SOIL MICROBIAL AND ROOT RESPIRATIONS FROM THREE ECOSYSTEMS IN TROPICAL PEATLAND OF SARAWAK, MALAYSIA

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ABSTRACT

The partitioning of soil respiration (SR) to root respiration (RR) and microbial respiration (MR) was conducted using the root exclusion and closed chamber method in three ecosystems on tropical peatlands. RR was estimated by differencing SR and MR. The forest ecosystem displayed significantly higher monthly MR compared with oil palm and sago ecosystems with the highest value of 219 mg CO_2 C m^{-2} hr^{-1}in May 2003. This might be attributed to its thick leaf litter and root mat, and water filled pore space which was conducive for microbial activity. The lowest range of MR, between 153 mg CO_2 C m^{-2} hr^{-1} (October) and 34 mg CO_2 C m^{-2} hr^{-1} (September), was found in the sago ecosystem probably due to its high water-table. The highest RR was recorded in the forest (172 mg CO_2 C m^{-2} hr^{-1}), followed by oil palm (128 mg CO_2 C m^{-2} hr^{-1}) and sago (95 mg CO_2 C m^{-2} hr^{-1}).The latter might be ascribed to its slow growth rate, while the former to higher root biomass and growth rate. The annual ratio of RR to SR was 52 % in the sago ecosystem and 60 to 62 % in both oil palm and forest ecosystems.

Keywords: Microbial respiration, root respiration, tropical peat, oil palm, sago.

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INTRODUCTION

Soil respiration (SR) is one of the main sources of carbon flux in most ecosystems. Thus, any agricultural practice that causes major changes to it may have a large impact on the global carbon budget and heat balance. With the extensive land development for agriculture purposes in Sarawak, there is an urgent need to carry out measurements to determine the potential of soil as a net source or sink for atmospheric CO_2 in the agro-ecosystems. Total CO_2 released from the soil is an effective indicator of both root system and microbial activities especially those involved in the organic matter mineralisation. Consequently, soil CO_2 is often used as an index of biological activity in soil (Lamade *et al*., 1996). However, it comprises two forms of respiration, *i.e.* autotrophic (root) and heterotrophic (microbial) respiration that need to be distinguished for better understanding of the below-ground carbon dynamics and the implication of environmental changes on soil carbon cycling (Hanson *et al*., 2000; Widén and Majdi, 2001) in the agro-ecosystems. Part of the variation can be ascribed to differences in site characteristics such as species, climate and stand age (Raich and Schlesinger, 1992).

Root respiration (RR) comprises all respiration processes of the organic compounds from the plants in the rhizosphere. This includes the respiration of living root tissue, the respiration of symbiotic mycorrhizal fungi and associated microorganisms in living roots, and the decomposing organisms operating on root exudates (Hanson *et al*., 2000). Exudates and root residues are energy rich. They enhance the underground carbon stock and are metabolised by soil microorganisms. These

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readily available carbon sources contribute to fast carbon turnover in the soil and C priming effect in the rhizosphere when compared with root-free soil (Dormar, 1990; Kuzyakov, 2002; Cheng and Kuzyakov, 2005). Contradictorily, CO_2 from RR cannot be used by microorganisms for growth because it is an energy-poor mineralisation product that does not affect the turnover of microbial biomass and soil organic matter. Therefore, an accurate carbon budget of the plants, soil and rhizosphere microorganisms cannot be determined, without estimating root respiration and microbial utilisation of root exudates, separately from microbial decomposition of organic matter (Kuzyakov, 2002). This is because the former is carbon neutral and does not cause a reduction in soil organic C.

A range of methods such as component integration, root exclusion and isotopic techniques (Hanson *et al*., 2000) have been used to quantify the RR and microbial respiration (MR) under field conditions. In general, the root contribution to SR generally ranges from 33%-89% in forests, 17%-40% in grasslands, 12%-38 % in croplands and 50%-93% in arctic tundra (Raich and Tufekcioglu, 2000). Studies using a root exclusion approach to measure the RR of oil palm in plantation on mineral soils in Sumatra, Indonesia (Lamade *et al*., 1996) and other crops on peat lands (Silvola *et al*., 1996) show 30%-80% and 35%-45% of RR to total SR, respectively.

Recently, considerable attention has been given to autotrophic respiration but its role in contributing to the total SR is still unclear particularly for perennial tree crops and forest in tropical peat swamps. *In situ* comparisons between SR and heterotrophic respiration in a continuous and simultaneous way are rare, but are valuable for improving our understanding of the different behaviour between RR and heterotrophic respiration (Tang *et al*., 2005). Moreover, there is a need to quantify heterotrophic respiration in tropical peat swamps because of its direct bearing on the atmospheric carbon dioxide concentration unlike root respiration.

Melling *et al*. (2005) had provided a comprehensive account of SR in three ecosystems in tropical peatland. This article extends it through partitioning SR in mixed peat swamp forest, and oil palm and sago ecosystems in the tropical peatland of Sarawak, Malaysia into root and MR by using the root exclusion technique. Unlike trenching, the root exclusion technique with sufficient incubation time, does not suffer problems with the presence of an abnormal amount of dead roots which contribute to the release of CO_2 (Hanson *et al*., 2000). Factors affecting the MR in this ombrotrophic peat land were studied as well.

MATERIALS AND METHODS

Sites Description

The three studied sites were all located in Mukah Division of Sarawak, Malaysia with an equatorial climate, characterised by high, even temperatures and heavy rainfall without a distinct dry season. The ecosystems comprised of a mixed peat swamp forest, oil palm (*Elaeis guineensis*) plantation and sago (*Metroxylon sagu*) plantation. The peat soils were classified as *Typic Tropofibrist* under the USDA soil classification system (Soil Survey Staff, 1992) and were categorised as deep peat because their soil depths were more than 250 cm.

The forest ecosystem is a mixed peat swamp forest of about 1200 ha which represents the climax vegetation of tropical peatland. It has an uneven canopy with a mean canopy height of about 21 m where the dominant species can reach a height of 40 m. Forest composition includes principal species such as Ramin (*Gonystylus bancanus*), Alan (*Shorea albida*), Jongkong (*Dactylocladus stenostachys*) and Kapur (*Drybalanops rappa*) (Anderson, 1972). The water-table in the forest was generally high throughout the year, at a depth of less than 40 cm, and the forest conditions were heavily shaded, damp and highly humid. The forest floor had thick root mats and leaf litter.

