CARBON CYCLING IN A BORNEAN TROPICAL FOREST

Exploring Carbon Allocation and Cycling of Tropical Forest in the 52-ha Lambir Hills Forest Dynamics Plot

by

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Common Abbreviations

Above-ground coarse wood net primary productivity	NPP_{ACW}	Leaf area index	LAI
Above-ground net primary productivity	NPP_{AG}	Litter respiration	R_{litter}
Amazon Forest Inventory Network	RAINFOR	Litterfall detritus	$D_{\mathrm{litterfall}}$
Analysis of variance	ANOVA	Litterfall net primary productivity	$NPP_{\mathrm{litterfall}}$
Autotrophic respiration	R_{a}	Lost to leaf herbivory net primary productivity	$NPP_{\mathrm{herbivory}}$
Below-ground net primary productivity	NPP_{BG}	Malaysian Palm Oil Board	MPOB
Branch turnover net primary productivity	$NPP_{\mathrm{branch\ turnover}}$	Mycorrhizae respiration	R_{myc}
Carbon dioxide	CO_2	Mycorrhizae treatment	T_{Myc}
Carbon use efficiency	CUE	Net primary productivity	NPP
Center for Tropical Forest Science	CTFS	No Input treatment	T_{NI}
Coarse roots net primary productivity	$NPP_{\mathrm{coarse\ roots}}$	No Litter treatment	T_{NL}
Coarse woody debris	CWD	No Root Disturbed treatment	T_{NRD}
Coarse woody debris detritus	D_{CWD}	No Root Undisturbed treatment	T_{NRUD}
Coarse woody debris respiration	R_{CWD}	Plant carbon expenditure	PCE
Control treatment	T_{C}	Reduced O/A horizon treatment	$T_{\mathrm{O/A}}$
Detritus Input and Removal Transfer	DIRT	Root detritus	D_{root}
Diameter at breast height	DBH	Root respiration	R_{root}
Doctor of Philosophy	D.Phil.	Stem area index	SAI
Double litter treatment	T_{DL}	Soil organic matter	SOM
El Niño Southern Oscillation	ENSO	Soil organic matter respiration	R_{SOM}
Fine roots net primary productivity	$NPP_{\mathrm{fine\ roots}}$	Specific leaf area	SLA
Global Ecosystem Monitoring network	GEM	Total net primary roductivity	NPP_{Total}
Gross primary productivity	GPP	Total ecosystem respiration	R_{Total}
Heterotrophic respiration	R_{h}	Total belowground carbon allocation	TBCA
Infra-red gas analyser	IRGA	Total soil respiration	R_{S}
International Biological Programme	IBP	Vapour pressure deficit	VPD

Declaration

I hereby declare that this thesis is my own work and composed by me. No part of this thesis is submitted for any other degree or qualification.

Kho Lip Khoon

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I dedicate this thesis to my baby boy, Ryoga.

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Abstract

The tropical forests on the island of Borneo are among of the richest in the world in terms of tree diversity, and their capacity to store a large reservoir of carbon. The Southeast Asian forests are fundamentally different from Neotropical and African forests, with their single-family dominance by dipterocarp trees, and with inherently greater stature and biomass. The carbon productivity and allocation in Asian tropical forests is still poorly quantified, and their responses to environmental drivers are still poorly understood. Almost all recent advances in tropical forest carbon cycling research have occurred in the Neotropics, with very few studies in Asia. The principal aim of this thesis is to quantify the carbon budget of a lowland dipterocarp forest in the Lambir Hills National Park, Miri, Sarawak, Malaysian Borneo. I examined and explored the productivity and carbon cycling processes and their responses to environmental factors across two major and contrasting soil types, in particular the clay and sandy loam soils. I recorded and analysed the Net Primary Productivity (NPP) and respiration for the above- and below-ground components, and observed the responses to seasonal variation and environmental drivers.

Total soil respiration was relatively high and contributed a great deal to ecosystem respiration. Variation in soil respiration rates appeared closely related to soil moisture content. I found a strong diurnal cycle in soil respiration. On the basis of the first soil carbon dioxide (CO_2) efflux partitioning study undertaken in a tropical forest, the diurnal cycle in total soil respiration appeared to be entirely driven by the diurnal cycle in litter respiration, and in turn litter is strongly controlled by moisture.

There was little seasonal variation in allocation of net primary productivity (NPP), but there was evidence showing potential inter-annual variability for several components of NPP. Further, the allocation of NPP showed a strong seasonal shift between the forest

plots on clay and sandy loam soils. Combining all the data measured and obtained in this D.Phil. thesis, the overall carbon budget assessed in this lowland dipterocarp forest showed a high level of agreement with other studies in Asia using micrometeorological techniques and the situation appears to be comparable to tropical forests in Amazonia. The key difference is that the aboveground NPP is higher and is the largest component contributing to the overall carbon budget, with relatively higher carbon use efficiency (CUE). The lowland dipterocarp forest in Lambir shows higher allocation in the above-ground NPP, and there were also differences in NPP and its allocation between sandy and clay-rich plots.

Chapter 1

Chapter 1: Introduction

1.1. The Terrestrial Carbon Cycle

The terrestrial biosphere plays a crucial role in the global carbon cycle. Changes in climate, land use and atmospheric chemistry can significantly influence biophysical interactions and biogeochemical exchanges with the atmosphere (Prentice *et al*., 2000), hence also affecting the potential feedback to terrestrial ecosystems. The terrestrial ecosystems constitute large reservoirs of exchangeable carbon – approximately 2,200 Petagrams (Pg) C, which are mainly stored in vegetation (~30%) and soils (~70%) (Saugier *et al*. 2001). A recent estimate of the net terrestrial biosphere exchange between land and atmosphere was about -0.9 ± 0.6 Pg C yr^{-1} between 2000 and 2005, which suggests a net uptake of atmospheric carbon dioxide (CO_2) by the terrestrial ecosystem (Denman *et al*., 2007). Despite decades of long-term observational records, there remain significant uncertainties in regard to predicting the long-term responses of the terrestrial carbon cycle to global environmental change (Schimel, 2007; Heimann and Reichstein, 2008) and the contribution of key ecological processes to the terrestrial carbon sink (Canadell *et al*., 2000; Schimel *et al*., 2001).

Tropical forests in particular play an important role in regional and global biogeochemical cycles and regulate the climate. Tropical forest ecosystems contain approximately 471 ± 93 Pg C or 55% of terrestrial carbon storage (Pan *et al*., 2011). In Asia, tropical forests cover between 30% and 45% of the tropical land area (Achard *et al*., 2002; Achard *et al*., 2004; Hansen *et al*., 2010), with ~36.7 x 10^6 ha of extant forest area in Borneo (Miettinen *et al*., 2011). At the same time, deforestation and forest degradation contributed 1.30 ± 0.24 Pg C yr^{-1} to the atmosphere between 2000 and 2005, and about 47% of these emissions were from tropical Asia (Malhi, 2010). As anthropogenic pressure to clear land for agriculture continues to change land use and forest cover in the tropical region, the carbon cycling of terrestrial ecosystems is expected to shift and could significantly affect the atmospheric CO_2 concentration, and hence the global climate. In addition, analyses of climatic trends in tropical forest regions showed substantial inter-annual climate variability, primarily driven by the El Niño Southern Oscillation (ENSO) (Malhi and Wright, 2004), corresponding to enhanced rates of global CO_2 rise during El Niño years (Timmermann *et al*., 1999). For instance, the intense ENSO event of 1997–1998 (Webster and Palmer, 1997) induced the longest and one of the most severe droughts recorded in north-western Borneo. Such periodic short-term droughts have substantially increased plant mortality (Becker *et al*. 1998; Nakagawa *et al*. 2000), altered plant phenology (Harrison, 2000; Harrison, 2001; Potts, 2003), and often caused high fire incidence in lowland tropical forests (Nykvist, 1996; Toma, 1999). These disturbances may potentially influence the biogeochemical cycles and atmospheric CO_2 concentrations.

There is now a considerable body of evidence showing that the dynamics and biomass of tropical forests are responding to contemporary atmospheric change and climate variability (Grace and Rayment, 2000; Malhi and Phillips, 2004; Malhi and Wright, 2004; Lewis *et al*., 2009a; Hector *et al*., 2011). The changing ecology of tropical forests may be attributed to atmospheric CO_2 concentration, nutrient deposition, temperature, drought, and solar irradiance (Lloyd and Farquhar, 1996; Post *et al*., 1997; Graham *et al*., 2003; Nemani *et al*., 2003; Cox *et al*., 2004; Cowling and Shin, 2006). The old-growth tropical forests are showing evidence of accelerating dynamics and increasing biomass (Phillips and Gentry, 1994; Baker *et al*., 2004; Phillips *et al*., 2004; Chave *et al*., 2008). A recent study showed that tropical forest trees in research plots in Southeast Asia increased in both forest biomass and net primary productivity (NPP) (Chave *et al*., 2008). On the other hand, there is a possibility that trees may be responding to environmental changes through shifts in allocation of carbon from stem growth to other pathways (Curtis and Wang, 1998; LaDeau and Clark, 2001; Lewis *et al*., 2004; Metcalfe *et al*., 2010).

The tropical forests on the island of Borneo are the most diverse terrestrial ecosystem on Earth. The wet tropical forests of this region are mainly dominated by dipterocarp species and they are characterised by high above-ground biomass (Anderson *et al*., 1983; Proctor *et al*., 1983; Yamakura *et al*., 1986; Yamakura *et al*., 1996; Paoli *et al*., 2008; Slik *et al*., 2010). However, carbon cycling in Southeast Asian tropical forests has received little attention since the inception of the International Biological Programme (IBP) in 1970 (Soepadmo and Kira, 1977; Kira, 1987) and remains poorly understood. Despite important early work in the 1970s in Pasoh Forest Reserve, Peninsular Malaysia, most recent advances in our understanding of forest carbon dynamics have mainly come from sites in Amazonia (Clark *et al*., 2001b; Chambers *et al*., 2004; Aragão *et al*., 2009; Malhi *et al*., 2009; Malhi *et al*., 2011). For this reason, my D.Phil. research study sets out to focus on exploring the carbon cycle in a lowland dipterocarp forest in Borneo and to evaluate the differences with similar studies in tropical forest elsewhere. Discerning the carbon cycle of tropical forests in this region is very valuable to better understand how this ecosystem contributes to the total biospheric carbon cycle and may influence global environmental change.

