples were oven-dried at 80 °C, and the oven-dry mass was recorded periodically.

Measurement of fine roots (diameter  $\leq$  2 mm) involves root decomposition and fine root biomass (living and dead) to estimate fine root production. Root bags were prepared for the root decomposition study. To prepare root bags, fine roots were collected in bulk outside the designated plots amounting to 5 kg (fresh weight) of fine roots at 20 cm soil depth using a 150 mm in length and 80 mm in diameter soil coring probe. Roots were washed, air-dried, and oven-dried at 80 °C and inserted into 120 root bags of 1.0 g each. The root bags had a mesh opening size of 211  $\mu$ m with a dimension of 10  $\times$  10 cm (Sefar PET 1500), which blocked practically the ingrowth of fine roots; however, fine soil particles, water, and microorganisms can penetrate through the sheet. Root bags were buried at 10-15 cm soil depth and collected at corresponding time intervals every 4 months. Collected root bags were washed and then oven-dried for the remaining mass. The decomposition was estimated as  $y_i = (\text{initial mass} - \text{remained mass})/\text{initial mass}$ . For each responding time interval, 18 root bags were collected up to 840 days (October 2017- February 2020). After collecting, root bags were air-dried and oven-dried at 80 °C for constant weight and recorded.

Sequence soil cores were collected every 4 months on the same dates with litter collection and other data to estimate fine root biomass. On each date, 30 soil cores were collected using the same stainless steel tube to a depth of 20 cm. The soil core positions were identified systematically in the main plot. To avoid errors, the soil corings points were positioned so as not to overlap with the root bag study, litterfall collections, and the soil respiration subplots. The collected soil was then washed and sieved using a 0.05 mm mesh size to collect fine roots. The living and dead roots were separated based on color, texture, and resilience (Hishi & Takeda 2005). For example, dark/black colored roots that could break were deemed dead, and bright/yellow colored roots that were resilient were categorized as living roots. Afterward, the roots were air-dried (Hishi & Takeda 2005) followed by oven-drying at 80 °C until a constant weight was obtained. Living roots and dead fine roots, together with the root decomposition ratio, were obtained to calculate the fine root production.

Soil surface respiration ( $R_s$ ) is the production of carbon dioxide by organisms and plant parts in soil. The  $R_s$  is the sum of autotrophic respiration ( $R_a$ ) of roots and rhizosphere organisms and heterotrophic respiration ( $R_h$ ) of bacteria and fungi decomposition of organic matter and soil faunal activity in the organic and mineral horizons (Hanson et al. 2000). Thus, to capture only  $R_h$ , trenched plots were prepared using a chopper in April 2017, 6 months before data collection. The dimensions were 1  $\times$  1



**Fig. 1** - Monthly rainfall and air temperature at Jengka VJR forest, Malaysia from October 2017 to June 2020.

m with a depth of 0.8 m. A six-month period before measurements was allowed for dead root decomposition to ensure that only Rh was recorded in trenched plots. Trenches were inspected periodically to remove the organic debris and clip intruding roots, so as to ensure that only heterotrophic respiration was recorded for the estimation of NEP.

#### Estimation methodology

Carbon accumulation of forest or net ecosystem production (NEP) in a forest ecosystem was simply estimated by using eqn. 1 (O'Connell et al. 2003), which assumes that inputs of C other than net primary production (NPP) and losses of C other than heterotrophic respiration (Rh) are negligible (eqn. 1):

$$NEP = NPP - Rh \quad (1)$$

#### NPP Estimation

NPP includes four components, namely, the aboveground living biomass increment ( $\Delta M$ ), the coarse root increment ( $\Delta Cr$ ), the aboveground litterfall (Lf), and the fine root production (Lf) (eqn. 2):

$$NPP = \Delta M + \Delta Cr + Lf + Pr \quad (2)$$

Firstly, the aboveground biomass (AGB, kg dry weight) of each stem was estimated based on allometry according to Chave et al. (2005), a well-known method for tropical forests receiving 1500-4000 mm annual rainfall, based on the diameter at breast height (DBH) and the wood-specific gravity ( $\rho$ ). DBH was measured for the study period, while species average  $\rho$  was obtained from the Global Wood Density Database. The equation was fitted for each tree in the plots estimated. Finally, the value for each plot was totaled to obtain the aboveground biomass of carbon and extrapolated to one hectare to facilitate calculations as (eqn. 3):

$$AGB = \rho \cdot \exp(-1.499 + 2.148 \cdot \ln d + 0.207 \cdot \ln d^2 - 0.0281 - \ln d^3) \quad (3)$$

where AGB is the aboveground biomass (kg) and  $d = \ln(DBH)$ .

