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Reduced soil respiration in gaps in logged lowland dipterocarp forests

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ABSTRACT

We studied the effects of forest composition and structure, and related biotic and abiotic factors on soil respiration rates in a tropical logged forest in Malaysian Borneo. Forest stands were classified into gap, pioneer, non-pioneer and mixed (pioneer, non-pioneer and unclassified trees) based on the species composition of trees >10 cm diameter breast height. Soil respiration rates did not differ significantly between non-gap sites (1290 ± 210 mg CO_2 m^{-2} h^{-1}) but were double those in gap sites (640 ± 130 mg CO_2 m^{-2} h^{-1}). Post hoc analyses found that an increase in soil temperature and a decrease in litterfall and fine root biomass explained 72% of the difference between gap and non-gap sites. The significant decrease of soil respiration rates in gaps, irrespective of day or night time, suggests that autotrophic respiration may be an important contributor to total soil respiration in logged forests. We conclude that biosphere-atmosphere carbon exchange models in tropical systems should incorporate gap frequency and that future research in tropical forest should emphasize the contribution of autotrophic respiration to total soil respiration.

1. Introduction

Forest ecosystems contain an estimated 638 Gt (60%) of the carbon stored in terrestrial ecosystems and could potentially absorb about 10% of global carbon emissions projected for the first half of this century (Streck et al., 2008). At the same time, 13 million hectares of tropical deforestation per year contribute to 20% of global carbon emissions (Canadell et al., 2008). The increasing importance of the remaining tropical forests for climate change mitigation is therefore a topic of broad interest (Chazdon, 2008; Putz et al., 2008). Intact forest cover of the Indo-Malaya region (including South Asia, South-East Asia and Papua New Guinea) was less than 40% of the original area by 2000 (Wright and Muller-Landau, 2006). At a regional scale, logged forests cover more than 85% of the remaining forest area in the state of Sabah (Malaysian Borneo) where the present study was undertaken (Sabah Forestry Department, unpubl. data). In the light of these current trends it is crucial to better understand biogeochemical cycling in tropical forest ecosystems and in particular in logged forest over the long-term (Sayer et al., 2007). Compared to a primary forest the altered vegetation composition and structure of a logged forest leads to changes in microclimatic conditions. For example logged forests are known to be more susceptible to fires than unlogged forests, mainly due to drying of the forest floor (Collins et al., 2004). Further, the absence of large trees and the resulting lower frequency and size of canopy gaps have been shown to disturb succession in regenerating forests of peninsular Malaysia (Numata et al., 2006). However, to date little is known about how changes in forest structure and composition influence biogeochemical cycles and in particular total CO_2 efflux at the soil surface, known as soil respiration (Ostertag et al., 2008).

Soil respiration is a substrate driven process consisting of four main sources of carbon compounds, namely carbon from litter, soil organic matter (SOM), roots, and root exudation processes (Berg and McClaugherty, 2003). Based on the source of the carbon, total soil respiration can be divided into heterotrophic respiration by microbes (mainly litter and SOM) plus autotrophic respiration by roots, mycorrhiza and the rhizosphere (Hansen et al., 2001). Differences among tree species in litter quality, quantity, timing of litter input and respiratory activities in roots have been shown recently (Bjornlund and Christensen, 2005; Hattenschwiler and Gasser, 2005; Scherer-Lorenzen et al., 2007). Studies from boreal systems show that litter decomposition and the turnover of soil organic matter (SOM) are affected by tree species composition and diversity, and that forest composition may alter soil respiration rates (Borken and Beese, 2005). Further factors that were shown to alter changes of heterotrophic and autotrophic respiration in forest ecosystems in either gaps or under closed canopy include soil

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temperature and soil water content (Davidson et al., 2000; Ritter et al., 2005), precipitation (Raich and Schlesinger, 1992), light interception (Zhang and Zak, 1995), root biomass (Soe and Buchmann, 2005) and nutrient availability (Cleveland and Townsend, 2006). Ohashi et al. (2008) showed that spatial variation in soil respiration may be higher than either seasonal or diurnal variation in tropical forests of South-East Asia. Based on these findings the principal objective of our work was to determine if changes in forest composition and structure could explain some of the spatial patterns of soil respiration in logged forests. We were interested in the following research questions:

Do soil respiration rates change depending on forest composition?
Do soil respiration rates differ in gap sites compared to non-gap sites?
Do soil respiration rates differ between day and night time?
Which abiotic and biotic factors explain the changes found?