1.2. Literature Review

1.2.1. Lowland Dipterocarp Forest

The third largest block of tropical forest (after Amazonia and the Congo Basin) lies in the eastern tropics (Mayaux *et al.*, 2005). Located mainly in the countries of Malaysia and Indonesia, this is also known as the Malesian region (Richards, 1952; Ashton, 1964; Whitmore, 1984). In this region, the Malesian forests encompass most of Peninsular Malaysia, Borneo, Sumatra, Java, and the Philippines (Ashton, 1964; Whitmore, 1984). The climate is typically wet every month, with no regular annual dry season (mean monthly precipitation less than 100 mm). The aseasonal lowland Malesian forest is exceptionally diverse in species and genera (Ashton, 1964; Whitmore, 1984). Distinctively different from any tropical forest elsewhere, Malesian forest is largely dominated by a single tree family – the Dipterocarpaceae (Ashton, 1982). The dipterocarp family accounts for approximately 10% of all tree species and 80% of all emergent individuals in a typical lowland forest (Ashton, 1982).

In Borneo, the lowland dipterocarp forests have been described as the richest tree communities in the Old World (Whitmore, 1984; Ashton, 2005; Ashton, 2009). One of the most well-documented floristic composition studies is from Lambir, Sarawak, with 1,192 species from 288 genera (Lee *et al.*, 2002). This high level of species diversity is typically aggregated on deep soils with relatively low nutrient status (Ashton, 1998; Potts *et al.*, 2002; Davies *et al.*, 2005; Paoli *et al.*, 2006). The lofty and dense dipterocarp forest typically constitutes tall trees of greater stature than tropical forest elsewhere. Trees may reach a height of up to 70–80 m and occur in groups (Ashton, 1982). A unique feature of dipterocarp forest is the phenomenon of mass flowering, followed by mast fruiting (Foxworthy, 1932; Medway, 1972; Janzen, 1974; Ashton, 1989; Kelly, 1994). The irregular phenomenon occurs at intervals of between two and 10 years, and takes place when simultaneous flowering takes place among most species of dipterocarps and several other canopy tree families (Foxworthy, 1932; Chan and Appanah, 1980; Ashton *et al*., 1988; Appanah, 1993; Sakai *et al*., 1999; Numata *et al*., 2003; Sakai *et al*., 2006).

1.2.2. Tropical Forest and the Carbon Cycle

The carbon cycle is an important biogeochemical cycle that involves the movement and exchange of carbon between the biosphere and organisms. The processes of photosynthesis and respiration are the basis of the carbon cycle. Photosynthesis is a metabolic process by which plants, algae and photosynthetic bacteria utilise solar energy and fix CO_2 from the atmosphere to produce carbohydrate and oxygen. The overall chemical reaction is:

$$6H_2O + 6CO_2 \xrightarrow{\text{sunlight}} C_6H_{12}O_6 + 6O_2 \qquad \text{(Eq. 1.1)}$$

where $[CH_2O]$ represents carbohydrate. In the presence of the light energy, water molecules are split. When water breaks up, it releases oxygen, electrons and protons. Oxygen is used by the mitochondria for respiration and the remainder is respired to the atmosphere. The energetic electrons and protons are combined with CO_2 to produce carbohydrate (e.g. glucose). Carbohydrate produced in plants is stored as energy and biomass (i.e. leaves, stems, roots), which are essential for metabolism. The rate of CO_2 uptake in photosynthesis is defined as gross primary productivity (GPP). At a global scale, the highest GPP in natural ecosystems is found in tropical biomes, and averages 35.5 ± 1.6 Mg C ha^{-1} yr^{-1} (Luyssaert *et al*., 2007). In a recent review, the mean GPP has been reported at 29.9 ± 5.9 Mg C ha^{-1} yr^{-1} (mean ± standard deviation) across six tropical forests sites (Vicca *et al*., 2012).

At the same time, plants return CO_2 to the atmosphere via respiration. In respiration, carbohydrate is oxidised and converted (photosynthates) back into energy for growth, reproduction, maintenance, and other vital metabolic functions. Photosynthates are combined with oxygen to produce energy and water, and release CO_2 back to the atmosphere. This process in plants is defined as autotrophic respiration (R_a). R_a contributes approximately 23.2 ± 1.4 Mg C ha^{-1} yr^{-1} across tropical biomes (Luyssaert *et al*., 2007). Hence, the remaining photosynthates in plants are allocated for biomass production, also termed as the NPP.

1.2.3. Tropical Forests' Net Primary Productivity

Carbon enters terrestrial ecosystems solely through photosynthesis and is returned to the atmosphere through a variety of respiration processes. The difference between photosynthesis and plant respiration or R_a represents the potential NPP. Hence, NPP is the difference between GPP and total plant respiration or R_a:

$$NPP = GPP - R_a \qquad \text{(Eq. 1.2)}$$

Moreover, NPP is the rate of biomass construction or gains in organic structures such as wood, leaves, root tissues, and some poorly described NPP components, such as root exudates production and volatile organic compounds release. These components of NPP primarily determine the magnitude and turnover of carbon and nutrient cycles in terrestrial ecosystems.

Terrestrial NPP is among the most important ecosystem variable in the global carbon cycle and the main driving force of ecological processes. It has been the subject of long and extensive studies in various major ecosystems (Whittaker 1970). The net sources and sinks of terrestrial biosphere have been estimated using several methods that include integration of field measurements (Whittaker and Likens, 1973; Ajtay *et al*., 1979; Roy *et al*., 2001), a combination of models for remote sensing (Melillo *et al*., 1993; Dixon *et al*., 1994; Ruimy *et al*., 1994; Prince and Goward, 1995; Schimel, 1995; Field *et al*., 1998; Brown and Schroeder, 1999; Jobbágy and Jackson, 2000; Knorr and Heimann, 2001; Goodale *et al*., 2002; Houghton, 2003), observation of atmospheric CO_2 data (Tans *et al*. 1990; Jacobson *et al*. 2007; Stephens *et al*. 2007), and isotopic analyses (Ciais *et al*. 1995; Rayner *et al*. 1999).

In Southeast Asia, the earliest detailed studies of NPP were conducted in Pasoh, Peninsular Malaysia (a lowland dipterocarp forest) and Khao Chong, Thailand (an evergreen seasonal forest), with multiple independent methods over a few selected plots that included the summation or harvesting method (Kira *et al*., 1967; Ogino *et al*., 1967; Kira, 1978), the canopy photosynthesis method (Kira, 1978), the micrometeorological or energy balance approach (Aoki *et al*. 1975). Summing all biomass components directly measured and quantified following destructive felling involves a laborious process and often introduces large errors in estimation (Clark *et al*., 2001a). The canopy photosynthesis method is calculated from the photosynthesis-light curve within a single day (Aoki *et al*., 1975; Kira, 1978). Recently, a growing number of studies have focused on the micrometeorological method, particularly the eddy covariance technique, in order to determine net ecosystem exchange and GPP (e.g. Mizoguchi *et al*., 2008). However, this technique requires validation from a bottom-up approach such as the summation or integration method.

The integration method repeatedly measures biomass components over time and employs allometric equations to calculate various components of NPP without the need to destructively harvest plants. In addition, long-term changes can be monitored on the same study site. Hence, the integration method, as employed in my D.Phil. study, potentially provides a suitably long-term and reliably consistent methodological approach. Moreover, employing proper correction to calculations and propagating plausible errors may increase the accuracy in estimating total NPP.

Tropical forest NPP has been estimated to contribute between 32% and 43% of the global terrestrial NPP (Melillo *et al.*, 1993; Field *et al.*, 1998). Following recent reviews of NPP studies in tropical forests, NPP in tropical forests has been estimated to range between 4–17 Mg C ha^{-1} yr^{-1} (Grace *et al.*, 2001; Clark *et al.*, 2001b; Malhi *et al.*, 2011). Early estimates of productivity at various tropical forest sites (UNESCO, 1978; Medina and Klinge, 1983) were often limited to above-ground production (woody growth and litterfall) with fewer estimates of below-ground production (Clark *et al.*, 2001b). Hence, the missing NPP components and the lack of NPP data across tropical forest sites are the major sources of uncertainty in NPP estimates (Clark *et al.*, 2001b; Malhi *et al.*, 2011).

NPP studies are relatively scarce in Asian tropical forests, and the available NPP data shows substantial variation across various vegetation types and methods applied (see Table 1.1). Total NPP from models and micrometeorological techniques exhibit slightly higher values than summation or integrated methods. For example, there appears to be an overestimate from Pasoh when total NPP was estimated using the micrometeorological technique and calculated from the photosynthesis-light curve within a single day of observation (Kira, 1978). However, it should also be noted that the current eddy covariance technique may generate estimates with greater accuracy. Nevertheless, total NPP estimates are within a plausible range when estimated from the harvesting, summation and integration methods (Table 1.1).

Total NPP from lowland dipterocarp forest in Pasoh is the highest, with the exception of the modelled data and overestimated value from Khao Chong forest (Table 1.1). In contrast, pre-montane forest is the lowest, with a recent study having recorded the lowest total NPP from a pre-montane forest in Sulawesi, Indonesia (Hertel *et al.*, 2009). Mean total NPP is significantly higher across the Asian tropical forests as compared to the Amazonian forests. However, the lack of data from the Asian region makes this estimate tentative.

The lowland Bornean forests are fundamentally different from Neotropical and African forests, being so dominated by dipterocarp trees (Ashton, 1964; Ashton, 1982; Whitmore, 1984; Ashton and Hall, 1992; Davies and Becker, 1996; Curran and Webb, 2000; Lee *et al.*, 2002; Potts *et al.*, 2004; Ashton, 2005). In addition, previous studies have reported higher values of above-ground NPP (Kitayama and Aiba, 2002; Paoli and Curran, 2007; Chave *et al.*, 2008).

Because of the lack of data for Asian tropical forest sites, it is still poorly understood whether apparent differences in primary production are driven by environmental factors, carbon allocation patterns, soil factors, or the missing NPP components (DeLucia *et al.*, 2007; Litton *et al.*, 2007; Malhi *et al.*, 2009; Cleveland *et al.*, 2011; Malhi *et al.*, 2011). In Amazonia, it has been suggested that large regional gradients in above-ground productivity across Neotropical forests may be explained by the variations in plant photosynthesis, the amount of carbon allocated to roots, and the amount of carbon lost through plant respiration (Malhi *et al.*, 2004).

