Reduced soil respiration in gaps in logged lowland dipterocarp forests

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A R T I C L E   I N F O

A B S T R A C T

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 $(1290 \pm 210 \, mg \, CO_2 \, m^{-2} \, h^{-1})$ but were double those in gap sites $(640 \pm 130 \, mg \, CO_2 \, m^{-2} \, h^{-1})$. 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.

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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 Town-send, 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 ecosystem 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 mechanisms 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