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 Pioneer, Non-Pioneer and a Mixture (Pioneer, Non-pioneer and Unclassified trees) thereof based on the species composition of trees >10 cm diameter breast height. Soil respiration rates did not differ significantly between the three forest classes (1293 ± 210 mg CO_2 m^{-2} h^{-1}) but were double those in gap sites (643 ± 126 mg CO_2 m^{-2} h^{-1}). Overall, an increase in abiotic factors (soil temperature and soil water content) and a decrease in biotic factors (litterfall and root biomass) explained 58% of the difference between gaps and forested sites, whereby soil temperature was the single most important factor. 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.

Introduction

Forest ecosystems contain an estimated 638 gigatonnes (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 13 million hectares of tropical deforestation per year contribute to 20% of global carbon emissions (Canadell 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, Southeast Asia, and Papua New Guinea) was less than 40 percent of the original area by 2000 (Wright and Muller-Landau, 2006). At a regional scale logged forests cover more than 85 percent of the remaining forest area in the province 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 logged forest ecosystems in the long term. Compared to a primary forest the altered vegetation composition and structure of a logged forest may lead 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 (IUCN, (Collins *et al.* 1991; Conservation Atlas of Tropical Forests: Asia and the Pacific)). 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 composition and structure 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 and in timing of litter inputs, but also in changed quantity of litter inputs 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 (e.g. Borken and Beese, 2005). Further factors that were shown to alter changes of heterotrophic and autotrophic respiration in forest ecosystems include soil temperature and soil water content (Davidson *et al.*, 2000; Marthews *et al.*, 2008), precipitation (Raich and Schlesinger, 1992), light interception (Zhang and Zak, 1995), root biomass (Soe and Buchmann, 2005) and nutrient availability (Cleveland and Townsend, 2006). 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 CO_2 efflux 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 forested sites compared to gap sites?

Do soil respiration rates differ between day- and night time?

Which abiotic and biotic factors explain the changes found?

Materials and Methods

Site description

Our study area (N05º05'20'' E117º38'32'', 102 m.a.s.l.) is located in the Malua Forest Reserve in the eastern part of the province of Malaysian Sabah in northern Borneo. 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 forest belongs to the the larger concession area of the Sabah Foundation and is classified as secondary lowland mixed dipterocarp production forest. The forest is aseasonal with an annual rainfall of ca. 3000 mm during the measurement period (2004-2008) (Saner, unpubl.data). The soil in this area is classified as orthic acrisol, which is acid (pH>5), highly weathered and with poor nutrient availability (0.36 % organic carbon, 81.26 % base saturation) (Saner, unpubl. data). Bedrock consists of a mixture of mudstone and sandstone areas with miscellaneous rocks (Forestry Department Sabah 2006, unpubl. data). The vegetation composition of a logged forest depends on its previous successional stage in primary condition, damage caused by logging operation and the time allowed for regeneration (Bischoff *et al.*, 2005). In our case the forest was logged by conventional methods about 30 years ago (early 1980s), whereby only trees > 45 cm diameter breast height (DBH) were harvested. Due to the heavy disturbance of the understorey seedling bank the forest developed thereafter into a mixed stand of areas that were dominated by Pioneer trees and other, less severely damaged sites which consisted mainly of Non-Pioneer trees (Turner 2001). Within one part of the experimental area seven transect lines were established 100 m apart from each other. Each of the 750 x 10 m transect lines was subdivided into seventy-five 10 x 10 m sites. Local taxonomic experts measured and identified all trees > 10 cm DBH to species level. The sites were then classified into Gap, Pioneer, Mix and Non-Pioneer based on the tree species composition. Gap sites were defined as an opening in the canopy layer (5 to 20 % of visible sky) as a result of tree- or branchfall. 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 have species which are 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 consists of higher concentrations in secondary compounds, such as polyphenols, condensed tannins or terpenoids (Grime *et al.*, 1996; Whitmore, 1998). These have been 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 stands consisted of a mixture of trees belonging to the functional groups of Pioneers and Non-Pioneers, as well as trees that could not be distinguished into either one of the two classifications (Unknown) (see Appendix, table S1).