Table 1.1: The mean (± standard error) total net primary productivity (NPP) of tropical forests

Site	Forest type	Method	Total NPP (Mg C ha^{-1} yr^{-1})	Reference
Asia				
Malaysia: Pasoh	Lowland dipterocarp	S	13.7 ± 1.4*	Kira (1978)
		S	12.8 ± 1.3*	Kira (1987)
		Met	24.5 ± 2.5*	Aoki *et al.* (1975)
Thailand: Khao Chong	Seasonal evergreen	S	14.3 ± 1.4*	Kira *et al.* (1967)
Indonesia: Sulawesi	Premontane	I	6.7 ± 0.3	Hertel *et al.* (2009)
Thailand: Central Thailand	Deciduous dipterocarp/ Dry evergreen	S/I	6.1 ± 0.6*	Ogino *et al.* (1967)
China	Tropical forest	Mod	17.8 ± 2.5	Wang *et al.* (2008)
		I	7.2 ± 1.6	Ni *et al.* (2001)
China: Fujian	Sub-tropical	S	11.2 ± 0.6	Yang *et al.* (2003)
China: Xishuangbanna	Tropical seasonal	S	8.8 ± 0.9*	Tan *et al.* (2010)
India: Western Ghats	Wet evergreen	I	11.9 ± 2.0	Swamy *et al.* (2010)
	Estimated Mean		**12.3 ± 0.5**	
Amazonia				
Brazil: Caxiuana	Moist old-growth	I	13.2 ± 0.8	Aragão *et al.* (2009)
		I	10.0 ± 1.2	Malhi *et al.* (2009)
Brazil: Tapajos	Moist old-growth	I	14.4 ± 1.3	Aragão *et al.* (2009)
		I	14.4 ± 1.3	Malhi *et al.* (2009)
Brazil: Manaus	Moist old-growth	I	11.4 ± 1.3	Aragão *et al.* (2009)
		I	10.1 ± 1.4	Malhi *et al.* (2009)
Peru: Tambopata	Lowland forest	I	15.4 ± 0.6	Aragão *et al.* (2009)
		I	15.3 ± 0.6	Girardin *et al.* (2010)
Peru: Tono	Pre-montane	I	7.1 ± 1.0	Girardin *et al.* (2010)
Peru: San Pedro	Lower montane	I	7.1 ± 0.4	Girardin *et al.* (2010)
Peru: Trocha Union	Lower and upper montane	I	5.1 ± 0.3	Girardin *et al.* (2010)
Peru: Wayquecha	Upper montane	I	5.1 ± 0.4	Girardin *et al.* (2010)
Colombia: Agua Pudre	Moist lowland	I	11.5 ± 0.5	Aragão *et al.* (2009)
Colombia: Zafire	Moist lowland	I	9.3 ± 1.3	Aragão *et al.* (2009)
Colombia: Porce	Lowland to pre-montane forest	I	12.8 ± 0.4	Sierra *et al.* (2007)
Venezuela: San Carlos	Moist white sand soil	I	6.0 ± 0.6*	Jordan and Escalante (1980)
	Estimated mean		**10.5 ± 0.2**	
Elsewhere				
Mexico: Chamela	Deciduous	I	4.7 ± 0.5*	Martinez-Yrizar *et al.* (1996)
USA: Hawaii	Montane	S	7.8 ± 0.3	Ostertag (2001)
Ghana: Kade	Moist semi-deciduous	S	12.5 ± 1.3*	Greenland and Kowal (1960)

* 10% standard error assigned (Aragão *et al.*, 2009; Malhi *et al.*, 2009)

NB: S, summation based on destructive method that measures actual accumulation of plant above- and below-ground biomass; Met, micrometeorology approach typically using eddy covariance technique that measures the flow of carbon dioxide between the forest canopy and the atmosphere; Mod, ecosystem simulation modelling to integrate observed meteorological data and carbon cycle; I, integrated sum of above- and below-ground biomass/NPP components measured continuously to capture increment and losses.

In addition, spatial variations of above-ground NPP appear driven by soil nutrients (Jordan and Herrera, 1981; Vitousek, 1984; Vitousek *et al*., 2010; Cleveland *et al*., 2011), particularly soil phosphorus (Harrington *et al*., 2001; Paoli *et al*., 2005; Paoli and Curran, 2007; Aragão *et al*., 2009; Quesada *et al*., 2009) and the availability of soil nitrogen (Cleveland *et al*., 1999; Vitousek *et al*., 2002; Cusack *et al*., 2010). A recent review suggested substantial variation in NPPallocation across sites (Malhi *et al*., 2011). The magnitude, spatial and temporal variations of NPP are of considerable interest with regard to testing our understanding of ecosystem functions, the role of the biosphere in global biogeochemical cycles, and the response of ecosystems to local and global perturbations.

1.2.4. Above-Ground Biomass and Productivity

Above-ground biomass in a forest ecosystem includes leaves, twigs, branches, woody materials, and trunks. These above-ground components are important contribution to total NPP, and hence the carbon balance. In the tropics, above-ground biomass has been reported over a large range of 20 to 330 Mg C ha^{-1} across various tropical forests (Clark *et al*., 2001b). The above-ground biomass of tropical forests seems relatively greater than in the temperate and boreal forests, yet the magnitude and spatial distributions are still uncertain (Goodale *et al*., 2002; Houghton *et al*., 2009; Malhi, 2010). Furthermore, the uncertainty is confounded by the rapid increase of tropical deforestation, which considerably alters carbon stocks and hence the global carbon cycle (Achard *et al*., 2002; DeFries *et al*., 2002; Houghton, 2003; Achard *et al*., 2004; van der Werf *et al*., 2009; DeFries *et al*., 2010; Miettinen *et al*., 2011).

A considerable number of studies assessing above-ground biomass are biased and inaccurate due to methodological inconsistencies related to measurements (Clark *et al*., 2001a). Moreover, the global and regional inventories and data available are limited, incomplete and out of date (Houghton *et al*., 2009; Malhi, 2010). The estimation of above-ground biomass can be determined through different methods. Destructive measurement is the conventional method used to quantify plant biomass (Ogawa *et al*., 1965; Kato *et al*., 1978; Klinge and Herrera, 1983; Rai and Proctor, 1986; Yamakura *et al*., 1986). Repeated field measurements to quantify biomass increment and losses are often challenging and time consuming. In tropical forest, this is made particularly difficult by the diversity of tree species, wood densities, tree architectures and life forms, as well as and the complexity of below-ground biomass components (Clark *et al*., 2001b). More advanced non-destructive measurements involve micrometeorology using the eddy covariance method (Aoki *et al*., 1975; Fan *et al*., 1990; Grace *et al*., 1995; Grace *et al*., 1996; Malhi *et al*., 1998; Araújo *et al*., 2002; Goulden *et al*., 2004; Saigusa *et al*., 2005; Saitoh *et al*., 2005; Takanashi *et al*., 2005; Kumagai *et al*., 2006; Hirata *et al*., 2008; Kosugi *et al*., 2008; Mizoguchi *et al*., 2008; Ohkubo *et al*., 2008), satellite optical data (Steininger, 2000), long-wavelength radar and lidar (Lefsky *et al*., 2002; Drake *et al*., 2003; Patenaude *et al*., 2004; Dubayah *et al*., 2010; Saatchi *et al*., 2011b), synthetic aperture radar (Ranson *et al*., 1997; Santos *et al*., 2003; Mitchard *et al*., 2009; Englhart *et al*., 2011; Morel *et al*., 2011; Saatchi *et al*., 2011a; Le Toan *et al*., 2011), and digital aerial image analysis (Brown *et al*., 2005; Tackenberg, 2007).

Although estimates of above-ground NPP in tropical forests are limited, it is nevertheless reasonably well known in regard to Amazonian forests as a result of continuous field measurements and monitoring of several permanent plots (Phillips *et al*., 1998; Clark, 2002; Chave *et al*., 2003; Baker *et al*., 2004; Chambers *et al*., 2004; Lewis *et al*., 2004; Malhi *et al*., 2004). In Southeast Asian forests, earlier measurements of above-ground biomass and NPP were conducted in the 1970s under the IBP (Soepadmo and Kira, 1977; Soepadmo, 1978; Kira, 1987). Thereafter, several sporadic estimations of above-ground biomass have been reported for various locations in the Southeast Asian region (see Table 1.2), but very few are above-ground NPP studies (Kitayama and Aiba, 2002; Paoli and Curran, 2007; Hertel *et al*., 2009).

Tropical forests in the Southeast Asian region often constitute substantial above-ground biomass. The variations in above-ground biomass are mainly attributed to different vegetation types observed across the region and the method employed, particularly the allometric equations. These values are significantly higher than those typically reported from forests in South America (see Table 1.2) or Africa (Malhi *et al*., 2006; Lewis *et al*., 2009b). One of the reasons that the above-ground biomass is higher in this region may be due to the mixed dipterocarp forests that are generally taller in stature and larger in size (Brown *et al*., 2001; Slik *et al*., 2010). In addition, this large above-ground carbon stock could be linked to soil fertility and demographic changes in species (Potts *et al*., 2004; Davies *et al*., 2005; Russo *et al*., 2005; Paoli *et al*., 2008). In north-western Borneo, mixed dipterocarp forests on red-yellow podzolic soils generally have much greater above-ground biomass than heath forests on podzols (Proctor *et al*., 1983; Ashton and Hall, 1992; Palmiotto *et al*., 2004; Potts *et al*., 2004). Furthermore, a recent review found that the substantial differences in NPP allocation between canopy and woody tissue in Asian lowland forests are mainly due to highly variable resources (Malhi *et al*., 2011). However, the lack of data in this region makes it difficult to evaluate the allocation within above-ground productivity and the relationship to total NPP (Clark *et al*., 2001b; Malhi *et al*., 2011). Hence, this thesis will determine the allocation of NPP and explore the potential relationships to environmental factors in a lowland dipterocarp forest.