In the 4000 ha oil palm ecosystem, the oil palms were about four years old with an average height of 5.5 m and planting density of 160 palms ha^{-1} and their canopies were almost closed. The water-table was lowered to 50-70 cm by drainage and compaction. In a one year period, 103 kg N ha^{-1} urea were applied twice in the oil palm plantation; in November 2002 and May 2003. There was no clear build-up of leaf litter in this young oil palm plantation, and therefore the soil surface was clean with no obvious root mat. The sago palms were cultivated on the 5700 ha of cleared peatland without any soil compaction. No agrochemical was applied to the site. The palms were also four-year-old at the commencement of study. They were about 4 m in height and their canopies had not closed. The sago plantation with a planting density of 100 palms ha^{-1} was cultivated after the forest was cleared. It was initially drained until the water-table was about 30 cm. A detailed description of the vegetation, climate and soil properties of SR plots at the sites is provided by Melling *et al*. (2005). This paper discusses the climate and soil properties of root exclusion (MR) plots only, which have not been presented before.

Soil CO_2 Respiration Measurements

Total soil and MR were measured at monthly intervals for a year using a closed-chamber method (Crill, 1991). In order to measure SR, three stainless steel open-ended cylinders, each 20 cm in diameter and 25 cm in height, were placed directly on the soil surface at each site (Melling *et al*., 2005). The chamber was placed at the edge of canopy for oil palm and sago plantation where root activity was expected to be highest while chamber for forest ecosystem was placed randomly since their roots were well distributed. Thus, the placement of the chambers was varied in each ecosystem because the canopy dimensions and root distributions differed substantially among them. The soil along the edge of each cylinder was cut with a very sharp knife so that the cylinder could be pushed 3 cm into the soil to prevent gas leakage from the bottom of the cylinder.

The root exclusion technique was used to measure the microbial (root-free) respiration. The roots were first severed but not removed to minimise disturbances. Stainless steel open-ended cylinders of 20 cm in diameter and 50 cm in length were then driven into the soil profile to act as a barrier to inhibit the growth of future root. The stainless steel open- ended chambers were left below the ground throughout the year without any disturbance. The chambers were left to stand for two months before the first CO_2 measurements were taken in August 2002 to reduce the effect of root decomposition on the CO_2 flux. The decomposition of roots occur two to three months after exclusion, therefore it is assumed that the RR in the plots is negligible in the root-excised plot after two months. No significant root invasion was observed during the sampling period. Had there been any green vegetation seen on the measuring plots, they would be removed. Similar to the measurement of SR as described earlier, another stainless steel open-ended cylinder of 25 cm in height was placed directly on the soil surface, above the 50-cm open-ended column at each site to measure CO_2 released. The distance between chambers was fixed at 7.5 m intervals between the inter-row of two oil palms. The first chamber was placed 2 m from the trees in the three ecosystems. The chambers, with and without roots, in each ecosystem were located about 1.5 to 2 m apart to minimise border effect and disturbance during measurements.

The open cylinders were left, standing for 30 min to establish an equilibrium state before gas sampling (Norman *et al*., 1997). When the equilibrium was achieved, 500 ml of gas sample from the headspace of each cylinder were extracted into airtight bags (Tedlar Bag) using 50 ml polypropylene syringe and this measurement was regarded as time 0 min. The top of the cylinder was then immediately sealed with acrylic cover which had two ports; one for gas sampling and the other for attaching a sampling bag to equilibrate the chamber pressure with the atmospheric pressure. After 6 min under closed chamber condition, another 500 ml of headspace gas samples from each chamber were extracted into airtight bags. Hence, the length of the measurement between two gas samples was 6 min under similar conditions. The gas measurements in each ecosystem were conducted between 1000 and 1300 hr on the same day for both plots, with or without roots.

CO_2 Concentration Analysis

The CO_2 gas concentrations were determined in the laboratory within 4 hr using CO_2 infrared gas analyser (Fuji Electric ZFP-5). The gas analyser was calibrated using standard calibration gas mixture of 0 and 1887 ppm CO_2 in N_2. Two-point regressions of CO_2 concentrations in the headspace and air temperature in the chamber were used to estimate the CO_2 fluxes at each sampling point according to Nakano *et al*. (2004), who demonstrated that the increase in the gas concentration in the chamber was linear for gas flux measurements taken within 10 min. The detectable limit in the study was 6.9 mg C m^{-2} hr^{-1}.

Environmental Variables

The air and soil temperatures, and relative humidity (*Table 1*) were measured simultaneously with the gaseous flux at monthly intervals. Air temperature and relative humidity were measured with a digital thermometer and a digital relative humidity meter respectively. Soil temperatures at 5 and 10 cm below the soil surface were measured with a portable temperature probe. Perforated PVC pipes of diameter 6 cm were inserted close to the chambers to measure water-table. The depth of ground water-table was recorded when the CO_2 flux was measured. Precipitation was measured with a rain gauge (area 706.9 cm^2) at the study sites.

Three peat soil samples at depths of 0 – 25 cm and 25 – 50 cm were collected monthly from each ecosystem at the same time as the gas sampling. The three soil samples at each depth were bulked for both physical and chemical analyses as shown in *Table 2*. Three further undisturbed core samples were also taken for measurement of volume at the laboratory by using a soil volume analyser (Model DIK-1110 Daiki Rika Kogyo Co., Ltd). The cores were then oven dried at 105°C for 48 hr and reweighed to determine their bulk density and moisture content. Soil moisture content of the peat was expressed as a percentage of the total pore space that was filled with water (percent water filled pore space, %WFPS), which was the ratio of

TABLE 1. ENVIRONMENTAL CHARACTERISTICS OF ROOT-EXCISED PLOTS IN THE MIXED PEAT SWAMP, OIL PALM AND SAGO ECOSYSTEMS IN SARAWAK

	Forest	Oil Palm	Sago
	2˚49′N, 111˚51′E	2˚49′N, 111˚56′E	2˚47′N, 111˚50′E
Site code	F	P	S
Annual rainfall (mm)	2163	2471[a]	2928
Mean monthly air temperature (°C)	27.7 ± 0.2	32.8 ± 0.6	34.5 ± 0.5
Mean monthly soil temperature at 5 cm (°C)	25.8 ± 0.1	30.7 ± 0.3	30.2 ± 0.3
Mean monthly soil temperature at 10 cm (°C)	25.8 ± 0.1	28.5 ± 0.2	27.6 ± 0.1
Mean monthly water table (cm)	45.5 ± 3.8	57.6 ± 2.6	23.6 ± 3.1
Mean monthly water-filled pore space (%) (0-5 cm)	66.6 ± 2.3	60.0 ± 2.0	75.1 ± 1.9
Mean monthly relative humidity (%)	89.1 ± 0.9	65.6 ± 2.0	59.5 ± 1.9
Peat thickness (cm)	480	555	650
Bulk density (kg m^{-3})	150 ± 0.003	200 ± 0.006	150 ± 0.003

Note: aThe rainfall value excludes the month of June 2003 because the rain gauge was stolen.