Ten sites with 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 forest classifications (Gap, Pioneer, Mix and Non-Pioneer) are therefore replicated ten times each, resulting in fourty measured sites.

Measuring soil respiration

One single PVC pipe (7 cm deep x 21 cm diameter) was inserted two centimeters into the soil at each of the fourty selected sites two weeks prior to start of the experiment. We excluded riverbeds and skid trails due to possible effects of soil compaction on soil respiration rates. The soil respiration box with diffusion-aspirated CO_2 measurement consisted of an airtight, non-through-flow PVC cylinder (30 cm deep x 21 cm diameter) that was put over the previously inserted PVC pipe. During chamber placement we opened a blow-off valve to control for overpressure inside the chamber. Air circulation within the chamber was provided by a small battery-run fan (Uusima, 2003). CO_2 measurements were taken at all sites between May to June 2007 using an Infrared Gas Analyzer CARBOCAP GMP343 (Vaisala, Finland). Day time measurements were taken once per site on seven days (n=280) between 08:00 am and noon. Night time measurements were taken once per site on two days (n=80) between 08:00 pm and 04:00 am. CO_2 measurements were taken over five minutes per site, whereby the first two minutes were disregarded to avoid disturbance effects caused by chamber placement. Soil respiration rates were calculated from the rate of CO_2 rise inside the chamber over the remaining three minute interval. Our measurement method may have influenced the result because of the small ventilator installed inside the chamber to provide sufficient turbulence to measure increases in CO_2 at the chamber headspace. This constant airflow disturbed the saturated CO_2 layer at the soil surface and prevented saturation of CO_2 concentration during the measurement period (Pumpanen *et al.*, 2004). However, even though our measurements may have overestimated absolute soil respiration rates, treatment effects between gaps and forested sites are informative, therefore relative changes in percentages are the focus of our study.

Measuring covariables

Light interception, defined here as the percentage of canopy openness at each site was determined using a Spherical Densiometer Model A (Lemmon, USA). Air relative humidity (%) and air temperature (ºC) were measured with a HMP75 probe (Vaisala, Finland). Soil moisture (%), pore water electroconductivity (ECp mS cm^{-1}) and soil temperature (ºC) were measured with a WET Sensor (Delta-T, UK). All soil measurements were taken at a depth of 5 cm, together with the soil respiration measurements. Cummulative daily rainfall was measured at 07:00 am using a standard rain gauge (Novalynx, USA). At all fourty selected sites we established $1m^2$ 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). Fine roots were extracted by washing the soil cores over a 210 µm sieve (Retsch, Germany). Litterfall traps ($1m^2$) were established next to the selected quadrats at 1.3 m height, using fine meshed plastic net. Litter was collected twice after two weeks during the measurement period. All collected root and litter samples were dried (60ºC for 48h) to constant weight before weighing with an electronic balance (precision 0.1g). Litter was further separated into leaves, twigs (typically < 1cm 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}).

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. The lmer function currently does not provide F-tests for fixed effects. Instead we performed pre-planned contrasts of the 3 forest sites (Pioneer, Mix, Non-Pioneer) relative to the Gap sites. We present point estimates of the means with their standard errors (SEM). 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, Mix 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 known from literature and only tested if not highly correlated. Selected covariables were then fitted individually into the model to test for their overall effect on day soil respiration rates. Data were checked for normal distribution and heterogeneity of residuals. F-tests were reported for this second analysis of a standard least squares linear model. We also examined a small number of multiple regressions using variables selected a priori for testing.

Results

The importance of forest composition and structure

Soil respiration rates were highly variable over time (73% of the summed variance components from the mixed-effects model) but less so in space (5%). However, there was no particular positive or negative trend over time. Soil respiration rates in Gap sites (mean ± SEM; 643 ± 126 mg CO_2 m^{-2} h^{-1}) were significantly lower than in Pioneer sites (1259 ± 193; t=4.6, p<0.001), Mixed sites (1257 ± 195; t=4.5, p<0.001) and Non-Pioneer sites (1364 ± 210; t=5.0, p<0.001). Differences in soil respiration rates between the forest stands were not significant. The average of all forested sites (1293 ± 210 mg CO_2 m^{-2} h^{-1}) was approximately double gap sites (643 ± 126 mg CO_2 m^{-2} h^{-1}) (Tab.1).