1.2.5. Below-Ground Biomass and Productivity

Little is known about increment and losses of below-ground biomass and the relationship to above-ground productivity in tropical forests (Raich and Nadelhoffer, 1989; Clark *et al.*, 2001b). Below-ground biomass is often unaccounted for or is estimated as some theoretical proportion of above-ground production (Whittaker and Marks, 1975). Based on a steady-state assumption, total below-ground carbon allocation (TBCA) was roughly twice the annual above-ground litterfall in forest ecosystems (Raich and Nadelhoffer, 1989; Trumbore *et al.*, 1995; Davidson *et al.*, 2002a). Early accounts of TBCA in several Bornean tropical forests were estimated between 4.8 and 17.7 Mg C ha^{-1} yr^{-1} (Anderson *et al.*, 1983; Proctor *et al.*, 1983). By comparison, TBCA in the Amazonian forests was relatively higher at between 1.5 and 39.0 Mg C ha^{-1} yr^{-1}. Recent reviews of 39 tropical forest sites estimate below-ground productivity to be in the range of 0.1–17.0 Mg C ha^{-1} yr^{-1}, although there are still considerable methodological uncertainties (Clark *et al.*, 2001b). Hence, the allocation of above-ground carbon to below-ground biomass often equals or exceeds the above-ground litterfall and respiration of forest ecosystems (Janssens *et al.*, 2001).

Below-ground productivity includes turnover of fine and coarse roots, losses of root material to below-ground consumers, rhizodeposition, and the carbohydrate inputs to mycorrhizal fungi and root nodule symbionts (Clark *et al* 2001a). In the forest ecosystems, roots constitute the largest amount of below-ground productivity (Raich and Nadelhoffer, 1989; Vogt *et al.*, 1996; Schlesinger, 1997). Root production has been suggested to contribute one-third of the global annual NPP (Jackson *et al.*, 1996).

Table 1.2: Summary of above-ground biomass (Mg C ha^{-1}) in Southeast Asian tropical forest and several sites in the Amazonian tropical forest

Site	**Vegetation**	**Carbon stock (Mg C ha^{-1})**	**Reference**
Southeast Asia			
Pasoh: Peninsular Malaysia	Lowland dipterocarp forest	238	Kato et al. (1978)
Pasoh: Peninsular Malaysia	Lowland dipterocarp forest	208	Hoshizaki et al. (2004)
Pasoh: Peninsular Malaysia	Lowland dipterocarp forest	268	Niiyama et al. (2010)
Pasoh: Peninsular Malaysia	Lowland dipterocarp forest	155	Okuda et al. (2004)
Lambir: Borneo Malaysia	Lowland dipterocarp forest	260	Yamakura et al. (1996)
Lambir: Borneo Malaysia	Lowland dipterocarp forest	249	Chave et al. (2008)
Gunung Mulu: Borneo Malaysia	Alluvial forest	125	Proctor *et al.* (1983)
	Dipterocarp forest	325	Proctor *et al.* (1983)
	Heath forest	235	Proctor *et al.* (1983)
	Forest over limestone	190	Proctor *et al.* (1983)
Danum Valley: Borneo Malaysia	Lowland dipterocarp forest	128	Saner et al. (2012)
Gunung Kinabalu: Borneo Malaysia	Dipterocarp montane forest	248	Kitayama and Aiba (2002)
East Kalimantan: Borneo Indonesia	Lowland dipterocarp forest	255	Yamakura *et al.* (1986)
Central Kalimantan: Borneo Indonesia	Heath forest	120	Miyamoto *et al.* (2007)
Central Sulawesi: Indonesia	Pre-montane forest	286	Hertel *et al.* (2009)
Borneo	Lowland tropical forest	238	Slik et al. (2010)
Khao Chong: Thailand	Seasonal evergreen forest	166	Kira *et al.* (1967)
Cheko: Cambodia	Seasonal evergreen forest	161	Hozumi *et al.* (1969)
Cambodia	Deciduous forest	144	Kiyono *et al.* (2010)
	Evergreen forest	223	Kiyono *et al.* (2010)
West Kalimantan: Borneo Indonesia	Lowland tropical forest	215	Paoli *et al.* (2008)
Peninsular Malaysia	Superior	245	Forestry Department (1987)
	Moderate hill	310	
Nam Phrom: Thailand	Semi-deciduous seasonal	170	Kyuma *et al.* (1985)
Estimated mean (± standard error)		**215 ± 12**	
Amazonia			
Manaus: Brazil	Moist old-growth forest	163	Chambers *et al.* (2004) Malhi *et al.* (2006) Pyle *et al.* (2008)
Tapajós: Brazil	Moist old-growth forest	153	Rice *et al.* (2004) Malhi *et al.* (2006) Pyle *et al.* (2008)
Caxiuanã: Brazil	Moist old-growth forest	201	Malhi *et al.* (2006)
Tambopata: Peru	Lowland Amazonian forest	124	Girardin *et al.* (2010)
Nouragues: French Guiana	Lowland wet forest	149	Chave *et al.* (2001)
Estimated mean (± standard error)		**158 ± 12**	

Despite this importance, however, accurate estimates and understanding of root dynamics remain a controversial problem beset by methodological uncertainties and analytical difficulties (Vogt *et al*., 1986a; Nadelhoffer and Raich, 1992; Vogt *et al*., 1998; Hanson *et al*., 2000; Norby and Jackson, 2000; Hendricks *et al*., 2006). Vogt *et al*. (1998) argued that there is no single best method to quantify root biomass, unless these various methods can derive comparable estimates to total carbon budgets in a system. Confounded by these issues, the interaction of root dynamics with global climate change, plant physiology, and below-ground production remains poorly understood (Norby and Jackson, 2000).

Root biomass mainly consists of coarse and fine roots. Large coarse roots are suggested to contribute to biomass increment owing to their slow turnover, while fine roots contribute to biomass loss due to their rapid turnover in forest ecosystems (Vogt *et al*., 1986b; Aerts *et al*., 1992; Gill and Jackson, 2000; Clark *et al*., 2001a). There are only a few studies that focus on structural coarse roots (Hozumi *et al*., 1969; Kenzo *et al*., 2009; Niiyama *et al*., 2010) and fine roots (Yoda, 1978; Yamashita *et al*., 2003; Green *et al*., 2005) in Southeast Asian tropical forests. Based upon a global review across tropical sites in Asia, the allocation of NPP to fine roots is relatively low but with higher allocation of woody tissue (Malhi *et al*., 2011). Fine roots have been found to make up more than 50% of total carbon in the upper 10 cm (Silver *et al*., 2000; Telles *et al*., 2003). The dynamics of roots are controlled by the soil environment (Pregitzer *et al*., 1993; Eissenstat *et al*., 2000; Pregitzer *et al*., 2000; Green *et al*., 2005) and above- and below-ground substrates (Hogberg *et al*., 2001; Pregitzer, 2003; Hendricks *et al*., 2006). Fine roots are particularly difficult to measure due to temporal and spatial variability including the prevailing environmental conditions, with the result being that any such measurements necessarily include a large degree of uncertainty (Hendrick and Pregitzer, 1993; Carvalheiro and Nepstad, 1996; Silver *et al*., 2000; Silver *et al*., 2005). In addition, the uncertainty in distinguishing live from dead fine roots is one of the other difficulties in assessing the dynamics of fine roots (Clark *et al*., 2001a).

The complexity of below-ground carbon cycling has emerged as a central obstacle to accurately model ecosystem carbon cycling and its response to environmental change (Raich and Nadelhoffer, 1989; Vogt *et al*., 1996; Hanson *et al*., 2000; Clark *et al*., 2001b). Hence, this D.Phil. study aims to examine the contribution of below-ground components to total NPP and its response to environmental factors.

1.2.6. Respiration Rates

Total respiration over an ecosystem (R_{Total}) is the sum of two large fluxes: the R_{a} and heterotrophic respiration (R_{h}). The components of R_{a} include leaf, wood (stem, branches, and coarse woody debris), and root (coarse and fine root), while R_{h} mainly involves below-ground components from litter, soil organic matter, and microbial decomposition. It is widely recognised that plants respire approximately 50% of the net carbon taken up by photosynthesis or GPP (DeLucia *et al*., 2007; Van Oijen *et al*., 2010). In addition, R_{h} has been estimated at 8.77 ± 0.96 Mg C $\mathrm{ha^{-1}\ yr^{-1}}$ across tropical biomes. These large fluxes of respiration are equally important to photosynthesis in determining the carbon balance in an ecosystem. However, accurately quantifying the components of respiration and scaling these fluxes over a large area is challenging. Over an ecosystem, the balance between GPP and R_{Total} is the net ecosystem productivity (NEP) and is given as:

$$\mathrm{NEP} = \mathrm{GPP} - R_{\mathrm{Total}} \qquad \text{(Eq. 1.3)}$$

Attempts to quantify NEP are increasingly important because it determines the potential of carbon sinks and sources of an ecosystem. Chambers et al. (2004) indicated that even a small NEP flux scaled over large areas may significantly increase the global accumulative sink. Although there is a growing interest in evaluating R_{Total} in tropical forests (Chambers *et al*., 2004; Cavaleri *et al*., 2008; Metcalfe *et al*., 2010; Tan *et al*., 2010), the quantifying and scaling of the components of respiration in regard to the ecosystem level remains at the early stages compared to its global importance.

1.2.7. Soil Respiration

Soil respiration is the second largest terrestrial carbon flux (Schlesinger, 1977; Raich and Schlesinger, 1992; Raich and Potter, 1995; Luo and Zhou, 2006), and typically contributes 30% to 80% of annual total ecosystem respiration (Janssens *et al*., 2001; Xu and Qi, 2001; Yuste *et al*., 2005; Davidson *et al*., 2006). Soil releases approximately 75–100 Pg of C (Schlesinger, 1977; Raich and Potter, 1995; Raich *et al*., 2002; Bond-Lamberty and Thomson, 2010), which is approximately 10% of annual atmospheric CO_2 cycling through the soil (Reichstein and Beer, 2008). By comparison, this large annual fraction of soil respiration is an order of magnitude larger than anthropogenic fossil fuels combustion (Boden *et al*., 2010). In addition, approximately 30% of the total global forest ecosystem respiration comes from tropical and sub-tropical evergreen broad-leaved forests (Raich *et al*., 2002).

In general, tropical moist forests have the highest recorded mean soil respiration of 12.6 Mg C ha^{-1} yr^{-1} across vegetation types as reviewed by Raich and Schlesinger (1992). A large number of soil respiration studies have been reported across the tropics (Table 1.3). In the Southeast Asian region, earlier studies based on the conventional method estimated mean annual soil respiration as being 14–16 Mg C ha^{-1} yr^{-1} in Khao Chong forest, Thailand and the Pasoh Forest Reserve, Malaysia (Yoda and Kira, 1969; Ogawa, 1978).