The coarse roots were also estimated using the allometric equation by Niiyama et al. (2010), which is suitable for Malaysian ecological conditions. Coarse roots were defined as  $\geq 2$  mm in diameter and estimated as (eqn. 4):

$$W_B = 0.023 \cdot d^{2.59} \quad (4)$$

where  $W_B$  is the belowground biomass and  $d$  is the diameter at breast height (1.3 m).

#### Estimation of aboveground and coarse roots increment

The change in the aboveground biomass (AGB, in kg) between 2017, 2018 and 2019 were estimated by calculating the variation

$\Delta M$ , following Clark et al. (2001 - eqn. 5):

$$\Delta M = \sum (AGB_{a-t_j} - AGB_{a-t_i}) + \sum (iAGB_{b-t_j} - dAGB_{b-t_i}) \quad (5)$$

where  $AGB_{a-t_j}$  and  $AGB_{a-t_i}$  are the AGB of stem  $a$  at time  $t_j$  and  $t_i$ , respectively,  $iAGB_{b-t_j}$  is the ingrowth of stem  $b$  at time  $t_j$ ,  $dAGB_{b-t_i}$  is the ingrowth of stem  $b$  at  $dbh = 5$  cm, and  $t_j > t_i$ . The variation in coarse root increment ( $\Delta Cr$ ) for the given years were estimated in a similar way (eqn. 6):

$$\Delta Cr = W_{B-t_j} - W_{B-t_i} \quad (6)$$

#### Aboveground litterfall

Lf (including all falling materials as leaves, branches, productive organs etc.) was estimated using 20 litter traps which were collected and totalled over the years 2018 and 2019.

#### Fine root production and turnover

Pr (fine root production) was estimated through the dry mass of living roots and dead roots at all collected dates (Osawa & Aizawa 2012 - eqn. 7):

$$P_r = (B_j - B_i) + (N_j - N_i) + \Delta \ln(1 - \gamma_{ij}) \cdot \left[ -(N_j - N_i) - \left( \frac{N_j - N_i}{\gamma_{ij}} + N_i \right) \right] \quad (7)$$

where  $B_i$  and  $B_j$  are the masses of living fine roots  $\leq 2$  mm in diameter (biomass) at time  $t_i$  and  $t_j$ , respectively ( $t_j > t_i$ ),  $N_i$  and  $N_j$  are the masses of dead fine roots (necromass), and  $\gamma_{ij}$  is the decomposition ratio of dead fine-roots at a corresponding time interval.  $B_i$ ,  $B_j$ ,  $N_i$ , and  $N_j$  were obtained by soil core sampling and  $\gamma_{ij}$  was calculated by using the root bag technique (see above). Fine root turnover (FrT) was calculated according to Kubisch et al. (2006 - eqn. 8):

$$FrT = \frac{FrP}{sFrB} \quad (8)$$

where  $FrP$  is the annual belowground fine root production and  $sFrB$  is the standing belowground fine root biomass.

#### Soil respiration measurement

An automated soil CO<sub>2</sub> flux system (LI-8100, Li-COR Biosciences, Lincoln, NC, USA) was used to measure soil CO<sub>2</sub> fluxes to the atmosphere. Measurements were taken between 10:00 and 12:00 pm when daily soil CO<sub>2</sub> fluxes were assumed to be at the highest rate (Luo & Zhou 2006). Periodic nighttime soil respiration was not accounted for, as random measurements done in October 2018 and February 2018 showed minimal diurnal variations. All measurements were done in 8 trenched plots, accounting for soil heterotrophic respiration only and not root respiration. Before measurements, soil collars with a 10 × 10 cm dimension were placed on the soil surface and inserted into the soil, leaving a headspace of 3 cm. Soil disturbance during