TABLE 2. CHEMICAL PROPERTIES OF THE PEAT SOIL AT DIFFERENT DEPTHS OF ROOT-EXCISED PLOTS IN THE MIXED PEAT SWAMP, OIL PALM AND SAGO ECOSYSTEMS IN SARAWAK

Ecosystem	Forest		Oil palm		Sago	
Soil depth (cm)	0-25	25-50	0-25	25-50	0-25	25-50
Soil pH (1:2.5)	3.6 ± 0.03	3.5 ± 0.02	3.3 ± 0.04	3.3 ± 0.02	3.6 ± 0.04	3.5 ± 0.02
LOI (%)	98.6 ± 0.1	99.2 ± 0.1	97.8 ± 1.3	99.3 ± 0.1	98.7 ± 0.1	99.0 ± 0.1
Total C (%)	48.1 ± 0.6	48.2 ± 0.7	45.5 ± 0.9	45.3 ± 0.7	45.2 ± 1.0	45.9 ± 0.8
Total N (%)	1.8 ± 0.04	1.5 ± 0.05	1.8 ± 0.08	1.6 ± 0.05	2.0 ± 0.05	1.7 ± 0.07
C:N	27.6 ± 0.9	34.0 ± 2.1	26.3 ± 1.2	29.2 ± 0.9	22.3 ± 0.6	27.0 ± 1.5
NH_4-N (mg kg^{-1})	54.6 ± 12.0	13.5 ± 5.0	51.6 ± 16.3	24.5 ± 11.9	47.7 ± 10.9	28.1 ± 5.6
NO_3-N (mg kg^{-1})	81.1 ± 36.3	27.5 ± 10.2	241.0 ± 104.7	149.9 ± 55.6	92.5 ± 54.3	22.8 ± 6.4
CEC[b] (cmolc kg^{-1})	48.7 ± 3.5	48.1 ± 4.3	45.3 ± 3.7	50.3 ± 6.4	47.0 ± 3.9	44.5 ± 3.9
Base saturation (%)	22.7 ± 1.5	19.2 ± 2.0	27.6 ± 5.2	28.5 ± 4.1	26.6 ± 2.7	24.6 ± 3.4

Note: LOI = loss on ignition.
CEC = cation exchange capacity.
Figures show mean ± standard error (n =12).

the volumetric moisture content (cm^3 H_2O cm^{-3}) to the total porosity of the soil.

Estimation of the Root Respiration

As the freshly-severed root material decomposes, SR decreases, eventually reaching a horizontal asymptote. The respiration rate at this asymptote represents soil MR. RR is then obtained by subtracting the MR rate from total SR rate (Kelting *et al*., 1998).

$$RR = SR - MR$$

where SR and MR denote the total soil respiration and microbial respiration, respectively.

Following this principle and the above equation, three assumptions were made. Firstly, the soil carbon only gets input from leaf and root litters; where carbon leached from rainfall is considered negligible. This is because the organic matter derived from the dead roots may not be able to move downwards until the root litter has undergone certain degree of humification (Nakane, 1978). Secondly, any carbon depletion from the soil is due to mineralisation of litter, root residues and organic matter only. Finally, interactions between microbial activity and carbon supply (litter and soil organic matter decomposition) are assumed to be negligible (Lamade *et al*., 1996). In the latter, we also assumed that carbon supply from root exudates was small, compared to carbon emission from RR.

Statistical Analysis

Repeated measure analyses were used to compare soil CO_2 fluxes with the ecosystems as the subject and time as repeated measurements using STATISTICA version 6.0 (StatSoft, 2001). Principal component analysis (PCA) was done using the data from the three ecosystems to determine the major principal components that have relationships with environmental variables. Multicollinearity among the environmental variables was eliminated by using PCA without rotation with eigenvalue of 1.0 as the lower limit.

Non-parametric tree regression test was carried out to establish the correlation between the environmental variables and microbial respiration rates using S-PLUS 2000 (Mathsoft, 1999). A decision tree based on a binary partitioning algorithm was built to partition data in a recursive manner until each group was either homogenous or contain a user-defined minimum numbers of observation. At each split, the algorithm considers each explanatory variable and chooses the one that results in the greatest reduction in deviance. It is not affected by multicollinearity between independent variables, shows the transparency of results and assesses the relative importance of inputs. This approach resulted in a complex decision tree that needed to be pruned, in order to obtain the most important information. Minimisation of deviance and the minimum number of observations per node (equal to 5) were specified to split the tree and stopping the algorithm (Melling *et al*., 2005).

RESULTS

Environmental Variables

The mean air temperature of the root-excised plots in the forest ecosystem was 27.7°C, whereas the sago and oil palm ecosystems were higher at 34.5°C and 32.8°C respectively (*Table 1*). The monthly soil temperature at 5 and 10 cm for the three ecosystems had similar patterns and were relatively constant as indicated by their low standard errors. The lowest mean soil temperature was observed in the forest at about 25.8°C. Both sago and oil palm ecosystems had almost similar mean monthly soil temperatures at the two different depths, ranging between 27.6°C and 30.7°C. Thus, the relative humidity (RH) might be influenced by the surrounding temperatures of the ecosystems where the forest recorded 74%-99%, which were higher than those of the oil palm at 53%-80% and sago at 54%-88%. These results were similar to the SR plots discussed by Melling *et al*. (2005), probably due to their close proximity.