Table 1.3: Soil respiration in Southeast Asian tropical forests and several study sites in the Amazonian tropical forest

Site	**Soil**	**Method**	**Soil respiration ($\mathrm{Mg\ C\ ha^{-1}\ yr^{-1}}$)**	**Source**
Southeast Asia				
Khao Chong, Thailand	Sandy	Absorption	16.1	Yoda and Kira (1969)
Pasoh, Peninsular Malaysia	Sandy	Absorption	16.0	Ogawa (1978)
Gunung Mulu, Borneo	Clay-rich	Absorption	5.8	Anderson *et al*. (1983)
Bako, Borneo	Sandy loam	Absorption	5.3	Wanner (1970)
Tjibodas, Java, Indonesia	Montane	Absorption	4.0	Wanner (1970)
Lambir, Borneo	Clay to sandy loam	IRGA	22.7	Katayama *et al*. (2009)
Lambir, Borneo	Clay to sandy loam	IRGA	20.1	Ohashi *et al*. (2007)
Lambir, Borneo	Clay to sandy loam	IRGA	19.9	Ohashi *et al*. (2008)
Pasoh, Peninsular Malaysia	Clay-rich	IRGA	18.4	Adachi *et al*. (2005)
Pasoh, Peninsular Malaysia	Clay-rich	IRGA	19.9	Adachi *et al*. (2006)
Nam Phrom, Thailand	Clay to sandy	Absorption	15.0	Tulaphitak *et al*. (1983)
Kog-Ma, Chiang-Mai, Thailand	Sandy loam	IRGA	25.6	Hashimoto *et al*. (2004)
Pasir Mayang, Sumatra, Indonesia	Clay-rich	IRGA	13.4	Ishizuka *et al*. (2005)
Pasoh, Peninsular Malaysia	Clay-rich	IRGA	14.8	Kosugi *et al*. (2007)
Sabah, Borneo	Clay-rich	IRGA	23.1	Saner *et al*. (2009)
Estimated mean (± standard error)			**15.9 ± 1.7**	
Amazonia				
Manaus, Brazil	Clay-rich	IRGA	18.9	Chambers et al. (2004) Sotta et al. (2004)
Caxiuanã, Brazil	Clay-rich	IRGA	13.1	Sotta et al. (2004) Sotta et al. (2006) Metcalfe et al. (2007)
Tapajós, Brazil	Clay-rich	IRGA	11.9	Sotta *et al*. (2006) Metcalfe *et al*. (2007)
Paragominas, Brazil	Clay-rich	Model	24.0	Davidson and Trumbore (1995) Trumbore *et al*. (1995)
Paragominas, Brazil	Clay-rich	IRGA	20.0	Davidson *et al*. (2000)
Estimated mean (± standard error)			**17.6 ± 2.2**	

NB: Absorption, alkali absorption chamber method places static alkali solution within chamber followed by titration of chloric acid; IRGA, infrared gas analysers using dynamic chamber method that allows air to circulate between the chamber and sensor to measure CO_2 concentration in the chamber over time; Model, aggregated model based on estimated gas diffusivity and volumetric water content

A relatively lower level of soil respiration of 4–7 Mg C ha^{-1} yr^{-1} was found across contrasting tropical forests in Borneo (Wanner, 1970; Anderson *et al*., 1983). However, recent measurements, using the IRGA measurement method, have found relatively higher soil respiration between 20 and 23 Mg C ha^{-1} yr^{-1}, which has been attributed to TBCA and forest structure (Katayama *et al*., 2009), difference in measurement techniques (Davidson *et al*., 2000; Ohashi *et al*., 2008), spatial variation (Nakayama, 1990; Hashimoto *et al*., 2007; Kosugi *et al*., 2007; Ohashi *et al*., 2008), the canopy gap (Adachi *et al*., 2006; Saner *et al*., 2009), and the effects of hot spots (Ohashi *et al*., 2007) in addition to environmental drivers. For comparison, recent estimates of mean annual soil respiration reported from several sites in Amazonian forests were in the range of 12 to 19 Mg C ha^{-1} yr^{-1} (Chambers *et al*., 2004; Sotta *et al*., 2004; Silver *et al*., 2005; Sotta *et al*., 2006; Metcalfe *et al*., 2007), with several notable exceptions of higher soil respiration between 25 and 30 Mg C ha^{-1} yr^{-1} (Trumbore *et al*., 1995; Sotta *et al*., 2004; Valentini *et al*., 2008).

Soil respiration is generally measured manually and typically during daytime. Daytime manual soil respiration measurements omit significant variations in biophysical parameters (e.g. temperature, soil moisture, precipitation, and photosynthesis), and assume that the magnitude of soil CO_2 efflux is consistent over a diurnal cycle. Hence, the estimation of long-term soil carbon dynamics may be constrained. Several studies have investigated the diurnal cycle of soil respiration in tropical forest regions (Meir *et al*., 1996; Kiese and Butterbach-Bahl, 2002; Sotta *et al*., 2004; Ohashi *et al*., 2008; Zanchi *et al*., 2009; Zimmermann *et al*., 2009), but none have captured long-term measurements or paid attention to the diurnal variation of soil components. The variation of soil respiration over the diurnal cycle can be substantial and has shown a distinctive response to environmental drivers (Vargas and Allen, 2008; Zanchi *et al*., 2009; Zimmermann *et al*., 2009) and photosynthesis in forest ecosystems (Tang *et al*., 2005; Vargas *et al*., 2011).

Thus, elucidating the relative magnitude of diurnal soil respiration and its underlying soil components, as well as exploring their diurnal response to abiotic and biotic factors, is crucial to further our understanding of the contribution of soil respiration.

Soil respiration is sensitive to environmental drivers – mainly temperature and moisture. On a global scale, soil respiration is positively correlated to temperature (Raich and Schlesinger, 1992; Raich *et al*., 2002; Reichstein *et al*., 2003; Bond-Lamberty and Thomson, 2010). Comprehensive reviews suggest that soil respiration often increases exponentially with temperature (Singh and Gupta, 1977; Lloyd and Taylor, 1994; Kätterer *et al*., 1998). However, the relationship does vary across different sites (Raich and Schlesinger, 1992) and may not always be evident (Davidson *et al*., 1998; Sotta *et al*., 2004). Several studies have found no clear relation between soil respiration and temperature (Valentini *et al*., 2000; Janssens *et al*., 2001; Adachi *et al*., 2006; Metcalfe *et al*., 2007; Katayama *et al*., 2009). In fact, the relationship may be confounded by other coordinated variables including plant and microbial metabolism (Malhi *et al*., 1998; Reichstein *et al*., 2003; Schwendenmann *et al*., 2003). Thus, soil temperature may not be the only factor that explains variation in soil respiration. The variability of temperature sensitivity (Q_{10}) is a critical environmental factor when seeking to understand the response of soil respiration to elevated temperature and global warming (Jenkinson *et al*., 1991; Schimel *et al*., 1994).

In tropical regions, soil respiration strongly depends on soil water content and typically shows a strong seasonal pattern, but the effects have been relatively variable. Studies in tropical forests on relations between soil water content and soil respiration have shown a parabolic response (Schwendenmann *et al*., 2003; Sotta *et al*., 2004; Sotta *et al*., 2006), and a negative linear relationship (Davidson *et al*., 2000; Chambers *et al*., 2004; Adachi *et al*., 2005; Kosugi *et al*., 2007). A recent study in a tropical seasonal forest has shown that seasonal and spatial variations of soil respiration are strongly correlated to soil water content (Hashimoto *et al*., 2007; Takahashi *et al*., 2011). Rewetting of dry soils considerably increased the rate of soil respiration (Davidson *et al*., 2000; Schwendenmann *et al*., 2003; Hashimoto *et al*., 2004; Sotta *et al*., 2004). However, a considerable amount of water as a result of heavy rain can inhibit CO_2 gas diffusion and significantly reduce R_s due to water-filled pores within the soil (Schwendenmann *et al*., 2003; Sotta *et al*., 2004; Takahashi *et al*., 2011). A previous study in Lambir showed that soil water content strongly explained the seasonal variation of soil respiration at deeper soil depths between 30 and 60 cm (Ohashi *et al*. 2008).

1.2.7.1. Partitioning Soil Respiration

Soil respiration is the sum of major soil components, which are mainly litter, root, mycorrhizae, and soil organic matter (SOM). The partitioning of soil respiration defines these components broadly into two groups: autotrophic and heterotrophic respiration. Establishing the long-term contribution of soil respiration from each soil component is essential in order to better understand the underlying mechanisms contributing to total soil respiration. Additionally, their responses to environmental drivers may have profound implications for soil and ecosystem carbon cycling.

Evaluating these soil components separately is complex and difficult without disrupting the structure and texture of the soil. In addition, the dynamics of below-ground processes are driven by substrate inputs mediated through the abiotic and biotic factors, which include above-ground plants, photosynthesis, decomposition, and root exudation in the soil. As such, there is a growing interest in determining the effects of soil priming attributed to above- and below-ground inputs in the soil. However, the effect of soil priming is understudied and poorly understood (Kuzyakov, 2006; Subke *et al*., 2006; Kuzyakov, 2010; Kuzyakov, 2011).

Over the years, growing interest in the partitioning of soil respiration has resulted in numerous methods and techniques being used to separate soil components. Although considerable advances are showing good agreement among various soil partitioning approaches, estimated results are still interpreted in the light of assumptions and methodological caveats (Hanson *et al*., 2000; Kuzyakov, 2006; Subke *et al*., 2006). Furthermore, soil partitioning studies are rare in tropical forests. The following methods have been employed in tropical forests to partition soil components contributing to total soil respiration: 1) root exclusion/trenching (Li *et al*., 2004; Silver *et al*., 2005; Li *et al*., 2006; Chemidlin Prévost-Bouré *et al*., 2009; Sayer and Tanner, 2010; Takahashi *et al*., 2011); 2) component integration (Edwards and Harris, 1977; Davidson *et al*., 2002b; Metcalfe *et al*., 2007); 3) litter manipulation (Sayer *et al*., 2007; Zimmermann *et al*., 2009; Sayer *et al*., 2011); 4) isotopic labelling (Giardina *et al*., 2004); 5) mass balance (Nakane, 1980; Trumbore *et al*., 1995); and 6) root regression (Behera *et al*., 1990; Subke *et al*., 2006).