2. Materials and methods

2.1. Site description

Our study area (N05°05′20″ E117°38′32″, 102 m.a.s.l.) was located in the eastern part of the province of Malaysian Sabah in northern Borneo. The region is aseasonal with an annual rainfall of ca. 3000 mm during the measurement period (2004–2008) (Saner, unpubl.data). Cumulative daily rainfall was measured at 07:00 am using a standard rain gauge (Novalynx, USA). The forest belongs to a one million hectare concession area of the Sabah Foundation and is classified as secondary lowland mixed dipterocarp production forest. It is situated 65 km north to the Danum Valley Field Centre, which forms part of the Danum Valley Conservation Area (Marsh and Greer, 1992). The study was set up within a large-scale forest rehabilitation project called the Sabah Biodiversity Experiment which covers an area of 500 hectares of logged forest in the Malua Forest Reserve. The experiment aims to study the importance of tree species diversity, composition and life history traits for providing fundamental ecoystem services, such as carbon sequestration (Scherer-Lorenzen et al., 2005). The vegetation composition of a logged forest depends on its previous successional stage in primary condition, damage caused by the logging operation and the time allowed for regeneration (Bischoff et al., 2005). In our case the forest was logged by conventional methods about thirty years ago (early 1980s), whereby only trees >45 cm diameter breast height (DBH) were harvested. Due to heavy disturbance of the understorey seedling bank the forest developed thereafter into a mixed stand of sites that were dominated by pioneer trees and other, less severely damaged sites that consisted of non-pioneer trees (Turner, 2001). Overall, the basal area for trees >10 cm was 25.0 ± 0.9 (SEM) m^2 ha^{-1} and tree density was estimated as 417 per hectare (Saner, unpubl. data). Litterfall (11.7 ± 0.3 t ha^{-1} $year^{-1}$) measured over one year was comparable to close-by primary forest (Burghouts et al., 1992) and at the upper end of reported estimates from old-growth Amazonian forests (5.2–12.5 t ha^{-1} $year^{-1}$) (Chave et al., 2009). The soil was classified as orthic acrisol, which is acidic (pH > 5), highly weathered with poor nutrient availability (81% base saturation) and a low organic carbon content (topsoil: 1.2%, 1 m depth: 0.6%) (Saner, unpubl. data). Bedrock consisted of a mixture of mudstone and sandstone areas with miscellaneous rocks (Forestry Department 2006, Sabah, unpubl. data).

2.2. Forest structure and composition

Seven transect lines (750 m × 10 m) were established 100 m apart from each other and each line was subdivided into 75, 10 × 10 m sites. Local taxonomic experts measured and identified all trees >10 cm DBH along the transect lines to species level. The sites were then classified into gap, pioneer, mixed and non-pioneer based on the tree species composition. Gap sites were defined as openings in the canopy layer (5–20% of visible sky) as a result of tree- or branchfall. Light interception, defined here as the percentage of canopy openness at each site was determined at the start of the experiment using a Spherical Densiometer Model A (Lemmon, USA). They were selected by visual examination, based on experience of estimating canopy openness using densiometers, hemispherical photographs and measurements of photosynthetic active radiation (PAR) in other studies in Danum Valley (Whitmore et al., 1993). Pioneer sites were defined as areas covered by highly light demanding species. We identified *Duabanga moluccana* Bl. (Sonneratiacea), *Macaranga* sp. Muell. Arg. (Euphorbiaceae), *Melicope luna-akenda* T.G. Hartley (Rutaceae), *Octomeles sumatrana* Miq. (Datiscaceae) and *Ludecia bornensis*, *Nauclea subdita* Steud., *Neolamarckia cadamba* Bosser, *Neonauclea* sp. Merr. (Rubiaceae) as pioneer trees. Non-pioneer sites were identified as those that had species which were slow growing with a high wood density, in particular from the families of the Dipteroarpaceae, Ebenaceae, Flacourtiaceae, Lauraceae, Meliaceae, Myristicaceae, Sabiaceae, Sapindaceae, Sapotaceae and Tiliaceae. Non-pioneer trees were expected to invest more photoassimilates into defense mechansims which would result in leaf litter that consisted of higher concentrations in secondary compounds, such as polyphenols, condensed tannins or terpenoids (Grime et al., 1996; Whitmore, 1998). These were shown to be relatively resistant to microbial decay and therefore may alter soil respiration rates (Ostertag et al., 2008), but see Kurokawa and Nakashizuka (2008). Mixed sites consisted of trees belonging to both pioneers and non-pioneers (as well as trees that could not be distinguished into either one of the two classifications; unknown) (see Appendix, Table A).