The water-filled pore space (WFPS) of the root-excised plots in sago ecosystem was 75.1%, forest 66.6% and oil palm 60.0% following the decreasing order of their respective mean water tables (*Table 1*). In fact, the WFPS declined by 0.44% for every cm drop in the mean water-table. The rainfall and water-table at the three ecosystems showed a distinct seasonal trend. The highest values were observed during the month of January at all sites. The monthly ranges of rainfall in these ecosystems were as followed: forest (33-418 mm), sago (37-610 mm) and oil palm (43-537 mm). On average, the sago ecosystem was found to have the highest water-table at 23.6 cm as compared with the forest at 45.5 cm and oil palm 57.6 cm. The monthly depths of water-table were observed to be mainly a direct consequence of the precipitation. Furthermore, due to drainage prior to planting, the water-table in the oil palm ecosystem was the lowest amongst the current studied ecosystems. It also had the highest bulk density among the three ecosystems as it had been drained and compacted earlier, as part of the best management practice in the plantation.

The chemical characteristics of the peat soil samples of root-excised plots at the depths of 0-25 and 25-50 cm are given in *Table 2*. Generally, the peat soil was acidic with soil pH below 4.0 which means high availability of exchangeable hydrogen ions. Due to the high values of loss of ignition (LOI) at about 99%, the peat soils were found to contain large amount of organic materials, with the organic C ranging from 45% to 48%. This contributed to the ratio of C:N exceeding 22:1 in the three peat ecosystems with the forest having the highest C:N ratio of 28:1 in the top soil. The oil palm ecosystem was observed to have the highest NO_3-N concentration in the soil, due to the regular applications of urea fertiliser since its planting, unlike the forest and sago ecosystem which did not receive any fertiliser application throughout the studies. These results were similar to those of SR plots reported by Melling *et al*. (2007).

CO_2 Respiration

The trends of CO_2 flux for soil and MR were compared separately according to the study sites from August 2002 to July 2003 (*Figure 1*). In the forest ecosystem, CO_2 flux was only measured in September as approximately three months were required for the stabilisation of CO_2 production in the soil, due to the decomposition of the big roots. The forest did not only have the highest amount of root mats but also leaf litter on the ground leading to negative readings of the CO_2 flux during the initial measurements in August 2002, as compared to the oil palm and sago ecosystems.

A significant rise in RR may be expected in the first two to three months after root excision due to root injury and soil disturbance (Ewel *et al*., 1987; Uchida *et al*., 1998). With time, the respiration rate of the root-excised plot (MR) gradually became

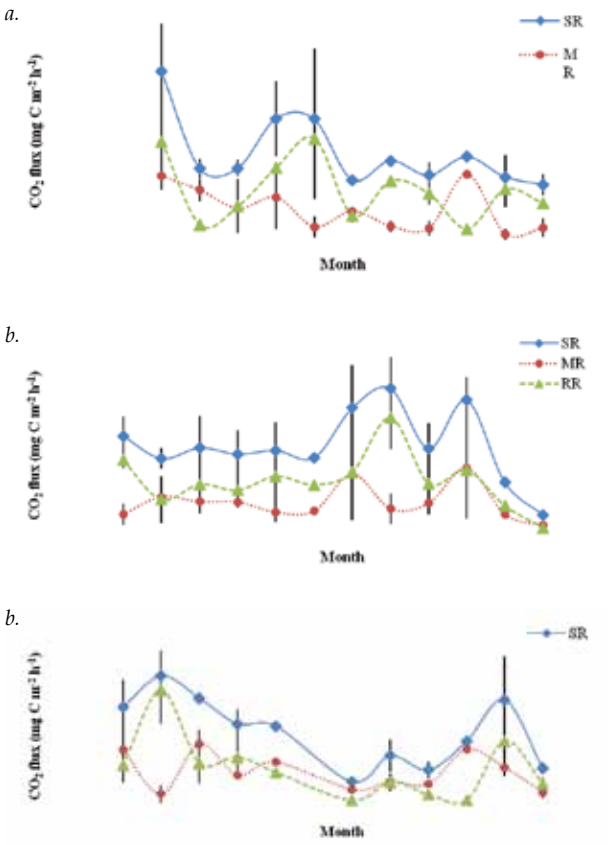

Figure 1. Monthly CO2 flux trends for soil, microbial and estimated root respirations in the (a) forest, (b) oil palm and (c) sago ecosystems. The measurement of CO2 flux in the forest began in September. Data represent means ± SE. Error bars indicate SE of the mean. Symbols without error bars have errors smaller than the symbols.

substantially lower than the control SR measured at 0-50 cm. In this study, the growth of new roots into the excised plot from below the base of the partitions was not prevented mechanically (Lee *et al*., 2003). Nevertheless, the possibility of this mechanism interfering with the experimental results was remote because the water-table was mainly above the depth of soil core (50 cm), while most oil palm roots were found in the top 50 cm of the soils (Lamade *et al*., 1996).

Most SR values were observed to fall below 300 mg CO_2 C m^{-2} hr^{-1} in all three ecosystems involved except for certain months. The highest SR was recorded in September for both forest and sago ecosystems. Oil palm showed the highest SR in the month of March. Forest ecosystem generally had higher monthly soil CO_2 emissions ranging from 188 to 533 mg CO_2 C m^{-2} hr^{-1} as compared to the sago plantation of 64 to 314 mg CO_2 C m^{-2} hr^{-1} and oil palm plantation 52 to 334 mg CO_2 C m^{-2} hr^{-1}.There was no significant difference among the three ecosystems in the soil CO_2-C and cumulative fluxes. However, as a strong and substantial trend was observed, it shows the effects of time and an interaction of factors such as relative humidity, WFPS and air temperature on the monthly CO_2 flux at the sites (Melling *et al*., 2005).

In the forest ecosystem, the MR fluctuated in the range of 115 to 214 mg CO_2 C m^{-2} hr^{-1} from September to December 2002. It was followed by a continual decline from January 2003 onwards, despite peaks at 108 mg CO_2 C m^{-2} hr^{-1} in February and 219 mg CO_2 C m^{-2} hr^{-1} in May**.** The flux for the CO_2 in the sago ecosystem fluctuated with the lowest and highest MR CO_2 recorded at 34 mg CO_2 C m^{-2} hr^{-1} (September) and 153 mg CO_2 C m^{-2} hr^{-1} (October), respectively. The range of MR for oil palm was 28 to 157 mg CO_2 C m^{-2} hr^{-1}.