The component-integration method, which will be employed and discussed in chapters 2 and 3, separates and measures each soil component that contributes to total soil respiration (litter, root, mycorrhizae, and SOM). However, although several recent advances have shown plausible estimates, disturbances to the soil profiles may considerably affect the respiration rate (Metcalfe *et al*., 2007; Fenn *et al*., 2010; Girardin *et al*., 2010; Nottingham *et al*., 2010).

1.2.8. Comparing Productivity and Soil Respiration between Tropical Forests in Southeast Asian and Amazonian Region

The tropical forests in Asia amount to only approximately 50% of the total forest carbon stock that there is in tropical America (Saatchi *et al*., 2011b; Baccini *et al*., 2012). In spite of this, the living biomass of trees in tropical Asia, particularly in Southeast Asia, contains a greater carbon density than in the tropical Amazon (Gibbs *et al*., 2007). Based on previously published data, the mean above-ground carbon stock across various vegetation types in Southeast Asia is approximately 36 ± 11% higher than the forests in Amazon (Table 1.4). This may be explained by the rate of biomass production for plants. However, the total NPP estimated from the available data (Table 1.1) in the tropical forests of Southeast Asia region is identical to the forests in Amazon (Table 1.4).

Table 1.4: Mean (± standard error) carbon stock, productivity and soil respiration for tropical forests in Southeast Asia and the Amazon.

	Southeast Asia	**Amazon**
Above-ground carbon stock Mg C ha^{-1}	215 ± 12	158 ± 12
Total net primary productivity (NPP) Mg C ha^{-1} yr^{-1}	10.7 ± 0.5	10.5 ± 0.2
Soil respiration Mg C ha^{-1} yr^{-1}	15.9 ± 1.7	17.6 ± 2.2

NB: Estimates are based on data presented in Table 1.1, Table 1.2, and Table 1.3.

The lack of data and the inconsistency in the methods employed to determine total NPP for tropical forests in Southeast Asia makes this estimated NPP tentative. Using an extensive dataset compiled from soil respiration studies comparing tropical forests in Southeast Asia and the Amazon, this large below-ground flux is much the same. The production and respiration terms essentially contribute to the understanding of the carbon budget and carbon cycling between these two contrasting tropical forest regions. Therefore, it is imperative to quantify these terms with greater consistency and accuracy over time, which has been a main focus during the course of my D.Phil. study.

1.3. Overview of Thesis

The ultimate aim of this thesis is to develop a comprehensive carbon budget and explore the relationship among environmental drivers, carbon allocation and the partitioning of soil respiration across two contrasting soil types in a Bornean lowland dipterocarp forest. To achieve this, measurements were employed in order to quantify the carbon allocation, fluxes and related environmental drivers to answer the research questions that make up the core of this thesis. Hence, this thesis consists of four independently linked chapters (Chapters 3–6), which have been prepared and to be submitted as scientific articles to peer-reviewed journals (Table 1.5). These chapters are bookended by the present background and introduction to the study (Chapter 1), the literature review and general explanation of field methodology (Chapter 2), and a discussion (Chapter 7). Here, I present an overview of chapter 3–6 to explain the aim of each article and its objectives.

Table 1.5: Publication status of chapters

Chapter	Status	Journal
3	Ready for submission	*Soil Biology and Biochemistry*
4	Ready for submission	*Forest Ecology and Management*
5	Ready for submission	*Journal of Ecology*
6	Ready for submission	*Global Change Biology*

Chapter 3: Diurnal Variation of Soil CO_2 Efflux in a Bornean Lowland Dipterocarp Forest

This is a novel study that explores the diurnal variation of soil CO_2 efflux and its components, including flux from litter, roots, soil organic matter and mycorrhizae. In addition, this study seeks to understand which of the soil components and environmental factors contribute to and drive the diurnal patterns.

Key research questions:

a) What is the diurnal variation of total soil CO_2 efflux?

b) What is the diurnal variation of CO_2 efflux from litter, root, soil organic matter, and mycorrhizae, and their relative contribution to total soil CO_2 efflux?

c) What is the relationship of total soil CO_2 efflux and its soil components to daily variation in environmental factors such as soil temperature, soil moisture, rainfall, ambient air temperature, relative humidity, and solar radiation?

Chapter 4: Magnitude and Seasonal Variation of Soil CO_2 Efflux in a Bornean Lowland Dipterocarp Forest

To provide a comparison with the diurnal variation of soil CO_2 efflux (Chapter 3), this chapter explores the magnitude and seasonal variation of soil CO_2 efflux based on typically manual measurements conducted during daytime from two contrasting soil types (clay and sandy loam). This article presents a detailed soil partitioning approach using a Detritus Input and Removal Treatment (DIRT) experiment. The relationships with environmental factors such as soil moisture, soil temperature, and air ambient temperature are explored.

Key research questions:

a) What is the mean annual soil CO_2 efflux, and which environmental factors control its temporal variation?
b) How is total soil CO_2 efflux partitioned into soil component fluxes from litter respiration, SOM respiration, root and mycorrhizae respiration, and how do these components respond seasonally and to environmental factors?

c) Are there any significant differences in soil CO_2 efflux and its partitioning between the contrasting soil types of clay and sandy loam soils?

Chapter 5: Annual Budget and Seasonal Variation of Above- and Below-ground Net Primary Productivity in a Lowland Dipterocarp Forest in Borneo

This article quantifies above-and below-ground NPP, exploring the seasonal variation on clay and sandy loam sites. This is the first attempt to describe the seasonal variation of NPP and its components in relation to a lowland Asian tropical forest. This article presents important insights into how productivity in a lowland dipterocarp forest differs from that in tropical forests elsewhere.

Key research questions:

a) What is the above- and below-ground NPP, and how is it partitioned into woody material, leaves, reproductive materials, fine roots and coarse roots in a lowland dipterocarp forest in Borneo?

b) What is the seasonal variation in the components of above- and below-ground NPP, and how are these related to environmental factors?

c) What is the overall allocation of NPP at this site, and how does it very between clay and sandy loam sites?

Chapter 6: Comprehensive Assessment of the Carbon Budget of a Bornean Lowland Dipterocarp Forest

Finally, this article synthesises a comprehensive carbon budget for a lowland dipterocarp forest. This chapter brings together results from the preceding chapters in order to estimate total NPP, GPP and carbon use efficiency in a lowland dipterocarp forest. The results are compared with recent data from Amazonian forests.

Key research questions:

a) What is the overall allocation of NPP components and respiration rates (autotrophic and heterotrophic) in a lowland dipterocarp forest, and how does it vary between clay and sandy loam sites?

b) What is the total budget of carbon productivity, carbon use efficiency (CUE), and GPP in Lambir, and how do these budgets differ between sites and tropical forests elsewhere?

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CHAPTER 2

Chapter 2: Site Description and Methods

2.1. Study Site

2.1.1. Lambir Hills National Park

Lambir Hills National Park (4^o 12’ N, 114^o 2’ E) was gazetted in 1975 as a totally protected area and serves as a reservoir of forest resources and biodiversity. Lambir is located approximately 30 km south of Miri Resort City in the state of Sarawak, the Malaysian part of the island of Borneo (Figure 2.1). Covering an area of 6,949 ha, Lambir is divided into two areas by the Pan-Borneo trunk road traversing the park. Approximately one-third of the area is isolated from the major portion of the park and has been under persistent pressure for development and agriculture. The topography of Lambir is hilly and the terrain is undulating with steep slopes. Approximately 85% of the total park area is dominated by slopes and the remaining area consists of ridges and valleys (Yamakura *et al*., 1995). The elevation in Lambir ranges from near sea level to the highest peak of rugged sandstone escarpment at 465 m in altitude (Watson, 1985; Yamakura *et al*., 1995). Lambir is geologically made up of Setap Shale formation, Sibuti formation, Lambir formation, and Tukau formation deposited during the Miocene period (Liechti *et al*., 1960).

2.1.2. Floristic Composition

Lambir hosts several forest types that include lowland mixed dipterocarp forest, patches of heath (kerangas) forest on the highest ridges, and small patches of swampy forests associated with streams. The lowland mixed dipterocarp forest has been widely studied and has the most diverse collection of tree species recorded in the Paleotropics (Ashton and Hall, 1992; Phillips *et al*., 1994; Davies and Becker, 1996; Lee *et al*., 2002), with approximately 1,200 tree species recorded in a 52 hectare forest dynamics plot (Condit

2000; Davies *et al*. 2005). The Euphorbiaceae and Dipterocarpaceae are the most species-rich families and approximately 87 species of the Dipterocarpaceae family have been recorded in the plot (Lee *et al*., 2002). A comprehensive floristic composition and stand structure has been described by Lee *et al*. (2002).