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 time were 20% (216 ± 99 mg CO_2 m^{-2} h^{-1}) lower than at daytime (t=2.2, p=0.04) (fig.1). Gap sites showed the smallest absolute decrease (180 mg CO_2 m^{-2} h^{-1}), but their relative change was highest (25%). Pioneer, Mix and Non-Pioneer sites had a decrease of (281, 246 and 215 mg CO_2 m^{-2} h^{-1}) with relative changes of 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 (tab.1).

The importance of selected abiotic and biotic factors

For subsequent analysis all forested sites (Pioneer, Mix and Non-Pioneer) were pooled to consider the gap versus forested site contrast only. Main covariables such as litterfall and root biomass were measured only twice or once, respectively during the 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 reduce the effect of the gap versus forested site contrast. To reduce collinearity only covariables that were not highly correlated with each other ($R<0.26$) were considered (with one exception: root biomass and soil water content were negatively correlated ($R=0.48$), but we decided to include both based on a priori assessment of the covariables likely to be most important).

Overall, an increase in soil temperature and soil water content and a decrease in litterfall and root biomass explained 58% of the difference between gaps and forested sites (fig.2). Soil temperature was the single most important covariable, explaining 10-11% (fitted first and last into the model) of the total variation and reducing the effect of the gap versus forested site contrast by 46% ($F_{1,24}=5.5$, $p<0.05$). Litterfall explained 3-7% of the total variation and reduced the contrast effect by 31%, but its effect on soil respiration was only marginally significant ($F_{1,24}=3.4$, $p=0.07$). Soil water content explained 2-3% of the total variation and reduced the contrast effect by 11% ($F_{1,24}=1.4$, $p=0.25$). Contrary to our expectations, root biomass (<1-2%) and standing litter (<1%) did not have a substantial influence on the total variation (tab.2A). Further, substituting litterfall and root biomass by basal area did not result in a better explanation of the gap versus forested site contrast (tab.2B).

Discussion

Our results showed that forest stand composition did not affect soil respiration rates differently. All sites (Pioneer, Mix and Non-Pioneer) showed similar 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 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) (Adachi *et al.*, 2006); 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 a higher soil water content and a lower fine root biomass in gaps compared to the sub-canopy. In gaps 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 forested sites (tab.1). 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 fourty 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 correlates 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. Scharenbroch and Bockheim (2008) found higher soil respiration rates in gap sites compared to gap edges and closed forest in old growth northern hardwood-hemlock forests in USA. They suggested that a higher gap soil respiration reflects more available decomposable substrate, in combination with increased solar radiation, soil moisture and soil temperature. This finding may hold true for tropical regions too, where an initial decomposition pulse after high organic matter decomposition was reported after hurrican events (Ostertag *et al.*, 2003). However, 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). Measured covariables of the present study explained the differences between gaps

and forested sites only to a minor extent, suggesting that other factors such as nitrogen concentration or soil organic matter (SOM) could have been important to consider. However these were found to be important shortly after gap formation rather than in established gaps (Denslow *et al.* 1998).

Total soil respiration in gaps is likely to depend on different relative shares of autotrophic and heterotrophic respiration compared to forested sites. We aimed at testing this by comparing day- to night time measures of soil respiration rates. We found a significant decrease in soil respiration rates from day to night measures in both, gaps and forested 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, similar to the findings of Vargas and Allen (2008) but in contrast to Sotta *et al.* (2004) (tab.1). Studies on gap dynamics discussed changes in heterotrophic respiration, however the contribution of autotrophic respiration and in particular mycorrhizal respiration could be an important explanatory for the decrease of total soil respiration rates in forest gaps. Brumme (1995) found that in temperate beech forest gaps CO_2 fluxes were 40% lower compared to a mature stand which they explained based on differences in root respiration. 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.