The forest ecosystem showed the highest annual means of SR and MR among the three ecosystems with 285 and 113 mg CO_2 C m^{-2} hr^{-1} respectively, which were taken from 11 months of data (*Table 3*). This was followed by the oil palm ecosystem at 207 mg CO_2 C m^{-2} hr^{-1} (SR). However, the MR in oil palm was the lowest among all ecosystems at only 79 mg CO_2 C m^{-2} hr^{-1}. A higher water-table of 20 cm, which was observed in the sago plantation resulted in the lowest SR of 182 mg CO_2 C m^{-2} $hr^{-1}$and approximately 87 mg CO_2 C m^{-2} hr^{-1} for its MR (*Table 3*). In the sago plantation, there was no reading recorded in January 2003, due to flooding, which coincided with the highest monthly rainfall.

The RR was estimated by subtracting the MR from SR on a monthly basis. The mean values for SR and RR increased significantly in each site with accompanying decreases in the MR. The RR was the highest in January 2003 at 328 mg CO_2 C m^{-2} hr^{-1} in the forest which corresponded to the highest value recorded for its SR in the same month. Similarly, the highest RR values were obtained in March for oil palm and September for sago at 269 mg CO_2 C m^{-2} hr^{-1} and 280 mg CO_2 C m^{-2} hr^{-1}, respectively. As for the mean annual RR, the forest was estimated to have the highest value at 172 mg CO_2 C m^{-2} hr^{-1}. The RR rates for the sago and oil palms were found to be only 95 and 128 mg CO_2 C m^{-2} hr^{-1} respectively. Consequently, the contribution of roots to total soil CO_2 release seems to be variable; where forest and oil palm showed a similar ratio of RR to SR at approximately 60% to 62%. The ratio of RR to SR in sago ecosystem was lower at 52 % only (*Table 3*).

Principal Component Analysis

The environmental variables in the three tropical peatland ecosystems were analysed using PCA. From the results of the initial eigenvalues, the first three principal components were considered (eigenvalue = 1.0), which accounted for 87.2 % of the total variance for the MR (*Table 4*). The first principal component (PC1) constituted the climatic status of the ecosystem which included air temperature, soil temperature at 5 and 10 cm and

TABLE 3. SUMMARY OF THE AVERAGE SOIL, MICROBIAL AND ESTIMATED ROOT RESPIRATIONS (Mg Co_2 cm^{-2} hr^{-1}) AND PERCENTAGE OF ROOT RESPIRATION IN THE FOREST, OIL PALM AND SAGO ECOSYSTEMS

	Forest	Oil Palm	Sago
Soil respiration	285.0 ± 32.3	206.7 ± 22.6	182.3 ± 24.7
Microbial respiration	113.3 ± 20.0	79.1 ± 10.8	87.0 ± 13.2
Root respiration	171.8 ± 28.1	127.6 ± 17.3	95.2 ± 22.9
% RR to SR	60	62	52
Months of data	11	12	12

Note: RR – root respiration.
SR – soil respiration.

TABLE 4. VARIANCE OF MICROBIAL RESPIRATION RATE AS EXPLAINED BY VARIOUS PCA COMPONENTS

Component	Eigen value	% of variance	Cumulative eigenvalue	Cumulative (%)
1	3.6	51.0	3.6	51.0
2	1.8	24.6	5.4	75.6
3	0.8	11.6	6.2	87.2

TABLE 5. VARIANCE OF ROOT RESPIRATION RATE AS EXPLAINED BY VARIOUS PCA COMPONENTS

Component	Eigenvalue	% of variance	Cumulative eigenvalue	Cumulative (%)
1	3.6	51.4	3.6	51.4
2	1.8	25.7	5.4	77.1
3	0.8	11.9	6.2	89.0

relative humidity. It explained 51.0 % of the total variance. PC2 accounted for 24.6 % of the total variance and it was correlated with the WFPS and water-table and thus, defined the water status of the peat soils. PC3, which only accounted for 11.6% of the total variance, represented the level of soil compaction as determined by the soil bulk density. The 89.0 % of the variance in RR was obtained from the first three factors which was similar to those in the MR. The distribution of percentage of variance among the three principal components was also similar, whereby PC1 accounted for 51.4% of the total variance, followed by PC2 at 25.7% and finally PC3 at 11.9%. The composition of variables constituting each principal component in the RR was similar to those obtained for MR except that the environment of oil palm plantation was now closer to the forest ecosystem than the sago plantation. The oil palm plantation did not alter the environmental factors for RR in the peat swamp much, probably because the water-table under the forest had been lowered by the neighbouring development.

The forest had the lowest air and soil temperatures and lower water-table compared to sago ecosystem. From *Table 5*, it is suggested that the microclimate in the forest on peat had been changed after the cultivations of oil palm and sago nearby. The PC1 scores could be used to separate the oil palm and sago ecosystems from the forest ecosystem because upon cultivation, their PC1 scores became negative compared to the positive values in the forest ecosystem. This was due to the higher air and soil temperatures upon the conversion of forest to perennial tree crops. PC2, which defines the water status of tropical peat swamp, might be used to differentiate the sago ecosystem from the other two ecosystems by virtue of its high water-table resulting in a negative score. The increase in the bulk density in the oil palm ecosystem, due to the compaction of peat before planting the palms and the lowering of water table through systematic ditches resulted in positive PC3 score. This might be used to distinguish it from the forest and sago ecosystems, which have negative scores. Therefore, the three PCA scores, which separated the three ecosystems, also clearly showed the anthropogenic changes caused by the land conversion of tropical peat swamp from forest to perennial tree crops.

Regression Trees

The regression tree for CO_2 flux due to MR in the forest ecosystem is shown in *Figure 2*. The most important predictor variables were identified as WFPS, depth of water-table and soil temperature at 5 cm depth (TCOF). WFPS at the critical level of 54.1% separated the high and low microbial CO_2 flux. The highest mean CO_2 flux was measured at 182 mg CO_2 C m^{-2} hr^{-1} when WFPS was less than 54.1%. However, when the WFPS exceeded 54.1% and mean water-table deeper than 53 cm, the lowest flux of CO_2 was seen at only 42 mg CO_2 C m^{-2} hr^{-1}. High surface soil temperature above 26ºC would increase MR.

