Differences in soil respiration between different tropical ecosystems

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Abstract

We examined the relationship between soil respiration rate and environmental determinants in three types of tropical forest ecosystem—primary forest, secondary forest, and an oil palm plantation in the Pasoh Forest Reserve on the Malaysian Peninsula. In August 2000, the soil respiration rate and environmental factors (soil temperature, soil water content, soil C and N contents, biomass of fine roots, and microbes) were measured at 12–16 points in research quadrats. Soil respiration rates were 831 ± 480, 1104 ± 995, 838 ± 143, 576 ± 374, and 966 ± 578 (mean ± S.D.) mg CO2 m⁻² h⁻¹ in the primary forest canopy and gap site, secondary forest canopy and gap site, and oil palm plantation, respectively. Although the mean soil respiration rates in the three forest ecosystems did not differ significantly, differences were evident in the environmental factors affecting the soil respiration. The major causes of spatial variation in soil respiration were fine root biomass, soil water content, and soil C content in the primary and secondary forests and oil palm plantation, respectively.

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Keywords: Land-use change; Secondary forest; Oil palm plantation; Soil C content; Root biomass; Microbial biomass

1. Introduction

The capacity of forests to absorb atmospheric CO₂ has been debated in previous studies (e.g., Dixon et al., 1994; Bousquet et al., 1999). A recent study has estimated that the annual net primary production of tropical regions is 32% of global terrestrial photosynthesis (Field et al., 1998). Tropical forests contain large amounts of C in the vegetation and soil, equivalent to 37% of global terrestrial C pools (Dixon et al., 1994).

Tropical forests are estimated to represent a C sink of 1–3 Pg C y⁻¹ (1 Pg = 10¹⁵ g) (Malhi and Grace, 2000). However, these studies were based on the micrometeorological method, which does not yield much insight into the contribution of each component to the C cycle. Malhi and Grace (2000) pointed out that net biotic C sinks can be over- or underestimated, because of insufficient sample areas for statistical analysis, especially in Asia and Africa. Tropical forests in Asia are rapidly being changed into secondary forests or plantations, and deforestation to create permanent croplands has accounted for approximately 75% of the total CO₂ emission from tropical Asia in the 1980s (Houghton and Hackler, 1999). Annual C flux to the atmosphere from changes in land use in tropical Asia...
was 0.88 Pg C y\(^{-1}\) in the 1980s and 1.09 Pg C y\(^{-1}\) in the 1990s (Houghton, 2003). Schimel et al. (2001) calculated net carbon flux using an atmospheric inverse model, and indicated that tropical areas offset emissions due to tropical deforestation.

Soil respiration, or CO\(_2\) efflux from the soil surface, is one of the most important components of the C cycle in forest ecosystems. Many studies of soil respiration have been reported in many ecosystems; temperate forest (Xu and Qi, 2001), boreal forest (Rayment and Jarvis, 2000; Søe and Buchmann, 2005), neotropical rain forest (Schwendenmann et al., 2003), semi-arid steppe (Maestre and Cortina, 2003), subalpine forest (Scott-Denton et al., 2003), tropical bare soil (La Scala et al., 2000), cropland (Rochette et al., 1991; Stoyan et al., 2000), and plantation (Epron et al., 2004; Fang et al., 1998). Generally, soil respiration varies with time and space, and soil temperature and water content are key factors responsible for the variation in soil respiration. In tropical forests, the most influential factor affecting temporal variation of the soil respiration rate is not so much the soil temperature as the soil water content or rainfall, because the soil temperature is relatively constant (Kursar, 1989; Davidson et al., 2000). On the other hand, soil respiration is composed of respiration from both roots and microbes, and some studies have reported the relationship between soil respiration and the underground environment (e.g., root biomass (Søe and Buchmann, 2005; Fang et al., 1998) and soil microbial biomass (Neergaard et al., 2002)). However, there are few data on soil respiration and the environment for forests and plantations in Southeast Asia.

Understanding the factors responsible for soil respiration is essential for predicting changes in this variable caused by changes in land use. Although there have been many studies on soil respiration rates, few have compared soil respiration in forest and plantation ecosystems using the same method. The objectives of the present study were to (1) identify small-scale spatial variations in soil respiration, and (2) examine the factors affecting the variation in soil respiration rates in primary and secondary forests and in an oil palm plantation in tropical Southeast Asia.