2.3. Experimental setup

Ten gaps were randomly chosen along the transect lines. Within 100 m of each gap site we selected a pioneer, a mixed and a non-pioneer site for direct comparison. The four sites (gap, pioneer, mixed and non-pioneer) were therefore replicated ten times each, resulting in forty measured sites which represented the forest classifications. We excluded riverbeds and skid trails due to possible effects of soil compaction on soil respiration rates. One single PVC collar (7 cm × 21 cm diameter) was inserted 2 cm into the soil at each of the forty selected sites two weeks prior to the start of the experiment.

2.4. Measuring soil respiration

The soil respiration chamber was self-made following Pumpanen et al. (2004). It consisted of an airtight, non-through-flow PVC cylinder (30 cm × 21 cm diameter) with a small ventilator connected to a 12 V battery (Uusima, 2003). Soil respiration measurements were taken at all collars between May and June 2007 using an Infrared Gas Analyzer CARBOCAP GMP343 (Vaisala, Finland). During chamber placement we opened a blow-off valve to control for overpressure inside the chamber. Day time measurements were taken once per collar on seven days ($n = 280$) between 08:00 am and noon. For logistic reasons we were unable to record the diurnal changes reported in previous studies (Ohashi et al., 2008). Night time measurements were taken once per collar on two days ($n = 80$) between 08:00 pm and 04:00 am. Soil respiration measurements were taken over 5 min per collar, whereby the first 2 min were disregarded to avoid disturbance effects caused by chamber placement. Soil respiration rates were calculated from the rate of CO_2 efflux inside the chamber over the remaining 3 min interval. Even though we measured over a relatively short time span, treatment effects between gap and non-gap sites were clear and it is relative changes in percentages that are the focus of our study.

2.5. Measuring covariables

All soil and air measurements were done in combination with the soil respiration measurements. Soil temperature and soil moisture were measured at 5 cm depth with a WET Sensor (Delta-T, UK). Air relative humidity (%) and air temperature (°C) were measured with a HMP75 probe (Vaisala, Finland). At all forty selected sites we established 1 m^2 quadrats to collect standing litter and root biomass at the start of the experiment to avoid effects of site disturbance. Soil cores (100 cm^3) were taken vertically from the top mineral soil layer (0–5 cm) of each quadrat using standard soil corers (Eijkelkamp, Netherlands). Root biomass was extracted by washing the soil cores over a 210 μm sieve (Retsch, Germany). Litterfall traps (1 m^2) were established next to the selected quadrats at 1.3 m height, using fine (1 mm × 1 mm) meshed plastic net. Litter was collected twice during the measurement period. All collected root biomass and litter samples were dried (60 °C for 48 h) to constant weight before weighing. Litter was further separated into leaves, twigs (typically <1 cm in diameter) and reproductive organs (flowers and fruits). One litterfall measurement was discarded from the analysis because of a freshly fallen climber fruit that biased the litterfall rate of a non-pioneer site (>7 g day^{-1}).

2.6. Data analysis

We analyzed differences in continuous response variables with a mixed-effects ANOVA using restricted maximum likelihood with the lmer function from the lme4 library (Bates et al., 2008) for R 2.6.2 (R Development Core Team, 2008). The model was fitted to the data using an identity link function and specifying that the variance should increase as the square of the mean (Gamma error distribution). The lmer function currently does not provide *p* values for the approximate *F*-tests for fixed effects. Instead we performed pre-planned contrasts of the three non-gap sites (forest composition: pioneer, mixed, non-pioneer) relative to the gap sites using *t*-tests. We present point estimates of the means with their standard errors (SEM) from the fitted model. We included time when analyzing the importance of forest composition and structure on soil respiration rates. Spatial and temporal replicates were included as random terms into the model. Forest classification (gap, pioneer, mixed and non-pioneer) and measurement time (day, night) were included as fixed effects.

For subsequent analysis of the importance of measured covariables the dataset had to be collapsed as values of all covariates were not taken at all time points. Therefore, we used a linear analysis of covariance (ANCOVA). Rather than averaging the day and night measurements that had unequal replication, the two night time measurements were omitted and we used day respiration rates only for further analysis. Covariables were chosen based on their importance from literature and if not highly correlated with one another. Selected covariables were then fitted individually into the model to test for their potential effect on day soil respiration rates. Data were checked for normal distribution and heterogeneity of residuals. We also examined a small number of multiple regressions using variables selected a priori for testing.