collar insertion was minimized. During measurement, the chamber lid was closed, and the air was circulated in a gap between the collar headspace and the chamber. Once the CO<sub>2</sub> concentration in the chamber had stabilized (approximately 30 seconds), the concentration was recorded for about 60 seconds. After every measurement, the automated soil CO<sub>2</sub> flux system was moved from one sampling point to another. Each measurement was repeated twice at each sampling point. The systems software determined the flux rate by calculating the initial slope of a fitted exponential curve at the ambient CO<sub>2</sub> concentration and given in units of  $\mu\text{g mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . These values were converted to  $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  by mathematical functions. Ancillary variable such as water-filled pore space (WFPS) was calculated from the soil water content and bulk density (Jeyanny et al. 2021) and ranged between 52.80% and 57.97%

#### Conversion to Carbon

NPP was first estimated as dry biomass ( $\text{Mg ha}^{-1} \text{ year}^{-1}$ ), then converted to carbon ( $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ), which equals 50% of dry biomass (Sarmiento & Pinillos Garay 2005). This was done for  $\Delta M$ ,  $\Delta Cr$ , and Lf and Pr. Meanwhile, Rh was measured as  $\mu\text{g mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , then converted to carbon ( $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ). The difference between NPP and Rh is the carbon accumulation ( $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ), from which NEP was finally derived.

#### Statistical analysis

The growth variables of the sampled trees according to tree families were computed using descriptive statistics. Spatial variations of M and Cr were also quantified. All data corresponding to the time intervals were estimated and calculated separately according to individual trees and reported as means with standard errors for the years 2017 to 2019. However, mean values of Lf and Pr were computed similarly in separate plots and reported for the years 2018 and 2019 only. The total NPP was computed by summing up  $\Delta M$ ,  $\Delta Cr$ ,  $\Delta Lf$ , and  $\Delta Pr$  for the years 2018 and 2019 respectively. The sum of NPP, according to the years determined, was subtracted from the annual heterotrophic respiration (Rh), and the NEP for 2019 and 2018 was reported.

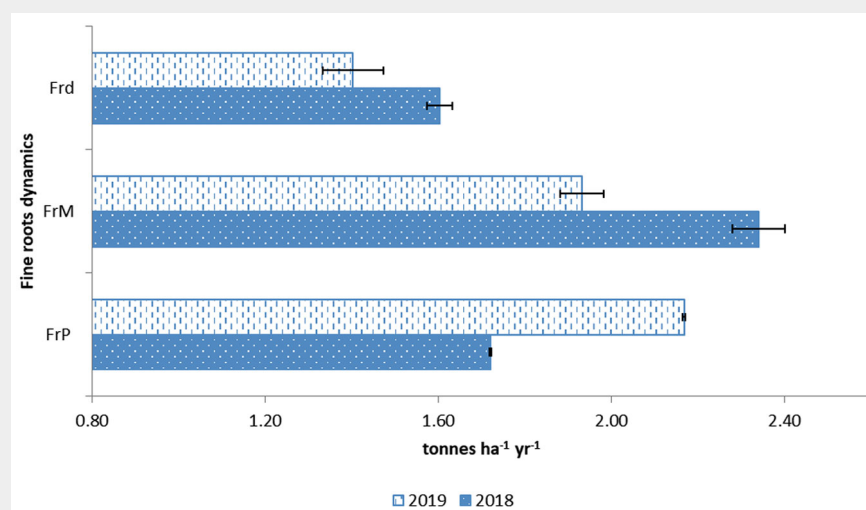
#### Results and discussion

The primary botanical families (Tab. 1) recorded of trees were Phyllanthaceae, Euphorbiaceae, and Dipterocarpaceae. Trees ranged from 4 to 50 m in height (median: 8 m), and DBH ranged from 5 to 70 cm (median: 8.35 cm). The stand basal area was  $22.8 \text{ m}^2 \text{ ha}^{-1}$ . Common genera were *Shorea*, *Aporosa* and *Croton*.