2. Materials and methods

2.1. Site description

Our study was conducted in primary and secondary forests in the Pasoh Forest Reserve in the state of Negeri Sembilan, Malaysian Peninsula (2°5’N, 102°18’W), and in an oil palm plantation adjacent to the Reserve. Here, the primary and secondary forests are dominated by Dipterocarpaceae (Tang et al., 1996). The total above-ground biomass was 403 Mg ha\(^{-1}\) (1 Mg = 10\(^3\) kg) in the primary forest (Hoshizaki et al., 2004). The secondary forest site is located in an area where all trees with a DBH (diameter of trunk at breast height) of ≥45 cm were selectively logged in 1958, and then left to regenerate naturally (Okuda et al., 2003). In the oil palm plantation, *Elaeis guineensis* (African oil-palm) seedlings were planted in 1976, and since then the site has been fertilized and weeded every year. Mean monthly maximum air temperature is 32.5 ± 1.1 °C and minimum air temperature is 22.5 ± 0.5 °C (Manokaran et al., 2004). Mean annual precipitation is 1450–2341 mm y\(^{-1}\) in the Pasoh Forest Reserve (Malaysian Meteorological Services, 1995–2000). The pH of the topsoil (0–5 cm) was 3.8 ± 0.2 (mean ± S.D., \(n = 28\)) in the primary forest, 4.2 ± 0.2 (\(n = 32\)) in the secondary forest, and 4.7 ± 0.4 (\(n = 16\)) in the oil palm plantation.

2.2. Measurement of soil respiration

We selected the three different ecosystems (primary and secondary forests, and oil palm plantation) and established two quadrats (under the canopy and gap) in the primary and secondary forests to consider the spatial variability of the forest ecosystems. Canopy and gap sites in the primary and secondary forests were established to compare the soil respiration and environmental factors between the two sites. Soil respiration rate was measured in a grid pattern at 16 points in a 64-m\(^2\) quadrat (under the canopy) and at 12 points in a 48-m\(^2\) quadrat (under the gap) in the primary forest (\(n = 28\)), at 16 points in two 64-m\(^2\) quadrats (under the canopy and gap) in the secondary forest (\(n = 32\)), and at 16 points in a 64-m\(^2\) quadrat in the oil palm plantation (\(n = 16\)); all points were at least 2 m apart. The required sample size for estimating large-scale soil respiration rates within ±20% at the 95% probability level were 19, 18, and 21 in the primary and secondary forests, and oil palm plantation, respectively (Adachi et al., 2005). The required sample size in the oil palm plantation was thus greater than in the forest sites. However, we selected the canopy and gap sites in the primary and secondary forests to consider the difference in the soil environment between the canopy and gap.

Soil respiration was measured between 09:00 and 14:00 on 26 August 2000 in the primary forest, 28 August in the secondary forest, and 30 August in the oil palm plantation.
palm plantation. To minimize the effects of chamber installation, 24 h before the soil respiration measurements were made a soil collar (5 cm high and 13 cm in diameter) was set into the soil to a depth of about 1 cm at each sampling point, taking care not to disturb the soil structure. The soil respiration rate was measured with a portable soil respiration rate measuring system (LI-6400, LI-COR, Lincoln, NB, USA) fitted with a soil respiration chamber (6400-09, LI-COR, NB, USA).

2.3. Measurement of environmental factors

Simultaneously with the soil respiration measurements, soil temperatures at depths of 1 and 5 cm and soil water content at 5 cm depth were measured at each point. Soil temperatures were measured using a thermometer (TM-150, Custom, Tokyo, Japan), and the soil water content was measured with a time domain reflectometry sensor (TDR; TRIME-FM, IMKO, Ettlingen, Germany). At the same sites where soil respiration had been measured in the three ecosystems, soil, and plant roots were sampled to a depth of 10 cm in a circular area 13 cm in diameter during 4–7 September 2000. Fine roots (diameter <1 mm) were collected by handpicking, rinsed with water, dried at 85 °C for 24 h, and weighed. The soil samples were sieved with a 2-mm mesh and mixed well, then part of each soil sample was stored at −20 °C for later measurement of soil microbial biomass by an adenosine triphosphate (ATP) method (Jenkinson and Oades, 1979). The ATP concentrations in the soil (nmol g⁻¹ soil dry weight) were measured by an ATP taster (AF-70, TOA DKK, Tokyo, Japan). The rest of the soil sample was dried at room temperature (about 25 °C) for a week, and then soil C and N contents were measured with a N/C analyzer (C-R6A, Shimadzu, Kyoto, Japan).