The significant predictors for MR in the sago ecosystem were the same as for the forest ecosystem except that TCOF was now more important than the other two variables (*Figure 3*). When TCOF exceeded the critical level of 31.9°C, the highest mean CO_2 emission of 130 mg CO_2 C m^{-2} hr^{-1} was obtained in the ecosystem. Conversely, low mean CO_2 fluxes were measured when TCOF was lower than 31.9°C (67 mg CO_2 C m^{-2} hr^{-1}) and the peat soils were saturated with water as indicated by its WFPS exceeding 67.4% and mean water-table higher than 15.7 cm (42 mg CO_2 C m^{-2} hr^{-1}).

Unlike the forest and sago ecosystems, the tree regression analysis for the oil palm ecosystem shows that bulk density (BD) and WFPS were the main predictors for the CO_2 flux (*Figure 4*). At a critical level of 220 kg m^{-3}, BD was split into the

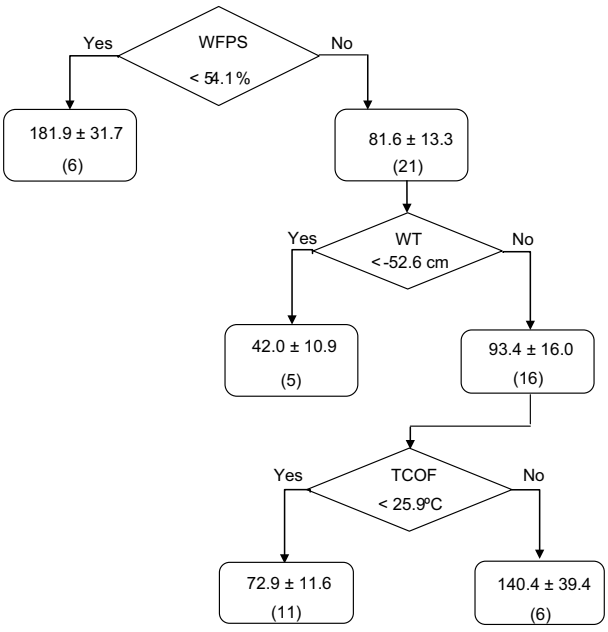

Figure 2. Regression tree for the forest ecosystem (r2 = 0.48). The microbial CO2 flux (mg C m-2 hr-1) in the group is shown in each box. Values are means ± SE. The number in brackets is the number of samples in the group. WPFS, WT and TCOF denote water filled pore space (%), depth of water-table (cm) and soil temperature at 5 cm depth (°C), respectively.

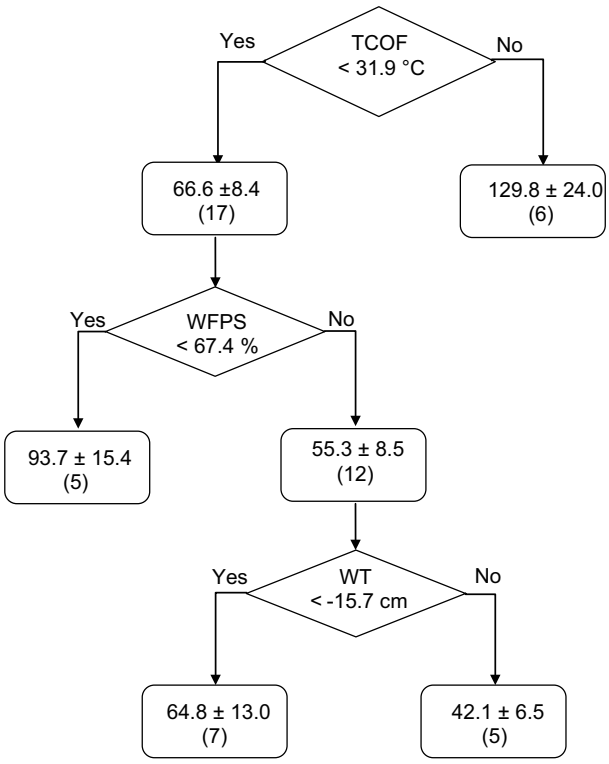

Figure 3. Regression tree for the sago ecosystem (r2 = 0.45). The microbial CO2 flux (mg C m-2 hr-1) in the group is shown in each box. Values are means ± SE. The number in brackets is the number of samples in the group. WPFS, WT and TCOF denote water filled pore space (%), depth of water-table (cm) and soil temperature at 5 cm depth (°C), respectively.

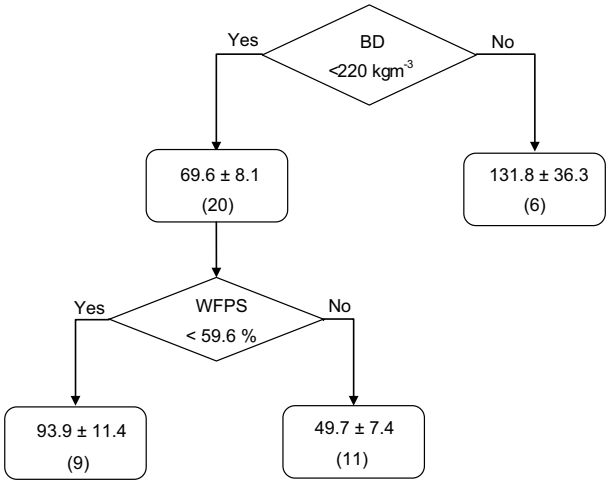

Figure 4. Regression tree for the oil palm ecosystem (r2 = 0.33). The microbial CO2 flux (mg C m-2 h-1) in the group is shown in each box. Values are means ± SE. The number in brackets is the number of samples in the group. BD and WFPS denote bulk density (kg m-3) and water filled pore space (%) respectively.

highest and lowest values of CO_2 under different determinant variables. When BD was greater than 220 kg m^{-3}, the highest CO_2 flux of 132 mg CO_2 C m^{-2} hr^{-1} was obtained. Only when the BD was less than 220 kg m^{-3} and WFPS more than 59.6% was the lowest CO_2 (49.7 mg CO_2 C m^{-2} hr^{-1}) obtained.