Conclusion

We conclude that forest structure, and in particular the frequency of gaps are relevant when quantifying soil respiration in a degraded secondary forest. Therefore we suggest that biosphere-atmosphere carbon exchange models in tropical systems should incorporate gap frequency.

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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	[ºC]	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	[ºC]	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 (> 5cm)	[g m^{-2}]	120 ± 13		156 ± 35		251 ± 56		218 ± 26	
Litterfall	[g m^{-2} d^{-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	

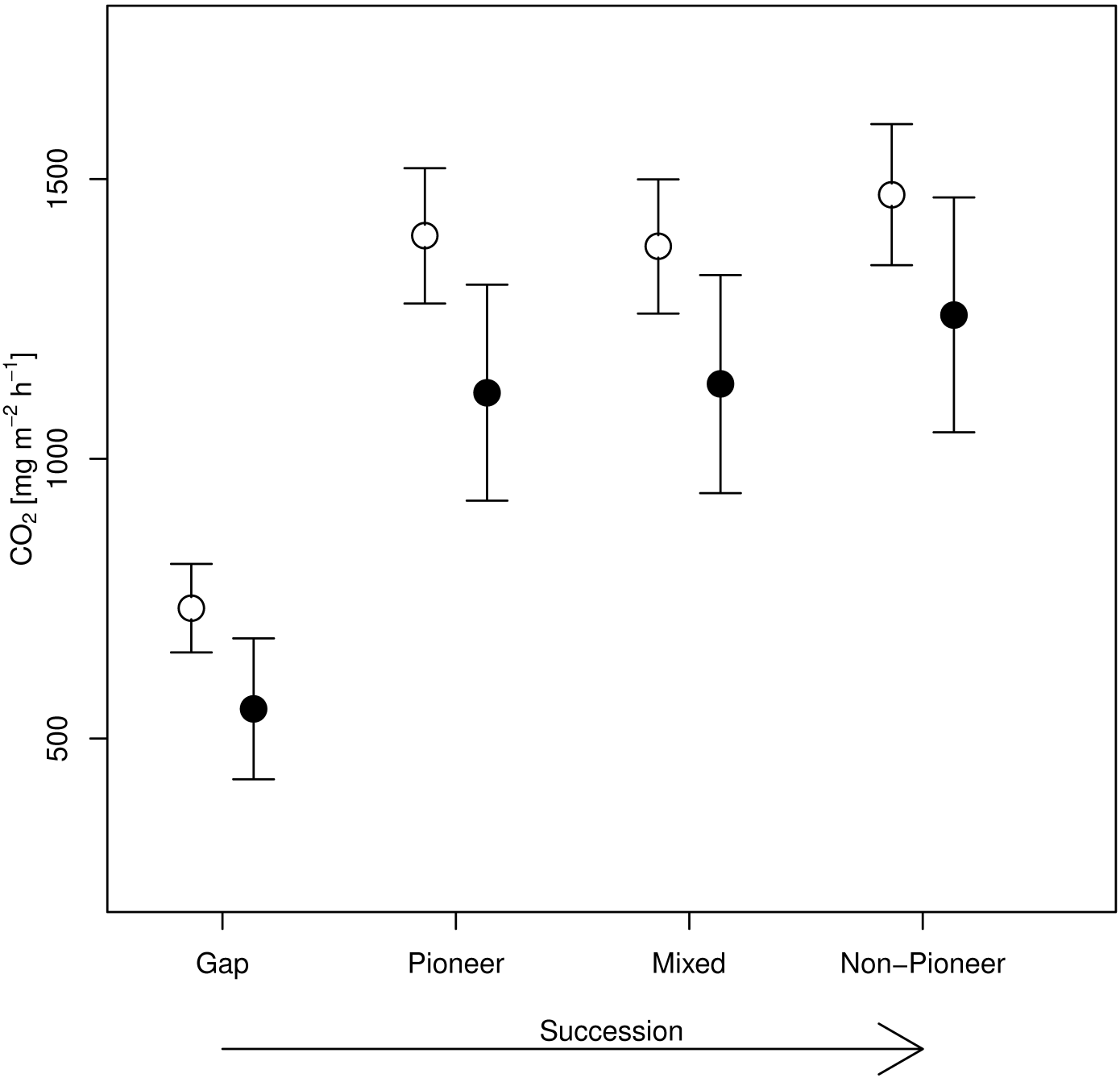
Table 2 Fitting the terms first and last in the ANCOVA model. F-value, percentage of total sum of squares and t-values are shown. Replication: block that consists of all four sites (n=10); Gap, Pioneer, Mixed, Non-Pioneer (n=40). Sites: Gap versus non-gap sites contrast. (a): Final model, (b): Fitting Basal Area instead of litterfall and fine root biomass.