2.4. Statistical analyses

All statistical analyses were conducted using the StatView 5.0 software package (SAS Institute, NC, USA). The distributions of soil respiration values were tested for normality using the Kolmogorov–Smirnov test, and we found that the data for each study site showed a normal distribution. ANOVA (Scheffé’s test) was used to determine the differences in average soil respiration and environmental factors between the primary and secondary forests, and the oil palm plantation, respectively (Table 1). Pearson Product–Moment correlations were used to clarify the relationship between soil respiration and environmental factors (Figs. 1 and 2). However, this analysis was done using the data for canopy and gap sites together in the primary and secondary forests, since these were treated as a single ecosystem. Step-wise selection analyses were used to examine the relationships between soil respiration rates and environmental factors. The soil N content was not included in this analysis, because the results of multiple regression analysis were strongly biased due to the strong correlation between the soil N and C contents at all sites.

3. Results

Soil respiration rates were 831 ± 480, 1104 ± 995, 838 ± 143, 576 ± 374, and 966 ± 578 (mean ± S.D.) mg CO₂ m⁻² h⁻¹ in the primary forest canopy and gap sites, secondary forest canopy and gap sites and oil palm plantation, respectively (Table 1). There was no significant difference in soil respiration among the sites (Scheffé’s test, p < 0.05). Soil water content at the secondary forest gap site was significantly lower than at the other sites. Soil C and N contents at the primary forest canopy site were significantly greater than at the other sites.

<table>
<thead>
<tr>
<th></th>
<th>Primary forest</th>
<th>Secondary forest</th>
<th>Oil palm plantation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Canopy (n = 16)</td>
<td>Gap (n = 12)</td>
<td>Canopy (n = 16)</td>
</tr>
<tr>
<td>Soil respiration (mg CO₂ m⁻² h⁻¹)</td>
<td>830.6 ± 480.0a</td>
<td>1103.7 ± 995.4a</td>
<td>837.8 ± 142.8a</td>
</tr>
<tr>
<td>Soil temperature (1 cm) (°C)</td>
<td>24.3 ± 0.3a</td>
<td>26.7 ± 0.6c</td>
<td>25.5 ± 0.5b</td>
</tr>
<tr>
<td>Soil water content (%)</td>
<td>17.5 ± 7.6a</td>
<td>20.0 ± 5.7a</td>
<td>15.2 ± 2.7a</td>
</tr>
<tr>
<td>Soil C content (%)</td>
<td>2.92 ± 0.9a</td>
<td>2.10 ± 0.8b</td>
<td>1.70 ± 0.3b</td>
</tr>
<tr>
<td>Soil N content (%)</td>
<td>0.2 ± 0.05a</td>
<td>0.15 ± 0.04bc</td>
<td>0.11 ± 0.02bcd</td>
</tr>
<tr>
<td>Fine root biomass (g)</td>
<td>1.78 ± 0.8a</td>
<td>1.60 ± 1.0a</td>
<td>2.05 ± 0.5a</td>
</tr>
<tr>
<td>Microbial biomass (nmol ATP/g d.w. soil)</td>
<td>0.79 ± 0.2a</td>
<td>0.45 ± 0.07b</td>
<td>0.58 ± 0.15ab</td>
</tr>
</tbody>
</table>

Means followed by the different letters (a–d) within a factor are significantly different (Scheffé’s test, p < 0.05).
Soil temperature did not correlate with the spatial variation in soil respiration rate, because soil temperatures (1 and 5 cm depths) were nearly the same in all the ecosystems (Fig. 1). In the primary forest, soil respiration had a significantly negative correlation with soil water content and a positive correlation with fine root biomass (Fig. 2). In the secondary forest, soil respiration had a negative correlation with soil water content and a positive correlation with soil C and N contents. In the oil palm plantation, soil respiration had a strong positive correlation with soil C and N contents, and a weaker positive correlation with biomass of fine roots and microbes. In the primary and secondary forests, soil water content had a strong negative correlation with fine root biomass (Fig. 3).