DISCUSSION

Environmental Changes and Controlling Factors in Microbial Respiration

The conversion of primary tropical forest on peat into plantations for sago and oil palms reduced the total soil CO_2 flux and its breakdown components such as SR, MR and RR. This might be attributed to the impact of cultivation of peat on the environmental conditions of the site such as the climate (PC1), soil moisture (PC2) and bulk density (PC3) as shown by the PCA analysis (Raich and Tufekcioglu, 2000; Melling *et al*., 2005). Compared with the forest ecosystem, the oil palm and sago ecosystems have higher air and soil temperatures. This might be due to the sparse canopies of the young oil palms and sago, which were planted only four to five years earlier, allowing direct sunlight to reach and warm the peat soil surface. The sago ecosystem has the best soil moisture status among the three ecosystems because systematic ditches were dug to maintain a high mean water-table of 23.6 cm particularly during the dry season. This was to meet the ideal growing conditions for the sago palms (Miyamoto *et al*., 2009). On the other hand, the water status of the oil palm was driest among the ecosystems (*Table 6*), again due to drainage to sustain its optimal growth and production. The bulk density of the peat soils under oil palm was increased intentionally by compacting with heavy machinery (Melling *et al*., 2005). This management practice improves the root system leading to better growth of oil palm. Altered environmental conditions of the cultivated sites have significant effects on the monthly variation in CO_2 fluxes within and between ecosystems (*Figure 1*).

Based on the tree regression, the monthly MR were found to be influenced by different environmental variables (*Figures 2* to *4*). This conforms to the findings for SR where Melling *et al*. (2005) found that the dominant environmental factors controlling total soil CO_2 to be relative humidity for forest, TCOF for sago and WFPS for oil palm. In the current study, the MR in the sago ecosystem was also mainly influenced by TCOF as for the SR. The mean MR doubled to 130 mg CO_2 C m^{-2} hr^{-1} when TCOF was higher than 31.9 ºC (*Figure 4*). It has been reported that the rate of MR is proportional to the decomposition of soil carbon. The elevation of environmental temperature increases the rate of carbon mineralisation and more carbon is being mineralised from the recalcitrant organic matter pool as predicted by many models (Lamade *et al*, 1996; Wang and Guo, 2006). Unlike MR, the RR rate is dependent on primary production and carbon partitioning in the plants and is usually independent of the changes in temperature (Wang and Guo, 2006). Furthermore, the fluctuation of RR can be attributed to changes in physiological activity such as growth respiration which is linked to the synthesis of new tissues and is unaffected by environmental changes such as temperature (Marshall *et al*., 1987; Tang *et al*., 2005).

TABLE 6. CORRELATION MATRIX OF PRINCIPAL COMPONENT ANALYSIS (PCA) FOR THE ENVIRONMENTAL FACTORS AND THEIR PCA SCORES ON THE ROOT RESPIRATION

Variable	PC 1	PC 2	PC 3
Water filled pore space	0.173	**-0.778**	0.446
Bulk density	-0.429	0.456	**0.727**
Air temperature	**-0.884**	-0.354	-0.197
Soil temperature at 5 cm	**-0.958**	-0.110	-0.027
Soil temperature at 10 cm	**-0.904**	0.158	0.151
Relative humidity	0.886	0.335	0.144
Water-table	0.287	**-0.841**	0.153
Proportion (%)	51.4	25.7	11.9
PCA scores			
Forest	2.17	0.59	-0.35
Oil palm	-1.38	0.94	0.47
Sago	-0.79	-1.53	-0.11

Note: The numbers in bold indicate definite assignation to a certain factor.

On the other hand, temperature is not only a direct factor which affects the soil MR, it also indirectly influences the change in temperature dependency of the microbial community in the soil (Fritze *et al*., 1993; Makiranta *et al*., 2009; Barcenas-Moreno *et al*., 2009). Two hypotheses which can explain the temporal pattern of respiration in the soil under field condition are: depletion of labile organic carbons based on theoretical models (Kirschbaum, 2004) and microbial adaptation to the increased temperatures (Luo *et al*., 2001). Thermal adaptation by the microorganisms includes physiological adjustment of individuals to species shifts and usually weakens the positive effect of warming on SR rates. In adapting to the change in temperature, there is an initial decline in the rate of MR per unit microbial biomass, but with time, the microbes are gradually able to perform better with every sustained increase in the temperature and *vice versa* (Bradford *et al*., 2008).

In the forest ecosystem, the microbial CO_2 flux was observed to be mainly affected by WFPS and temperature instead of relative humidity as found in the SR. This study has shown a substantial correlation between soil moisture and temperature on MR, which agrees well with the findings of Lamade *et al*. (1996) and Qiu *et al*. (2005) for an oil palm plantation on upland soils in Indonesia and Makiranta *et al*. (2009) for northern boreal peat lands. The effects of soil moisture on soil CO_2 production are usually inter-dependent with other factors at the site, such as spatial distribution of organic matter and the quantity of roots in the soil. Dry soils usually show lower emission of CO_2 than moist soils. Nevertheless, when the dry soil, which contains sufficient organic content is rehydrated, a substantially higher CO_2 is released. Killham (1994) mentions that the heterotrophic activity may also decrease in the drier soil due to the decline in the movement of microorganisms as the water film 'shrinks' around the soil particles. Hence, a certain level of moisture is required for microbial activities (Lamade *et al*., 1996; Ruser *et al*., 2006).

Moisture governs microbial activity by ensuring adequate supply for microbes since water is the major constituent of protoplasm. Therefore, sufficient but not excessive soil moisture is necessary to enhance the aerobic respiration in the water saturated peat through improved oxygen diffusion (Clymo, 1983; Adachi *et al*., 2006). Excessive moisture easily prevents microbial proliferation by limiting gaseous exchange and lowering oxygen supply thereby decreasing aerobic bacterial counts. This is supported by the present study which shows that very high water content in the forest ecosystem (WFPS > 54.1%) reduces microbial activity, hence MR dropped to 82 mg CO_2 C m^{-2} hr^{-1}. On the other hand, WFPS less than 54.1% resulted in the higher CO_2 flux of 182 mg CO_2 C m^{-2} hr^{-1} (*Figure 2*). Water content of more than 60% creates localised anaerobic condition that slows down the respiration rate and eventually the production of CO_2 (Ruser *et al*., 2006). Instead of releasing CO_2, methane may be produced from the anaerobic soil. Similar results were obtained for oil palm and sago ecosystems albeit at higher WFPS critical levels of 60% and 67%, respectively (*Figures 3* and *4*). This may be due to their higher environmental temperatures which increase soil water evaporation and cause the peat soils to dry up faster.