We conducted a complete biometric-based flux measurement over 2 years (2018-2019) and a partial biometric-based measurement (2017) in the Jengka Forest Reserve. Based on our results, it was displayed that there was a slight increment in

**Tab. 2** - Mean  $\pm$  standard error of Net Primary Production (NPP) and Net Ecosystem Production (NEP) at the Jengka Forest Reserve, Malaysia.

| Variables                           | Mg C ha <sup>-1</sup> year <sup>-1</sup> |                   |                   | NPP changes |      | Ratio (%) |
|-------------------------------------|------------------------------------------|-------------------|-------------------|-------------|------|-----------|
|                                     | 2019                                     | 2018              | 2017              | 2018        | 2019 |           |
| Aboveground biomass (M)             | 96.53 $\pm$ 27.53                        | 92.87 $\pm$ 27.71 | 91.89 $\pm$ 27.78 | 0.98        | 3.66 | 14-44     |
| Coarse Roots (Cr)                   | 34.07 $\pm$ 12.96                        | 33.19 $\pm$ 13.04 | 32.96 $\pm$ 13.07 | 0.23        | 0.88 | 3-10      |
| Litterfall (Lf)                     | 2.74 $\pm$ 0.01                          | 3.94 $\pm$ 0.02   | nd                | 3.94        | 2.74 | 32-58     |
| Fine roots production (Pr)          | 1.09                                     | 0.86              | nd                | 0.86        | 1.09 | 13-14     |
| Total                               | -                                        | -                 | -                 | 6.01        | 8.37 | -         |
| Soil heterotrophic respiration (Rh) | 12.23 $\pm$ 0.56                         | 8.9 $\pm$ 0.56    | 10.56 $\pm$ 0.24  | -           | -    | -         |
| Net ecosystem Production (NEP)      | -3.86                                    | -2.89             | nd                | -           | -    | -         |

**Fig. 2** - Fine roots production (FrP), mortality (FrM), decomposition (Frd) and turnover (FrT) in 2018 and 2019. Error bars indicate standard errors (n=3).

M for the years 2018 to 2019 compared to 2017, whereby the highest was between 2018 and 2019, close to 3.66 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Tab. 2). The Cr fraction was very minimal, less than 1 Mg C ha<sup>-1</sup> year<sup>-1</sup> and the Lf fraction showed values between 2.74 to 3.94 Mg C ha<sup>-1</sup> year<sup>-1</sup> for 2 years.

The total NPP was 6.01-8.37 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Tab. 2), whereby Lf accounted for the highest percentage (32%-58%) followed by M (14%-44%), and Pr (13%-14%). Based on the results, the abundant litterfall dominated the C budget, contributing to the soil organic matter pool that further allowed suitable woody increment in aboveground biomass via C mineralization/uptake. Van Do et al. (2015) reported similar trends where Lf and Fr constituted the biggest portions of evergreen broad leaf forests in Japan.

Fine root production (Pr) slightly increased (0.23 Mg C ha<sup>-1</sup> year<sup>-1</sup>). Our results for coarse roots are higher than those re-

**Tab. 3** - Net Ecosystem Production and measuring periods of selected forests.

| Forest type                                         | Study location                                                            | NEP (Mg C ha <sup>-1</sup> y <sup>-1</sup> ) | Measuring period | Sources               |
|-----------------------------------------------------|---------------------------------------------------------------------------|----------------------------------------------|------------------|-----------------------|
| Evergreen old- growth broad-leaved forest           | 21° 23' N, 103° 38' E (Northwest Vietnam)                                 | 2.6                                          | 2014-2015        | Do & Sato 2018        |
| Evergreen secondary broad-leaved forest             |                                                                           | 6.6                                          |                  |                       |
| Broad black spruce ( <i>Picea mariana</i> ) forest  | 54° N, 105° W (Saskatchewan, Canada)                                      | -1.3                                         | -                | O'Connell et al. 2003 |
| Cool-temperate deciduous broad-leaved forest        | 36° 08' N, 137° 25' E (Central Japan)                                     | 2.1                                          | 1999-2003        | Ohtsuka et al. 2010   |
|                                                     |                                                                           | 2.4                                          | 1994-2003        | Saigusa et al. 2008   |
| A young larch forest                                | 62° 13' N, 129° 10' E (Yakutsk, Russia)                                   | 2.4                                          | 1998-1999        | Sawamoto et al. 2003  |
| Japanese red pine ( <i>Pinus densiflora</i> ) stand | 35° 27' N, 138° 46' E (Mountain Fuji, Japan)                              | 2.9                                          | 1999-2008        | Otsuka et al. 2013    |
| Jack pine and aspen stands                          | 55° 51' N, 98° 29' E (Manitoba, Canada)                                   | 1.0                                          | 2003             | Goulden et al. 2011   |
| Dense stand of 500 cm tall jack pine                |                                                                           | 1.7                                          | 2003             |                       |
| Primary rainforest                                  | 2° 5' N, 102° 18' E (Pasoh Forest Reserve, Malaysia)                      | -1.9                                         | 2004             | Adachi et al. 2011    |
| Primary rainforest                                  | 2° 5' N, 102° 18' E (Pasoh Forest Reserve, Malaysia)                      | -5.0 to 2.1                                  | 1969-2012        | Yoneda et al. 2016    |
| Secondary rainforest                                | 3° 35' N, 102° 34' E (Jengka Virgin Jungle Reserve)                       | -3.4                                         | 2017-2019        | This study            |
| Dry evergreen forest                                | 14° 30' N, 101° 55' E (Sakaerat Environmental Research Station, Thailand) | 0.7                                          | 2004             | Adachi et al. 2011    |
| Previously logged peat swamp forest                 | Ketapang, West Kalimantan, Indonesia                                      | -0.1                                         | 2014-2015        | Basuki et al. 2021    |