3. Results

3.1. The importance of forest composition and structure

Soil respiration rates were highly variable over time and space (78% of the summed variance components from the mixed-effects model). However, there was no particular positive or negative trend over time. Soil respiration rates in gap sites (640 ± 130 mg CO_2 m^{-2} h^{-1}; $n = 10$) were significantly lower than in pioneer sites (1260 ± 190; $t = 4.6$, $p < 0.001$), mixed sites (1260 ± 200; $t = 4.5$, $p < 0.001$) and non-pioneer sites (1360 ± 210; $t = 5.0$, $p < 0.001$), suggesting that forest structure is an important factor determining spatial changes in soil respiration. The average of all non-gap sites (1290 ± 210 mg CO_2 m^{-2} h^{-1}) was approximately double gap sites. Differences between non-gap sites (pioneer, mixed and non-pioneer) were not significant, indicating that forest composition only had a minor influence on spatial patterns of soil respiration rates (Table 1).

3.2. Comparing day and night soil respiration rates

The effect of forest structure and composition on soil respiration rates was irrespective of the measurement period (day/night) (test of interaction: $t = 0.3$, $p = 0.36$). On average, measurements at night were 20% lower than at day time ($t = 2.2$, $p = 0.04$) (Fig. 1). Relative changes between day and night measurements were highest in gap sites (25%) and were lower for pioneer, mixed and non-pioneer sites (20%, 18% and 15%, respectively). Interestingly, environmental covariables did not show daily fluctuations, except for a slight increase in relative air humidity during the night (Table 1).

3.3. The importance of selected abiotic and biotic factors

For subsequent post hoc analysis all non-gap sites (pioneer, mixed and non-pioneer) were pooled to consider the gap versus non-gap site contrast only. Covariables such as litterfall and root biomass were measured only twice or once, respectively during the

Table 1

Mean (±SEM; calculated for each group individually) for all measured variables at gap and non-gap sites (pioneer, mixed, non-pioneer). Measurements that were taken together with soil respiration rates are reported separately for day ($n = 7$) and night ($n = 2$) time measures.

	Gap		Pioneer		Mix		Non-pioneer	
	Day	Night	Day	Night	Day	Night	Day	Night
Soil respiration [mg CO_2 m^{-2} h^{-1}]	733 ± 163	553 ± 133	1399 ± 216	1118 ± 256	1380 ± 223	1134 ± 159	1472 ± 187	1257 ± 193
Soil temperature [°C]	25.9 ± 0.3	26.2 ± 0.1	25.5 ± 0.2	25.9 ± 0.1	25.2 ± 0.1	25.6 ± 0.1	25.4 ± 0.1	25.7 ± 0.1
Air temperature [°C]	26.4 ± 0.3	26.5 ± 0.1	26 ± 0.2	26.1 ± 0.2	25.8 ± 0.1	26 ± 0.1	25.9 ± 0.1	25.7 ± 0.1
Soil water content [%]	37.5 ± 2.1	35.5 ± 2.4	35.3 ± 2.2	34 ± 2.7	30.4 ± 2.3	29.9 ± 2.5	29.9 ± 2.2	28.8 ± 2.2
Relative humidity [%]	91 ± 0.3	93.9 ± 0.3	90 ± 0.6	93 ± 0.5	90.2 ± 0.6	93.5 ± 0.3	90.4 ± 0.8	94 ± 0.3
Light interception [%]	12.2 ± 1.6		3.6 ± 1.1		3.1 ± 1.1		3.2 ± 0.8	
Standing litter [g m^{-2}]	153 ± 27		135 ± 14		178 ± 30		168 ± 20	
Root biomass (>5 cm) [g m^{-2}]	120 ± 13		156 ± 35		251 ± 56		218 ± 26	
Litterfall [g m^{-2} day^{-1}]	1.8 ± 0.3		2.4 ± 0.3		2.7 ± 0.4		2.0 ± 0.2	
Basal area [m^2 ha^{-1}]	9.5 ± 3.2		24.4 ± 3.0		31.5 ± 5.8		24.4 ± 3.4	