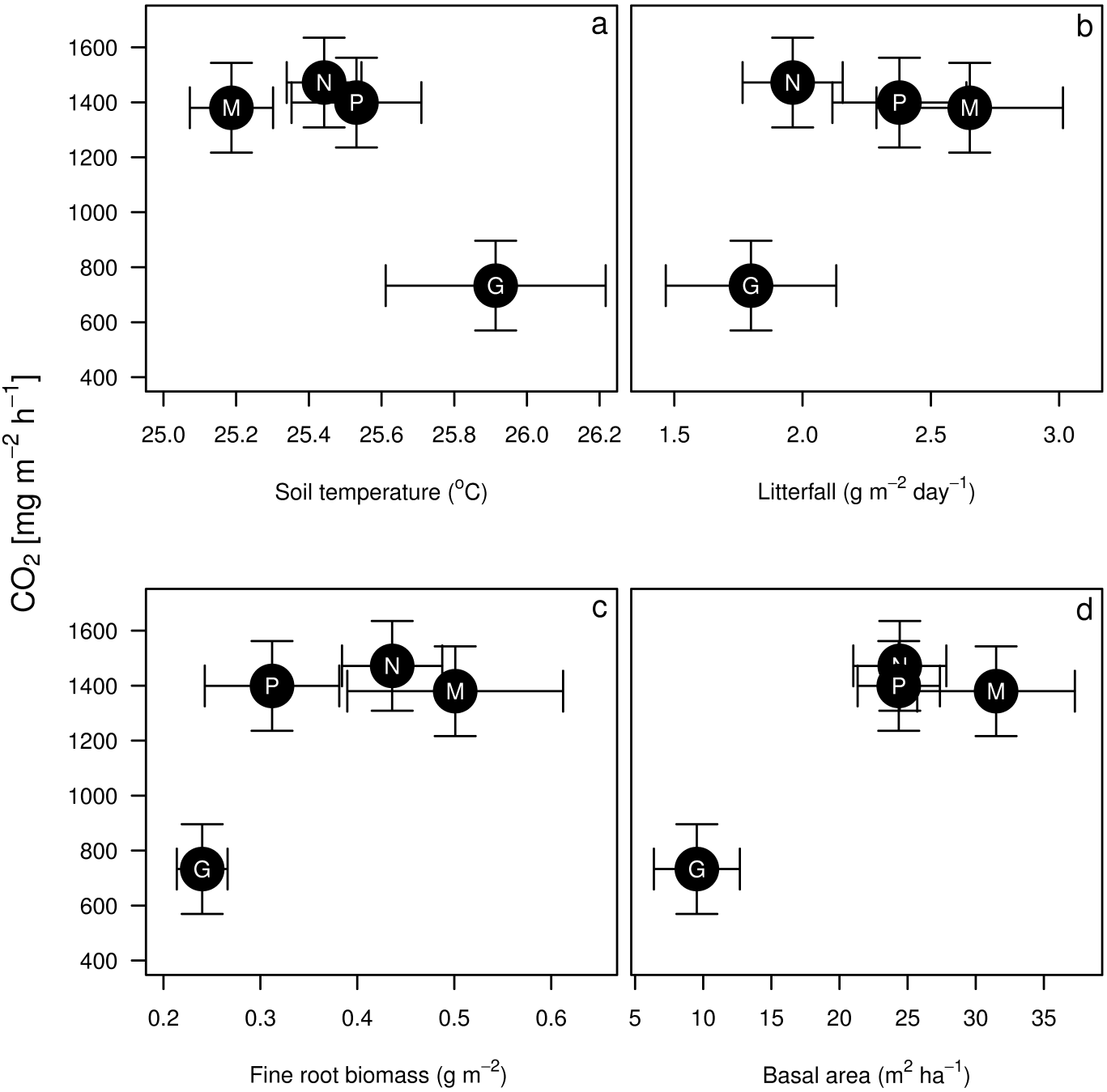
(a)	Fitted in first place		Fitted in last place		
	F	% SS	F	% SS	t
Replication	2.0	28.0	–	–	–
Soil temperature	10.0	15.9	9.0	14.3	1.8
Litterfall	7.2	11.5	5.7	9.1	0.9
Fine root biomass	< 0.1	< 1	0.4	< 1	1.4
Contrast	–	–	3.9	6.2	2.0