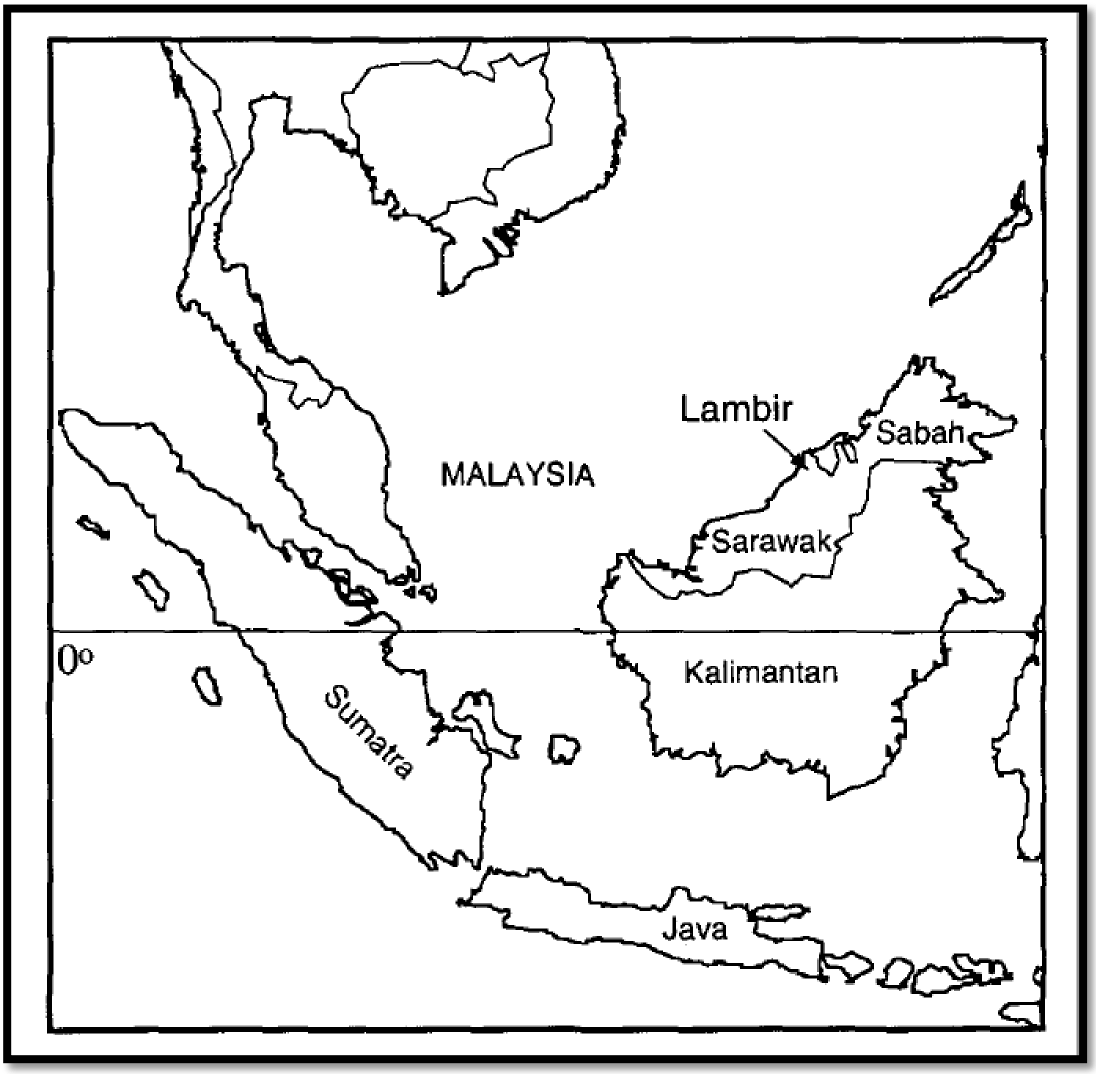

Figure 2.1: A map of Southeast Asia showing the location of the Lambir Hills National Park (after Lee *et al*., 2004).

The lowland dipterocarp forests of Lambir are tall in stature and complex in architecture, with trees between 40 – 60 m tall, a heterogeneous canopy and high stem turnover rates (Phillips *et al*., 1994). The basal area for trees ≥ 10 cm diameter at breast height (1.3 m DBH) is between 35 – 53 m^2 ha^{-1} (Phillips *et al*., 1994; Yamakura *et al*.,

1996) and the above-ground biomass is about 260 Mg C ha^{-1} (Yamakura *et al*. 1996; Chave *et al*. 2008). The rate of litterfall is consistent throughout the year and suggests little seasonal variation of leaf area index (LAI), with a mean estimated annual value of 6.2 m^{2} m^{-2} (Kumagai *et al*. 2004).

2.1.3. Soil

The soils in Lambir consist of red-yellow podzolic soils (Teng, 1996) or are classified as Acrisols (FAO, 2006) and udult Ultisols (Soil Survey Staff, 2006). Generally, they consist of high sand content (62–72%), a low pH (4.0–4.3) and high porosity (54–68%) (Ishizuka *et al*., 1998). The soils are mainly shale- and sandstone-derived and are from the Miocene-Pliocene Lambir Formation (Watson, 1985; Ishizuka *et al*., 1998; Baillie *et al*., 2006). Sandstone-derived soils (15% clay, 16% silt, and 68% sand) are humult Ultisols (Soil Survey Staff, 2006) and are densely matted with fine roots on the soil surface, have high sand content, are low in nutrients and low in water-holding capacity. The shale-derived soils, on the other hand, are clay-rich (typically 27% clay, 34% silt, and 40% sand) udult Ultisols (Soil Survey Staff, 2006), with a thin litter layer on the soil surface, and are relatively fertile and have higher water-holding capacity (Davies *et al*., 2005; Baillie *et al*., 2006; Tan *et al*., 2009). Humult Ultisols are mainly found on slopes and ridges and cover about 75% of the 52-ha plot, whilst the udult Ultisols are mostly on low-lying valleys and cover the remaining 25% (Davies *et al*., 1998). The soils and geomorphology of Lambir have previously been described in detail (Ishizuka *et al*., 1998; Baillie *et al*., 2006; Tan *et al*., 2009).

2.1.4. Climate

Lambir is an aseasonal lowland dipterocarp forest, with little seasonality in climate. The wet season associated with the northeastern monsoon is between September and January, while the drier period typically occurs between February and August. Lambir received approximately 2,630 mm of annual rainfall between 2000 and 2010 (recorded from an 80 m tall canopy crane approximately 3 km away from study plot), with an average monthly rainfall of more than 100 mm. Even during the drier period, mean monthly rainfall is more than 150 mm, which is well above the 100 mm mo^{-1} typically transpired from forest canopies (Fisher *et al.*, 2007). This indicates that Lambir may not experience water stress at any time of the year. However, Lambir experiences periodic severe droughts approximately once per decade (Walsh and Newbery, 1999; Malhi and Wright, 2004; Harrison, 2005). The mean annual temperature is approximately 27^{o}C with very little seasonality (Kumagai *et al.*, 2004).

2.1.5. Sampling Plot Design

The main experiment was carried out in a 52 hectare forest dynamics plot, which is part of the Center for Tropical Forest Science (CTFS) global network of large plots (Condit, 1995; Lee *et al.*, 2004). The 52-ha forest dynamics plot was established in 1992 (Yamakura *et al.*, 1995). All trees ≥ 1 cm in DBH were mapped, identified to species, and their DBH measured following standard methods (Condit, 1998). Censuses began in 1992 and were repeated every five years.

In the 52-ha plot, we established two one-hectare research plots (100 x 100 m), one each on clay (Line 5 – 9) and sandy loam (Line 42 – 46) soils (Figure 2.2). The one-hectare plot was further divided into 25 subplots measuring 20 x 20 m. These two contrasting soil types provide a direct comparison to several similar study sites established in the Amazonian forests (e.g. Chambers *et al*. 2004, Metcalfe *et al*. 2007, Aragão *et al*. 2009). The altitude difference between the highest and the lowest points is approximately 150 m, with steep slopes, undulating terrain and complex bisected topography (Yamakura *et al*., 1995).

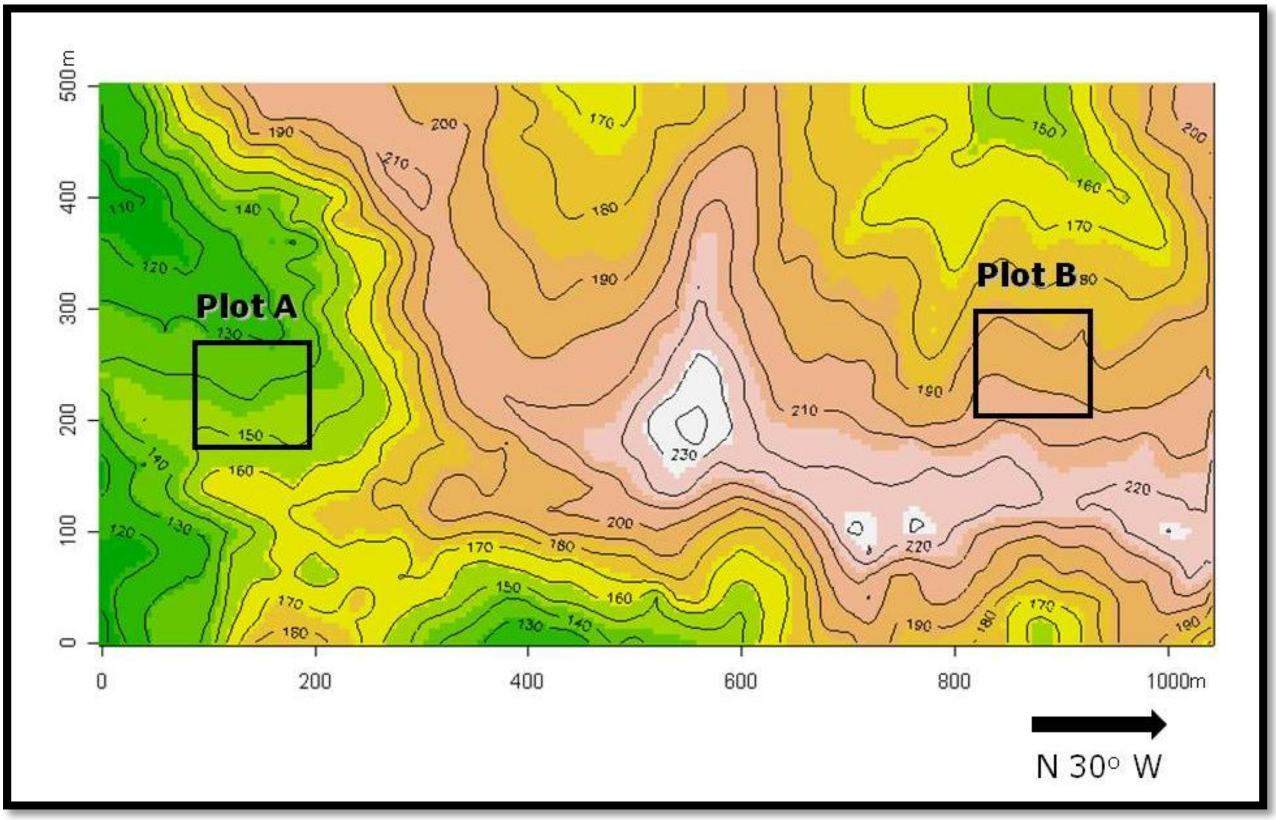

Figure 2.2: Topography map showing Plot A (clay) and Plot B (sandy loam) in the 52-ha plot in Lambir. The map is drawn at a scale of 1:20.

In addition, two smaller plots (20 x 20 m) were established on clay and sandy loam sites located outside of the 52-ha plot. These plots were established to monitor intensively the partitioning of soil respiration using the Detritus Input and Removal Treatment (DIRT) experimental plot (Sulzman *et al*., 2005; Nadelhoffer *et al*., 2006; Fekete *et al*., 2011). The clay and sandy loam sites were chosen so as to have soil types, species and elevation that were similar to and representative of the one-hectare plot. Analysis of soil characteristics was conducted on the clay soil prior to plot and treatment establishment, as described in Chapter 3. Each DIRT plot was divided into three subplots measuring 11 m x 5 m (T1, T2, and T3) as replicates, and then further divided into eight treatment plots measuring 2 m x 2 m (Figure 2.3; see section 2.2.5). The experimental design and treatment details are further discussed and illustrated in section 2.2.5 and in Chapter 4.