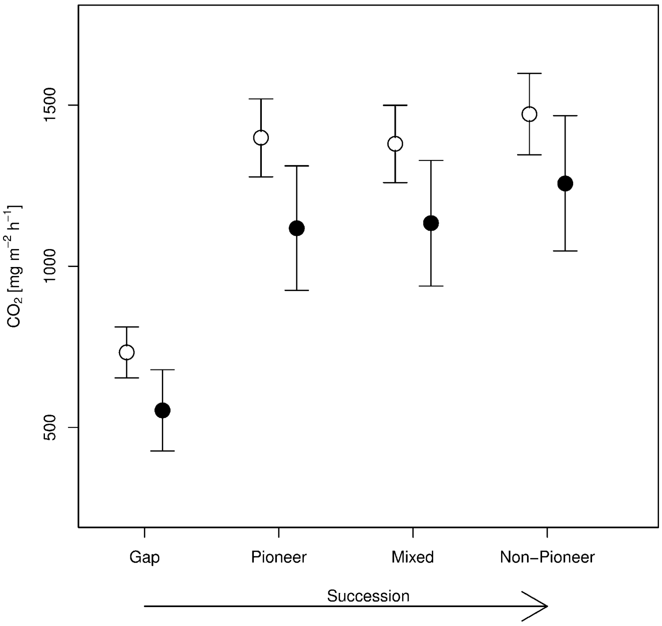

Fig. 1. Soil respiration rates (CO_2 [mg m^{-2} h^{-1}] (mean ± SEM)) along the successional gradient, ranging from gap sites to pioneer, mixed and non-pioneer sites. White circles indicate day soil respiration rates and black circles indicate night soil respiration rates.

period of soil respiration measurements. Therefore arithmetic means over time for all other covariables were used for the subsequent analysis of covariance (ANCOVA) too. The dataset was unbalanced and the sequential ANOVA order-dependent, therefore selected covariables were fitted both first and last in the model to bracket their effect on total variation (%) and how much they reduced the effect of the gap versus non-gap site contrast. Except for standing litter all covariables differed significantly between gap and non-gap sites: soil temperature ($t = 2.4$, $p < 0.05$), soil water content ($t = 2.2$, $p < 0.05$), litterfall ($t = 2.7$, $p < 0.05$), fine root biomass ($t = 2.1$, $p = < 0.05$), basal area ($t = 3.7$, $p < 0.001$), standing litter ($t = 0.3$, $p = 0.79$). To reduce collinearity only covariables that were not highly correlated with each other ($r < 0.27$) were considered for analysis (Table 2a). Overall, an increase in soil temperature and a decrease in litterfall and root biomass explained 72% of the difference between gap and non-gap sites (Fig. 2). Soil temperature was the single most important covariable, explaining 14–16% (fitted first and last into the model) of the total variation and reducing the effect of the gap versus non-gap sites contrast by 54% (test of soil temperature fitted in first place; $F_{1,25} = 10.0$, $p < 0.01$). Litterfall explained 7–9% of the total variation and reduced the contrast effect by 44% ($F_{1,25} = 7.2$, $p < 0.05$). Contrary to our expectations, fine root biomass explained <1% of the total variation (Table 2a). Neither soil water content nor standing litter did have a substantial influence on the total variation. Further, substituting litterfall and fine root biomass by tree basal area did not result in a better explanation of the gap versus non-gap sites contrast (Table 2b).

Table 2
Fitting the terms first and last in the ANCOVA model. *F*-value, percentage of total sum of squares and *t*-values are shown. Replication: block that consists of all four sites ($n = 10$); gap, pioneer, mixed, non-pioneer ($n = 40$). Sites: gap versus non-gap sites contrast: (a) final model and (b) fitting basal area instead of litterfall and fine root biomass.

	Fitted in first place		Fitted in last place		
	F	% SS	*F*	% SS	*t*
(a)					
Replication	2.0	28.0	–	–	–
Soil temperature	10.0	15.9	9.0	14.3	1.8
Litterfall	7.2	11.5	5.7	9.1	0.9
Fine root biomass	<0.1	<1	0.4	<1	1.4
Contrast	–	–	3.9	6.2	2.0
(b)					
Replication	1.9	26.9	–	–	–
Soil temperature	10.3	16.1	9.1	14.2	1.8
Basal area	1.3	2.0	0.1	<1	1.6
Sites	–	–	9.5	14.8	3.1