ported by Ngo et al. (2013) ( $18.8 \text{ Mg C ha}^{-1}$ ) but consistent with those reported by Lü et al. (2010) for aboveground biomass ( $136 \text{ Mg C ha}^{-1}$ ) and coarse roots ( $38.6 \text{ Mg C ha}^{-1}$ ) in a tropical forest ecosystem in Xishuangbanna, Southwestern China.

Before converting to C fractions, the fine root biomass production (FrP) for 2018 and 2019 were  $627.80$  and  $791.05 \text{ g m}^{-2} \text{ yr}^{-1}$ , respectively (data not shown). Still, upon conversion to tonnes  $\text{ha}^{-1}$ , it constitutes  $1.72 \pm 0.03 \text{ t ha}^{-1} \text{ yr}^{-1}$  (2018) and  $2.17 \pm 0.07 \text{ t ha}^{-1} \text{ yr}^{-1}$  (2019), as shown in Fig. 2. Generally, the fine roots mortality (FrM) were  $2.34 \pm 0.06 \text{ t ha}^{-1} \text{ yr}^{-1}$  (2018) and  $1.93 \pm 0.05 \text{ t ha}^{-1} \text{ yr}^{-1}$  (2019). The fine root decomposition fraction (Frd) was  $1.60 \pm 0.002 \text{ t ha}^{-1} \text{ yr}^{-1}$  (2018) and  $1.40 \pm 0.003 \text{ t ha}^{-1} \text{ yr}^{-1}$  (2019) for the same period. The fine root turnover (FrT) calculated for 2018 and 2019 was  $0.71 \text{ t yr}^{-1}$ . These values are similar to those reported by Gill & Jackson (2000) for tropics, ranging from  $0.60$  to  $0.75 \text{ t yr}^{-1}$  in broadleaf tropical forests of Meghalaya, India (Arunachalam et al. 1996) and *Acacia saligna* forest, ranging from  $0.87$  to  $1.97 \text{ t yr}^{-1}$ , in Northern Kenya (Lehmann & Zech 1998). The mean C allocation for fine roots in 2018 and 2019 was  $0.86$  and  $1.09 \text{ yr}^{-1} \text{ Mg C ha}^{-1}$ , respectively (Tab. 2).

In 2019 FrP was higher than FrM and Frd, and this was due to enhanced root decomposition (Frd), which increased root mortality in 2018, but it adversely affected FrP rates. The situation was reversed in the following year (Fig. 2). However, values for FrT were unchanged for both years. Approximately 70% of annual roots turned, consistent with those reported by Jiménez et al. (2009) and Silver et al. (2005) for tropical forests. When FrT is higher, it depicts its essential role in increased nutrient transformation rates for plant uptake, its control in fine root senescence dynamics, and the steady-state conditions of the study site (Gill & Jackson 2000). Our results for Pr were approximately half the Pr reported by Kho et al. (2013) in Lambir, Sarawak, Malaysia ( $1.96 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ). Our results for FrP were also higher ( $621.80$ – $791.05 \text{ g m}^{-2} \text{ yr}^{-1}$ ) as compared to a meta-data analysis done for tropical forest ( $372.00 \text{ g m}^{-2} \text{ yr}^{-1}$ ) by Finér et al. (2011) for sequential coring. The different values in 2018 and 2019 implied inter-annual variability of C fluxes (Silver et al. 2005) and the possibility of variable lifespans of fine roots (Gaudinski et al. 2001) at this study site.