The depth of the water-table also has a dominant effect on MR rates in forest and sago ecosystems (*Figures 2* and *4*). In the forest, although lowering the water table below 52.6 cm increases the aerobic layer, a reduction of MR occurred from a mean of 93 mg CO_2 C m^{-2} hr^{-1} to 42 mg CO_2 C m^{-2} hr^{-1}. This might be attributed to the reduction in microbial diversity and population when the peat is over drained (Makiranta *et al*., 2009). Conversely, flooding and a high water table (below 15.7 cm) in the sago ecosystem had decreased MR from 65 mg CO_2 C m^{-2} hr^{-1} to 42 mg CO_2 C m^{-2} hr^{-1}. In this instance, a slight decrease in the water-table in the sago ecosystem during the dry season may have deepened the oxic surface peat zone (Clymo, 1983; Hirano *et al*., 2009). Thus, the substrate availability for CO_2-releasing decomposition processes in the peat profile increase and results in enhancement of CO_2 production from the root-free zone (Jauhiainen *et al*., 2005) and peat subsidence. Since the water-table has been purposely maintained at a high level in the sago plantation, the negative effect of over drainage on MR was not obtained in this study.

The main environmental factor identified to be controlling the MR in the oil palm ecosystem was bulk density (*Figure 4*). Drainage and compaction of the peat prior to oil palm cultivation has successfully improved the bulk density of the peat soil. The MR in the oil palm increased from 70 mg CO_2 C m^{-2} hr^{-1} to 132 mg CO_2 C m^{-2} hr^{-1} when bulk density was greater than 220 kg m^{-3}. Following the drainage and cultivation, peat subsidence occurred rapidly and continuously within four to 10 years and various physical changes happened to the peat. The physical changes observed included increased bulk density, and decreased total porosity, oxygen diffusion, air capacity, available water volume and water infiltration rate (Radjagukguk, 2000). This condition not only provides better anchorage of the roots, but also improves the water retention capacity by increasing the micropores which in turn, are required for enhanced root activities. Water and air saturated macropores and micropores in

the soil could assist in the diffusion of oxygen-rich air and water soluble organic substrate. Under such conditions, the microbial and RR would most probably increase (Davidson *et al*., 2000; Melling *et al*, 2005) as obtained in this study. The effect of bulk density was not significant in the other two ecosystems because it remained low since compaction was not practiced.

Contribution of Roots to Soil Respiration among the Three Ecosystems

The contribution of RR to SR in the oil palm and forest ecosystems were similar in the range of 60% to 62%. Sago plantation showed the lowest RR to SR ratio with 52%. These findings agree with most studies where RR from the forest and croplands ranged from 33%-89% based on their corresponding total CO_2 efflux (Hanson *et al*., 2000). The type of vegetation and its species have substantial effects on the root dynamics (Vogt *et al*., 1996). Evergreen forests possess higher below-ground carbon allocation than deciduous forests (Gower *et al*. 1995) and young perennial crops such as sago and oil palms (Henson and Chang, 2000), leading to higher emission of soil CO_2 from the forest ecosystem. Additionally, high relative humidity and moist soil conditions in the closed canopy of the forest probably encourage microbial diversity and for population to maintain high MR. Our studies show that the rates of MR for oil palm and sago ecosystems were similar, despite their very different environmental conditions upon cultivation. However, a higher RR by the oil palm ecosystem was observed compared to the sago ecosystem. The oil palm has one of the highest carbon assimilation rate among the C3 plants and thus, a greater respiration rate which explains its high RR to SR ratio. Another plausible reason is the application of urea fertilisers which was carried out in the oil palm ecosystem only. As a result, the nutrients, particularly nitrogen (*Table 2*) enrich the roots of oil palm and improve its growth and production, with a corresponding increase in RR (Henson and Chang, 2000). A linear relationship exists between N concentration and respiration for temperate plant tissues and roots of trees, as a way for adapting their metabolic activities to the low temperatures (Reich *et al*., 1996; Burton *et al*., 1996).

The sago ecosystem, despite having the highest average soil temperature, due to its partially open canopy of young sago palms, showed the lowest overall CO_2 flux for both SR and RR than the other ecosystems (*Table 3*). This is because the sago plantation usually was inundated and the roots were below the water-table. Furthermore, the high monthly WFPS at 75% in the sago ecosystem will significantly reduce the rate of RR. The highest CO_2 flux was observed to occur at WFPS between 45% and 57% in our earlier study (Melling *et al*., 2005). Additionally, the young sago palms had lower root biomass and plant density compared to the more matured biomass in the forest and oil palm ecosystems.

CONCLUSION

The root exclusion method enables the determination of soil CO_2 with (SR) and without (MR) roots components in tropical peatlands. The RR could then be estimated along with the temporal variation in the ratio of RR to total soil respiration. The contribution of root and MR in terms of CO_2 changed dramatically across the ecosystems throughout the year and fluctuated irrespective of any single environmental conditions. The leading environmental controlling factors were found to be soil moisture, soil temperature at 5 cm and bulk density which influenced the biochemical and microbial processes in respective ecosystems. However, different combination of factors was involved in the MR rates in each ecosystem. The highest MR and estimated RR were observed in the forest with 113 and 172 mg CO_2 C m^{-2} hr^{-1} respectively. This was followed by oil palm with MR 79 mg CO_2 C m^{-2} $h^{-1}$and RR 128 mg CO_2 C m^{-2} hr^{-1}. In the sago ecosystem, the lowest RR was recorded with only 95 mg CO_2 C m^{-2} hr^{-1}, whereas the MR was measured at 87 mg CO_2 C m^{-2} hr^{-1}, which was slightly higher than the sago ecosystem. The contribution of root respiration to the total SR in each ecosystem was also determined where % RR to SR for oil palm ecosystem was agreeable with most published work, about 62%. The estimated annual RR to SR was also about 60% in the forest and 52% in the sago plantation.

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