4. Discussion

Our results showed that forest composition did not affect soil respiration rates: all non-gap sites (pioneer, mixed and non-pioneer) showed similar soil respiration rates, regardless of the vegetation type. In contrast, gap sites had significantly lower soil respiration rates. This result is in accordance with findings from secondary forests of peninsular Malaysia (Adachi et al., 2006) where they found a lower gap site C efflux (mean ± SEM; 576 ± 93 mg CO_2 m^{-2} h^{-1}) compared to the sub-canopy sites (838 ± 36) (our test based on reported SEM and sample size: $t = 2.62$, $p = 0.02$). Adachi et al. (2006) explained spatial variation in soil respiration in tropical primary and secondary forests of peninsular Malaysia with higher soil moisture and a lower fine root biomass in gaps compared to the sub-canopy. In gap sites we measured higher soil temperature, soil water content and light interception (Poulson and Platt, 1996; Scharenbroch and Bockheim, 2007) but lower fine litterfall rate (Bauhus and Bartsch, 1995), fine root biomass (Cuevas and Medina, 1988; Denslow et al., 1998) and basal area compared to non-gap sites (Table 1). These findings suggest that higher light interception led to a temperature increase on the soil surface, however the difference is relatively small across sites (<1 °C change between gap and non-gap sites for day time measurements). In addition, fewer trees in gap sites caused a higher soil water content due to lower water absorption (although soil in gap sites is not necessarily wetter than in understorey areas (Poorter, 2005) and simulation studies indicate a complex interaction between soil drying, gap size, litter level and the presence or absence of roots from surrounding vegetation (Marthews et al., 2008)). Measured covariables explained approximately two third of the difference between gap and non-gap sites. Other factors such as nitrogen concentration or soil organic matter (SOM), might have explained further variation, although these were found to be important shortly after gap formation rather than in established gaps (Denslow et al., 1998). In addition, studies on artificial gaps in Maracá Island, Brazil found that neither soil microbial biomass, soil respiration, nor nitrogen mineralization were enhanced in the forest compared to open areas (Luizao et al., 1998).

Studies from subtropical China found that gap size was a proximate factor of substrate-induced respiration, with the ultimate factor being soil moisture (Zhang and Zak, 1995). They measured gaps between five to forty meters in diameter, where small natural disturbances (gap size of 15 m in diameter) did not affect overall nutrient cycling rates, whereas large-scale disturbances inhibited nutrient release. They reported a decrease in litter decay from 57% to 44 % from closed forest to gap sites that correlated with a decrease in soil moisture from 19.2% to 11.4% in the large gaps. Based on these findings they suggested that abiotic conditions such as soil temperature and soil water content correlated positively with soil respiration if gaps and sub-canopy sites were compared. In contrast to such previous findings we could determine soil temperature, but not soil water content to be relevant for differences in soil respiration rates between gap and non-gap sites. However, small absolute differences in soil temperature suggest that biotic factors (e.g. litterfall and root biomass) may be relevant to explain observed changes in soil