(b)	Fitted in first place		Fitted in last place		
	F	% SS	F	% SS	t
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

Figure 1 Soil respiration rates (CO_2 mg m^{-2} h^{-1} (mean ± SEM)) along the successional gradient, ranging from Gap sites to Pioneer, Mix and Non-Pioneer sites. Open circles indicate day soil respiration rates, solid circles indicate night soil respiration rates.

Figure 2 Effects of different explanatory variables on soil respiration rates (CO_2 mg m^{-2} h^{-1} (mean ± SEM)). G: Gap, P: Pioneer, M: Mix, N: Non-Pioneer site


1500
1000
500
CO_2 [mg m^{-2} h^{-1}]
Gap
Pioneer
Mixed
Non−Pioneer
Succession


a
b
c
d
N
P
M
G
1600
1400
1200
1000
800
600
400
25.0
25.2
25.4
25.6
25.8
26.0
26.2
1.5
2.0
2.5
3.0
0.2
0.3
0.4
0.5
0.6
5
10
15
20
25
30
35
CO2 [mg m−2 h−1]
Soil temperature (°C)
Litterfall (g m−2 day−1)
Fine root biomass (g m−2)
Basal area (m2 ha−1)

Supplementary Electronic Material

Table A Overview of species grouped according to the classification (Pioneer, Unknown, Non–Pioneer)

Family	Botanical name	Classification
Datiscaceae	*Octomeles sumatrana* Miq.	Pioneer
Euphorbiaceae	*Macaranga conifera* Muell. Arg.	Pioneer
Euphorbiaceae	*Macaranga gigantea* Muell. Arg.	Pioneer
Euphorbiaceae	*Macaranga hypoleuca* Muell. Arg.	Pioneer
Rubiaceae	*Nauclea subdita* Steud.	Pioneer
Rubiaceae	*Neonauclea artocarpoiedes* Merr.	Pioneer
Rubiaceae	*Neonauclea gigantea* Merr.	Pioneer
Rubiaceae	*Neolamarckia cadamba* Bosser	Pioneer
Rubiaceae	*Ludecia bornensis*	Pioneer
Rutaceae	*Melicope luna-akenda* T.G. Hartley	Pioneer
Sonneratiaceae	*Duabanga moluccana* Bl.	Pioneer
Euphorbiaceae	*Aporusa accuminatissima* Merr.	Unknown
Euphorbiaceae	*Aporusa elmerii* Merr.	Unknown
Euphorbiaceae	*Aporusa grandistipula* Merr.	Unknown
Euphorbiaceae	*Baccaurea stipulata* J.J. Smith	Unknown
Euphorbiaceae	*Baccaurea tetandra*	Unknown
Euphorbiaceae	*Blumeodendron tokbrai* J.J. Smith	Unknown
Euphorbiaceae	*Cleistanthus myrianthus* Kurz	Unknown
Euphorbiaceae	*Cleistanthus paxii* Jabl.	Unknown
Euphorbiaceae	*Drypetes sp.* Vahl	Unknown
Euphorbiaceae	*Endorspermum diadenum* Airy Shaw	Unknown
Euphorbiaceae	*Endorspermum peltatum* Merr.	Unknown
Euphorbiaceae	*Glochidion rubrum* Bl.	Unknown
Euphorbiaceae	*Koilodepas longifolium* Hook.	Unknown
Euphorbiaceae	*Koilodepas pectinatum*	Unknown
Euphorbiaceae	*Mallotus muticus* Airy Shaw	Unknown
Euphorbiaceae	*Mallotus penangensis* Muell. Arg.	Unknown
Euphorbiaceae	*Mallotus phillippensis* Muell. Arg.	Unknown
Euphorbiaceae	*Mallotus stipularis* Airy Shaw	Unknown
Euphorbiaceae	*Mallotus wrayi* King *ex* Hook.	Unknown
Euphorbiaceae	*Ptychopyxis kingii* Miq.	Unknown
Euphorbiaceae	*Spathiostemon javensis*	Unknown
Leeaceae	*Leea indica* Merr.	Unknown
Leguminosae	*Archidendron sp.* Muell.	Unknown
Leguminosae	*Crudia reticulata* Merr.	Unknown
Leguminosae	*Cynometra inaequifolia* Knaap-v. M.	Unknown
Leguminosae	*Dialium indum* L.	Unknown
Leguminosae	*Peltophorum racemosum* Merr.	Unknown