In this study, the mean annual estimated Rs were highest in 2019 ( $12.23 \pm 0.56 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ), followed by 2017 ( $10.56 \pm 0.24 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ) and 2018 ( $8.90 \pm 0.56 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ). The complete information on the partitioning of heterotrophic and autotrophic respiration can be found in Jeyanny et al. (2021). Soil heterotrophic respiration (Rh) ranged between  $518.60$ – $784.08 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  (Jeyanny et al. 2021), which upon conversion is between  $8.90$  and  $12.23 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ .

Our results showed a negative NEP,

which indicates that Jengka FR was a source of carbon emission between 2018 and 2019 (Tab. 2), despite the high contributions from litterfall (Lf) and aboveground biomass (M) controlling the NPP. The results were also driven by high heterotrophic respiration. This was also possibly due to the specific characteristics of the location, which has been transformed into a fragmented forest with time, surrounded in adjacent areas by other crop plantations such as rubber and palm oil. Any drastic changes in these adjacent areas, such as the removal of vegetation, the introduction of water-demanding crops, and land use change, may affect the fragmented portion of forest in terms of environmental variables such as local air, soil temperatures and soil moisture retention in the forest site (Echeverría et al. 2007), thus relatively impacting the above ground biomass C density. Some trees at the forest edges experienced mortality due to wind throws. Logically, with increased soil temperatures and organic matter availability (i.e., from fallen trees and litter debris), the decomposition of fine roots and organic matter is expected, reducing the soil C stock in these areas. Emerging studies have shown that forest edges and fragments may only retain half as much of C as the forest interior (Ma et al. 2017), and this may have been one reason for the negative NEP obtained. Our study did not differentiate between edges and interior forest, and this is an emerging factor that has to be addressed in the future when reporting the C dynamics of a forest.

New studies reported that edge effects can translate into annual carbon emissions of  $450$ – $550 \text{ million Mt C year}^{-1}$  (Fischer et al. 2021). It was estimated that total carbon losses due to fragmented forests in the tropics globally is about  $0.34 \text{ Gt C year}^{-1}$  (Brinck et al. 2017). Similar results were also reported for negative NEP (Tab. 3), such as in Pasoh by Adachi et al. (2011) and Yoneda et al. (2016) ( $-1.9$  and  $-5.0$  to  $2.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , respectively) and in Kalimantan, Indonesia by Basuki et al. 2021 ( $-0.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ). The typical results obtained were between  $-5.0$  to  $6.6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  based on the literature (Tab. 3). Scientists do agree that very poor data are available on carbon budgets related to fragmented forests and further explorations are needed (Ma et al. 2017). Thus, it is important to note that carbon losses in the tropics, driven by external sources such as fragmented forests, may have experienced a change in microclimatic conditions, abundance of organic matter debris, shifts in species composition, and ecosystem functionality (Zhu et al. 2004). Inter-annual temporal patterns (Katayama et al. 2019, Jeyanny et al. 2021) also contributed to the changes in NPP and NEP. The results obtained for Pr, Lf, Cr, M, and Rh were similar to the findings for the Malaysian moist tropical forests such as in Pasoh (Adachi et al. 2006), Sarawak (Katayama et al. 2019),

and Sabah (Saner et al. 2012).

## Conclusions

In this study, the NEP values estimated for a tropical secondary forest in Malaysia were negative, indicating that the study area was a source rather than a sink of carbon due to direct and indirect drivers related to inter-annual variability and forest fragmentation. The most significant fraction that contributed to NPP changes were the above-ground biomass and the litterfall. The dynamics of fine root production changed according to seasonal variability; in this forest, the production was lower compared to mortality and decomposition. We strongly believe that future work in C dynamics should explore differences in an intact forest, forest edges, and modified forest landscape with a long-term monitoring approach for refined estimates of NEP. This work may be a foundation for conservation strategies related to REDD+ initiatives and offer important information for the development and validation of C density models in fragmented forests on a national and regional scale.

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