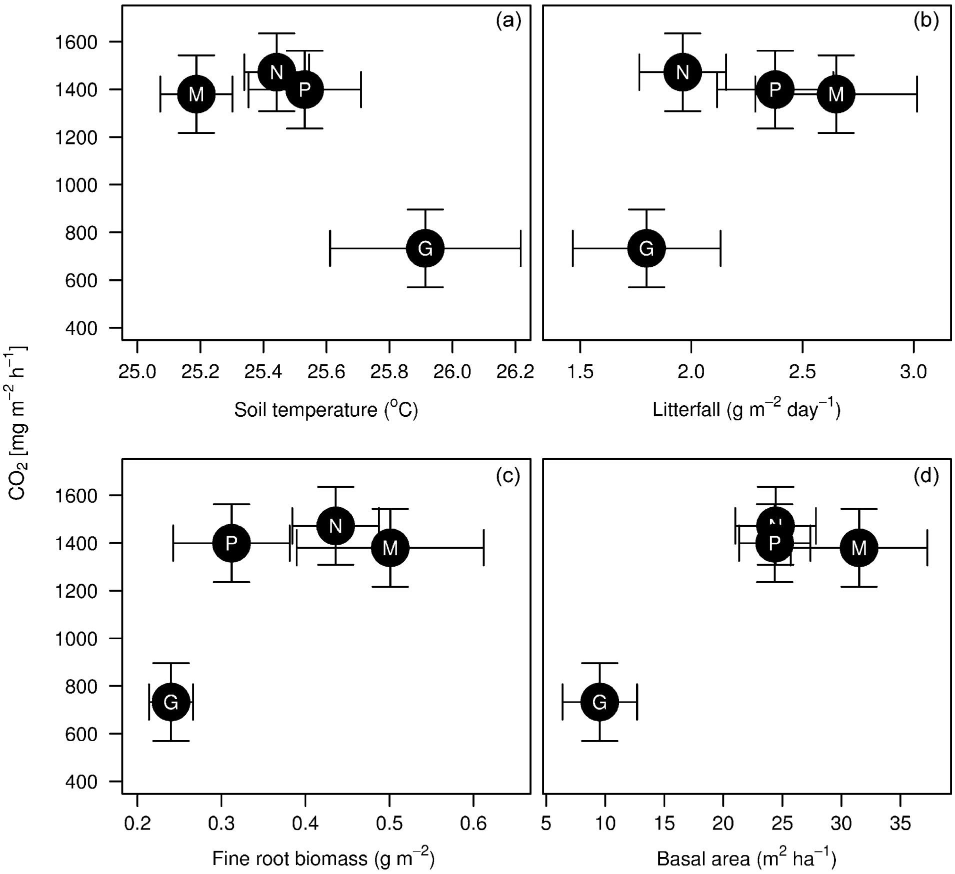

Fig. 2. Effects of the selected explanatory variables on day time measurements of soil respiration rates (CO_2 [mg m^{-2} h^{-1}] (mean ± SEM)): (a) soil temperature, (b) litterfall, (c) root biomass, (d) basal area. G: gap, P: pioneer, M: mixed, N: non-pioneer sites.

respiration rates between gap and non-gap sites. The lack of big trees in the gap sites resulted in a lower litterfall rate and lower fine root biomass (although decreased levels of fine root biomass could not explain altered soil respiration rates). A recent study by Katayama et al. (2009) reported the first evidence that soil respiration rates were positively related to mean diameter at breast height of trees within 6 m of the measurement point. Even though we could not find evidence for a relation between tree basal area and soil respiration rates, our results indirectly support their findings that tree presence increases soil respiration. Whether gap specific processes or the mere presence of large trees are more relevant for spatial variation in tropical forests would be interesting to test in the future.

Total soil respiration in gaps compared to non-gap sites is likely to depend on different relative shares of autotrophic and heterotrophic respiration. We found a significant decrease in soil respiration rates from day to night measures in both, gap and non-gap sites. Higher concentrations of photosynthetic assimilates in the roots and a resulting increase in autotrophic respiration during the day may partly explain the difference found. However, this assumption can be challenged since environmental variables such as light irradiance, air temperature, soil water content and air humidity are likely to change during the course of the day. In particular in gaps this may alter the contribution of heterotrophic respiration to total soil respiration rates. In our study, daily soil respiration fluctuations were decoupled from changes in environmental covariables and in particular from soil temperature (Table 1), similar to the findings of studies from Yucatan Peninsula in Mexico (Vargas and Allen, 2008) but in contrast to findings from the Amazonas, Brazil (Sotta et al., 2004). Such decoupled effects suggest that day and night time soil respiration should be measured separately when quantifying total ecosystem respiration (Katayama et al., 2009). Further, the day to night time difference in soil respiration rates between gap and non-gap sites could be simply due to the physical presence of a canopy, enhancing carbon storage during the night (Iwata et al., 2005). Studies of gap dynamics have focused on changes in heterotrophic respiration. However the contribution of autotrophic respiration, in particular mycorrhizal respiration, could be an important reason for the decrease of total soil respiration rates in forest gaps. Studies from temperate beech forest gaps showed that CO_2 fluxes were 40% lower compared to a mature stand which were explained based on differences in root respiration (Brumme, 1995). Girdling experiments or isotopic approaches (Hanson et al., 2000) would be necessary to draw further conclusions about the relative shares of the different components on total soil respiration rates in tropical lowland dipterocarp forests.

5. Conclusion

Forest structure, in particular the frequency of gaps, is relevant when quantifying soil respiration in logged forest. In addition, relative differences in soil respiration rates between day and night time may be important to consider when quantifying total ecosystem respiration. These findings are of particular interest for implementing biosphere-atmosphere carbon exchange models in tropical systems. We emphasize that future research in tropical forest should focus on the contribution of autotrophic respiration to total soil respiration.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.07.048.

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