Leguminosae	*Saraca declinata* Miq.	Unknown
Leguminosae	*Sindora sp.* Miq.	Unknown
Leguminosae	*Sympetalandra borneensis* Stapf	Unknown
Urticaceae	*Dendrocnide elliptica* Chew	Unknown
Dipterocarpaceae	*Anisoptera grossivenia* van Slooten	Non-Pioneer
Dipterocarpaceae	*Dipterocarpus caudiferus* Merr.	Non-Pioneer
Dipterocarpaceae	*Drobalanops lanceolata* Burck	Non-Pioneer
Dipterocarpaceae	*Hopea beccariana* Burck	Non-Pioneer
Dipterocarpaceae	*Hopea nervosa* King	Non-Pioneer
Dipterocarpaceae	*Hopea nutans* Ridl.	Non-Pioneer
Dipterocarpaceae	*Parashorea malaanonan* Merr.	Non-Pioneer
Dipterocarpaceae	*Parashorea tomentella* Meijer	Non-Pioneer
Dipterocarpaceae	*Shorea agamii* Ashton	Non-Pioneer
Dipterocarpaceae	*Shorea atrinervosa* Sym.	Non-Pioneer
Dipterocarpaceae	*Shorea faguetiana* Heim	Non-Pioneer
Dipterocarpaceae	*Shorea falciferoides* Foxw.	Non-Pioneer
Dipterocarpaceae	*Shorea fallax* Meijer	Non-Pioneer
Dipterocarpaceae	*Shorea gibbosa* Brandis	Non-Pioneer
Dipterocarpaceae	*Shorea johorensis* Foxw.	Non-Pioneer
Dipterocarpaceae	*Shorea leprosula* Miq.	Non-Pioneer
Dipterocarpaceae	*Shorea leptoderma* Meijer	Non-Pioneer
Dipterocarpaceae	*Shorea macroptera* Dyer	Non-Pioneer
Dipterocarpaceae	*Shorea parvifolia* Dyer	Non-Pioneer
Dipterocarpaceae	*Shorea parvistipulata* Heim	Non-Pioneer
Dipterocarpaceae	*Shorea pauciflora* King	Non-Pioneer
Dipterocarpaceae	*Shorea superba* Sym.	Non-Pioneer
Dipterocarpaceae	*Shorea symingtonii* Wood	Non-Pioneer
Dipterocarpaceae	*Vatica albiramis* van Slooten	Non-Pioneer
Dipterocarpaceae	*Vatica dulitensis* Sym.	Non-Pioneer
Ebenaceae	*Diospyros elliptifolia* Merr.	Non-Pioneer
Ebenaceae	*Diospyros macrocarpa* L.	Non-Pioneer
Ebenaceae	*Diospyros muricata* L.	Non-Pioneer
Flacourtiaceae	*Hydnocarpus borneensis* Sleumer	Non-Pioneer
Flacourtiaceae	*Hydnocarpus kunstleri*	Non-Pioneer
Flacourtiaceae	*Hydnocarpus polypetala*	Non-Pioneer
Flacourtiaceae	*Hydnocarpus sumatrana*	Non-Pioneer
Flacourtiaceae	*Hydnocarpus woodii* Merr.	Non-Pioneer
Flacourtiaceae	*Ryparosa sp.* Merr.	Non-Pioneer
Lauraceae	*Actinodaphne sp.* Nees	Non-Pioneer
Lauraceae	*Alseodaphne sp.* Miq.	Non-Pioneer
Lauraceae	*Beilschmiedia sp.* Merr.	Non-Pioneer
Lauraceae	*Cinnamomum sp.* Bl.	Non-Pioneer
Lauraceae	*Cryptocaria sp.* Wight	Non-Pioneer
Lauraceae	*Dehassia sp.* Kost.	Non-Pioneer
Lauraceae	*Endiandra rubescens* Miq.	Non-Pioneer