Table 2 shows the best single- and multiple-factor models using stepwise independent variable selection in the three different ecosystems. The major causes of soil respiration were fine root biomass, soil water content, and soil C content in the primary and secondary forests and oil palm plantation, respectively.

4. Discussion

Table 3 shows a comparison of soil respiration among tropical regions. Soil respiration rates observed in the present study were greater than in the previous studies. Although we did not obtain any data that might explain the higher rates observed in our study, Yamashita and Takeda (1998) reported that the litter decomposition rate ($k = 2.15$) in the primary forest study site we investigated was greater than those reported for other tropical forest ecosystems. Therefore, the high soil respiration observed in the present study may have been due to high microbial activity.

Soil respiration rates were negatively correlated with soil water content in the primary and secondary forests. The point to be considered is the influence of soil water content on soil gas diffusiveness and underground biotic activity. A higher soil water content decreases soil gas diffusiveness. Linn and Doran (1984) have suggested that aerobic microbial activity may be inhibited by low $O_2$ concentration when the soil water...
Fig. 2. The relationships between soil respiration and root biomass and microbial biomass in the three different ecosystems. P, S, and O indicate primary forest, secondary forest, and oil palm plantation, respectively. In the primary and secondary forests, canopy and gap sites are indicated by solid and clear circles, respectively. The correlation coefficient and \( p \)-value indicate significant relationships in the figure.

Fig. 3. The relationships between soil water content and fine root biomass in primary forest (P) and secondary forest (S). Canopy and gap sites are indicated by solid and clear circles, respectively.
content is high. In the present study, soil water content was not significantly correlated with soil microbial biomass in any of the three sites, although it had a significant negative correlation with fine root biomass (diameter < 1 mm) in the primary and secondary forests. Although in our study it is not clear why fine root biomass was low in soils with a higher water content, it is probable that a greater soil water content causes a lack of soil aeration, which inhibits the respiratory activity of plant roots. Gaertig et al. (2002) have reported that in German oak forests the density of fine roots showed a positive correlation with gas diffusion coefficient at the soil surface. This suggests that a high soil water content may directly or indirectly depress the soil respiration rate by affecting root biomass and soil gas diffusion.

The soil respiration rate showed a significant positive correlation with fine root biomass in the primary forest and the oil palm plantation. However, the magnitude and mode of contribution of fine root biomass to the soil respiration rate might differ between the two sites.

In the analysis of soil respiration versus fine root biomass between the natural forest (primary forest) and plantation (oil palm plantation), the regression equations for the primary forest (1), secondary forest (2), and oil palm plantation (3) were as follows:

\[ y = 650.05x - 150.27 \]  \hspace{1cm} (r^2 = 0.576, p < 0.01)  \hspace{1cm} (1)

\[ y = 155.42x + 472.41 \]  \hspace{1cm} (r^2 = 0.146, p = 0.0309)  \hspace{1cm} (2)

\[ y = 140.60x + 603.29 \]  \hspace{1cm} (r^2 = 0.311, p = 0.0247)  \hspace{1cm} (3)

As the regression equations for the primary forest and oil palm plantation were very different, we compared them. The y intercept of the regression equation for the primary forest was close to 0 mg CO₂ m⁻² h⁻¹, indicating that the soil respiration rate falls to almost 0 when fine root biomass is removed. However, in the oil palm plantation, the y intercept was about 600 mg CO₂ m⁻² h⁻¹, indicating that soil respiration in the absence of fine roots may be close to this value. In addition, the slopes of the regression lines show that the soil respiration rate per unit of fine root biomass was

### Table 2

Best single and multiple-factors models were generated using stepwise independent variable selection

<table>
<thead>
<tr>
<th>Site</th>
<th>Independent variables</th>
<th>Regression coefficient</th>
<th>Standardized partial regression coefficient</th>
<th>R²</th>
<th>Adj-R²</th>
<th>Regression ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary forest ( (n = 28) )</td>
<td>Intercepts</td>
<td>282.74</td>
<td>282.738</td>
<td>0.638</td>
<td>0.609</td>
<td>22.070 &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Fine root biomass</td>
<td>706.02</td>
<td>0.824</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Microbial biomass</td>
<td>-818.36</td>
<td>-0.258</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Secondary forest ( (n = 32) )</td>
<td>Intercepts</td>
<td>1189.82</td>
<td>1189.818</td>
<td>0.340</td>
<td>0.318</td>
<td>15.481 &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Soil water content</td>
<td>-21.58</td>
<td>-0.583</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oil palm plantation ( (n = 16) )</td>
<td>Intercepts</td>
<td>650.02</td>
<td>650.021</td>
<td>0.788</td>
<td>0.755</td>
<td>24.156 &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Soil water content</td>
<td>-34.60</td>
<td>-0.272</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil C content</td>
<td>551.97</td>
<td>0.778</td>
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<td></td>
</tr>
</tbody>
</table>

### Table 3

Soil respiration rate in different vegetation types in the tropical regions

<table>
<thead>
<tr>
<th>Soil respiration rate (mg CO₂ m⁻² h⁻¹)</th>
<th>Vegetation/location</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>948</td>
<td>Tropical forest (primary forest)/Malaysia</td>
<td>This study</td>
</tr>
<tr>
<td>707</td>
<td>Tropical forest (secondary forest)/Malaysia</td>
<td>This study</td>
</tr>
<tr>
<td>966</td>
<td>Oil palm plantation/Malaysia</td>
<td>This study</td>
</tr>
<tr>
<td>625</td>
<td>Tropical semi deciduous forest/Thailand</td>
<td>Tulaphitak et al. (1983)</td>
</tr>
<tr>
<td>338–503</td>
<td>Three types tropical forest/Australia</td>
<td>Kiese and Butterbach-Bahl (2002)</td>
</tr>
<tr>
<td>469–914</td>
<td>Tropical forest/Panama</td>
<td>Kursar (1989)</td>
</tr>
<tr>
<td>231–444</td>
<td>Tropical bare soil/Brazil</td>
<td>La Scala et al. (2000)</td>
</tr>
<tr>
<td>216–510</td>
<td>Tropical forest/Brazil</td>
<td>Fernandes et al. (2002)</td>
</tr>
<tr>
<td>183–1162</td>
<td>Pasture/Brazil</td>
<td>Fernandes et al. (2002)</td>
</tr>
<tr>
<td>430–675</td>
<td>Tropical forest/Costa Rica</td>
<td>Schwendenmann et al. (2003)</td>
</tr>
</tbody>
</table>

The values of soil respiration in primary and secondary forest in this study are average of canopy and gap sites.
greater in the primary forest than in the oil palm plantation. The difference in the regression intercepts and slopes was significant ($p < 0.01$). These results suggest that the respiration rate per unit of fine root biomass and/or microbial respiration associated with roots (e.g., mycorrhizae) are greater in the primary forest. In the oil palm plantation, we can consider that respiration by soil microbes that decompose soil organic matter is a more important factor affecting the soil respiration rate. This hypothesis is supported by the fact that soil respiration in the oil palm plantation was significantly correlated with soil microbial biomass and soil C content. Soil organic C is used by degradable microbes as the primary resource in soil microbial biomass and soil C content. Therefore, even though the soil respiration rate in both the primary forest and the oil palm plantation showed a positive relationship with fine root biomass, the magnitude and mode of the contribution of fine root biomass and associated soil microbes to soil respiration might differ, reflecting the different forms of land use. This supposition is supported by the results of multiple regression analysis of the data from the two sites; in the oil palm plantation, soil C content (the major energy source for soil microbes) was the major contributor to soil respiration rate.

In the present study, the mean soil respiration rate in the three ecosystems did not differ significantly; however, the environmental factors affecting soil respiration could be different. Differences in land use almost always lead to differences in the vegetation, density of above- and below-ground biomass, the amount of resources available for soil microbes, the physical and chemical characteristics of the soil, and so on. The mean soil respiration rate in each ecosystem is therefore of primary importance when considering the C cycle. However, alterations in the relationships between soil respiration and environmental factors caused by land-use changes are important when estimating variations in the C cycle and its response to environmental change.

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