Lauraceae	*Eusideroxylon zwageri* Teijs. & Binn.	Non-Pioneer
Lauraceae	*Litsea caulicarpa*	Non-Pioneer
Lauraceae	*Litsea firma* Hk.	Non-Pioneer
Meliaceae	*Aglaia elliptica* Bl.	Non-Pioneer
Meliaceae	*Aglaia macrocarpa*	Non-Pioneer
Meliaceae	*Aglaia odoratissima* Bl.	Non-Pioneer
Meliaceae	*Aglaia squamulosa* King	Non-Pioneer
Meliaceae	*Aglaia tomentosa* Teijs. & Binn.	Non-Pioneer
Meliaceae	*Azadiracta excelsa* Jacobs	Non-Pioneer
Meliaceae	*Chisocheton sp.* Blume	Non-Pioneer
Meliaceae	*Dysoxylum sp.* Blume	Non-Pioneer
Meliaceae	*Lansium sp.*	Non-Pioneer
Meliaceae	*Sandoricum koetjape* Merr.	Non-Pioneer
Meliaceae	*Walsura pinnata* Hassk.	Non-Pioneer
Myristicaceae	*Gymnacranthera sp.* Warb.	Non-Pioneer
Myristicaceae	*Knema sp.* Lour.	Non-Pioneer
Myristicaceae	*Myristica sp.* Gronov	Non-Pioneer
Sabiaceae	*Meliosma pinnata* Maxim.	Non-Pioneer
Sabiaceae	*Meliosma sumatrana* Walp.	Non-Pioneer
Sapindaceae	*Dimocarpus dentatus*	Non-Pioneer
Sapindaceae	*Dimocarpus longan* Lour.	Non-Pioneer
Sapindaceae	*Guioa pubescens*	Non-Pioneer
Sapindaceae	*Mischocarpus sp.*	Non-Pioneer
Sapindaceae	*Nephelium rambutan*	Non-Pioneer
Sapindaceae	*Paranephelium xestophyllum* Miq.	Non-Pioneer
Sapindaceae	*Pometia pinnata* Forst.	Non-Pioneer
Sapotaceae	*Madhuca sp.* Ham. *ex.* J. F. Gmel.	Non-Pioneer
Sapotaceae	*Palaquium sp.* Blanco	Non-Pioneer
Sapotaceae	*Payena sp.*	Non-Pioneer
Tiliaceae	*Brownlowia peltata* Benth.	Non-Pioneer
Tiliaceae	*Jarandersonia rinoreoides*	Non-Pioneer
Tiliaceae	*Microcos crassifolia* Burret	Non-Pioneer
Tiliaceae	*Pentace adenophora* Kost.	Non-Pioneer
Tiliaceae	*Pentace laxiflora* Merr.	Non-Pioneer