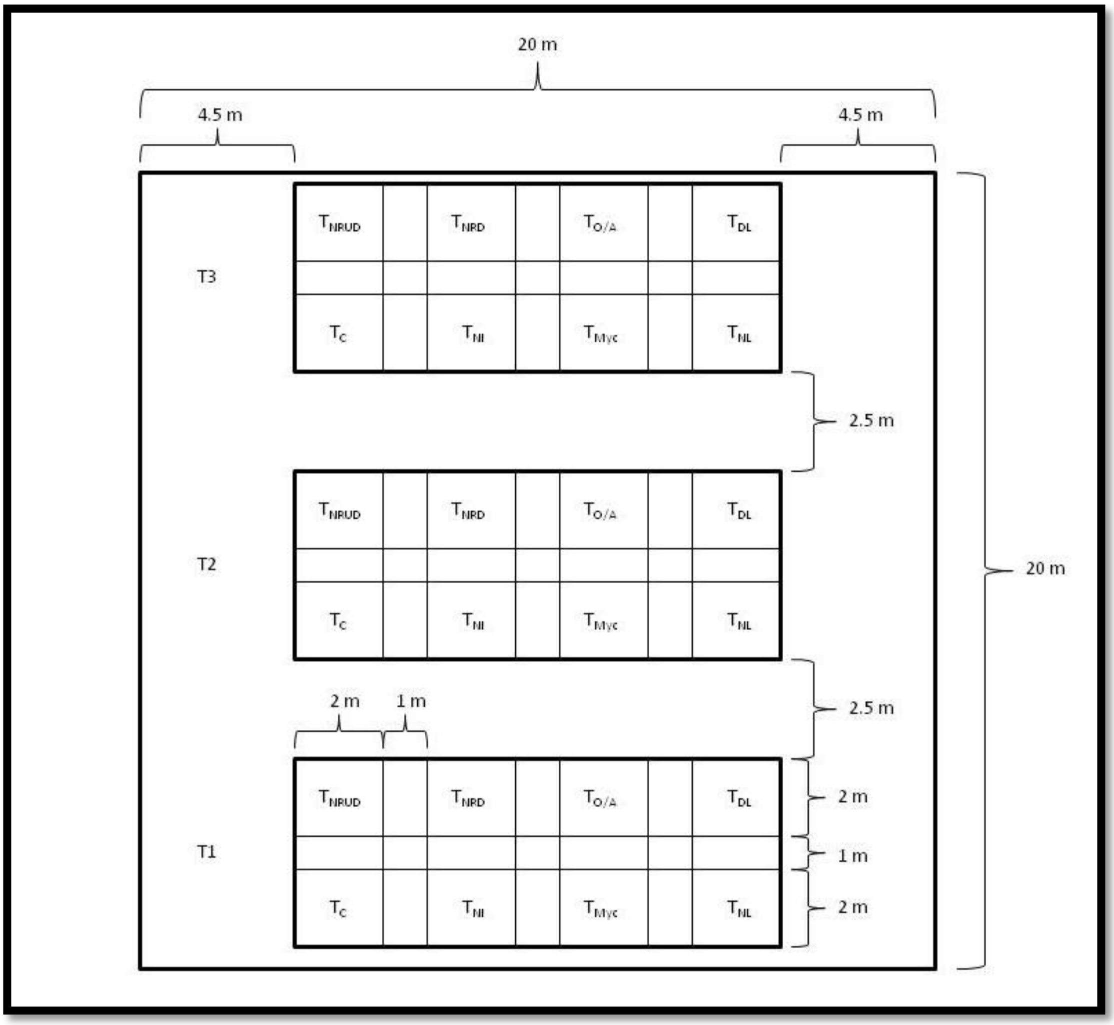

Figure 2.3: DIRT experimental plot with all treatments established on clay and sandy loam. The experimental design was adapted and modified from a similar experiment conducted in the Harvard Forest, USA (see Nadelhoffer *et al.*, 2006). Key: T_c, Control treatment; T_{NI}, No Input treatment; T_{Myc}, mycorrhizae treatment; T_{NL}, No Litter treatment; T_{DL}, Double Litter treatment; $T_{O/A}$, reduced O/A horizon treatment; T_{NRD}, No Root Disturbed treatment; T_{NRUD}, No Root Undisturbed treatment.

2.2. Measuring Biomass and Respiration

The sampling and measurement procedures were based on the protocols developed by the RAINFOR-GEM network, which are described in detail in a manual (available at http://gem.tropicalforests.ox.ac.uk/, Global Ecosystems Monitoring Network (GEM)).

2.2.1. Above-ground Biomass and Productivity

Multiple tree censuses from sandy loam and clay sites were used to determine above-ground woody biomass and production. All trees within the plots were identified to species by Lee *et al*. (2005). Using these tree censuses from both the one-hectare clay and sandy loam sites, the woody biomass and growth rate for all trees were determined using an allometric equation for moist tropical trees (Chave *et al*., 2005). A detailed description of the equation and calculation are provided in Chapter 5. Biomass values were converted by assuming that dry stem biomass has a carbon content of 47.4% (Martin and Thomas, 2011).

Dendrometer bands were installed (Figure 2.4a) on all trees (≥ 10 cm DBH) on both clay and sandy loam sites to capture seasonal variation in the above-ground coarse wood NPP. The dendrometers were installed in July 2008 on clay and sandy loam plots, but the first 10 and 3 months of data were not used to allow the dendrometers to settle onto the trees. Three-monthly increments from dendrometer bands were recorded from June 2009 to September 2010 (Figure 2.4b). In addition, 18 species of fast-growing trees (≥ 10 cm DBH) were randomly selected across each entire one hectare plot, and the monthly increments from dendrometer bands were recorded. Using these dendrometer data sets, monthly woody growth rates were estimated and scaled across all trees on clay and sandy loam sites. Chapter 5 further describes the methodology and the correction factor involved.

2.2.2. Litterfall NPP (*NPP*$_{\text{litterfall}}$)

Litterfall and dead woody material (< 2 cm diameter) was collected from litter traps (Figure 2.5a) measuring 0.25 m^2 (0.5 x 0.5 m). Collection began in July 2008 and continued until August 2009. Litterfall was collected every 14 days (Figure 2.5b), oven-dried at 80^{o}C to constant weight, and weighed immediately after removal from the oven. The litter was separated into: i) leaves; ii) branches (< 2 cm diameter); twigs and woody tissue; iii) fruits, flowers and seeds; and iv) undefined fine debris. Litterfall collection typically over one year or more in a steady state is approximately equivalent to canopy production, but excludes canopy herbivory and in-canopy decay or trapped leaves.

In addition, I combined the litterfall dataset with seasonal changes in LAI and mean values of specific leaf area (SLA) to determine the seasonal variation of leaf production (Doughty and Goulden, 2008). LAI was determined by recording monthly canopy hemispherical images from August 2009 to May 2010 using a digital camera (Nikon Coolpix 990) and a hemispherical lens (Nikon FC-E8 fisheye converter) (Figure 2.6a). Images (Figure 2.6b) were analysed with the CAN-EYE software (available at http://www4.paca.inra.fr/can-eye, Demarez *et al*., 2008; Weiss, 2012). The mean SLA was estimated by collecting nine samples of leaves per species (Figure 2.7a) from 11 specialist dominant tree species on sandy loam and five specialist dominant tree species on clay, as defined and categorised by Davies *et al*. (2005). Fresh leaf samples were scanned (Figure 2.7b), and oven-dried to constant mass. Leaf area was analysed using image analysis software (available at http://rsb.info.nih.gov/ij/index.html, ImageJ). SLA is fresh leaf area divided by dry mass of leaf. The methodology and analyses are further discussed in Chapter 5.

Figure 2.4: a) Dendrometer installed on tree, and b) measurement conducted using callipers.

Figure 2.5: a) Litter traps measuring 0.5 x 0.5 m, and b) two-weekly litterfall collection.

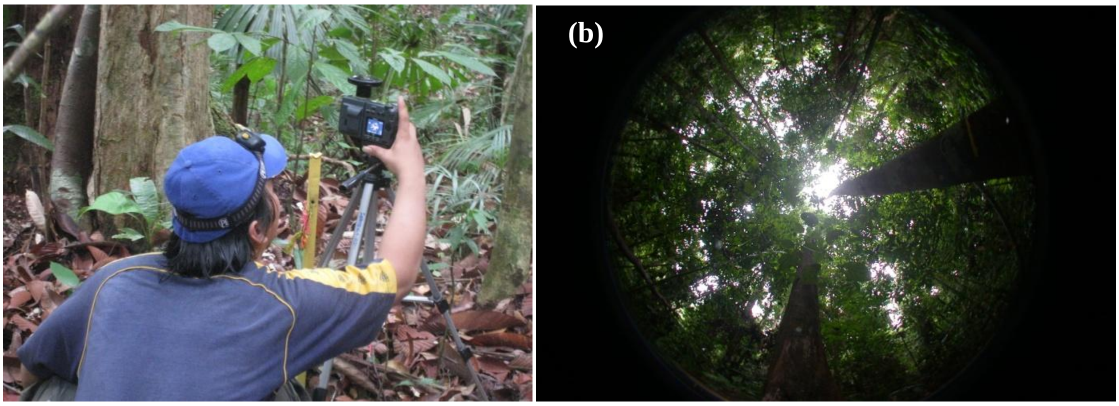

Figure 2.6: a) Recording images for LAI analysis by A. Deres and b) hemispherical image.

Figure 2.7: a) Leaves sampled using a slingshot by X. Tan and b) scanned to estimate SLA.

2.2.3. Branch Turnover NPP (*NPP*$_{\text{branch turnover}}$)

Four transects measuring 100 m x 1 m were established along the boundary in the one-hectare plot. Three-monthly censuses were conducted along the transects to collect fallen coarse woody materials (woody material > 2 cm diameter, including bark). Collections began in August 2009 and continued until July 2010. Branches that were easily lifted were cut to only include the transect-crossing component, removed and weighed directly. Heavier and larger branches that could not be removed were recorded for dimensions (diameter, height, and length), and were allocated a wood density value based on their decomposition stage. The state of decomposition was classified into four decomposition level woody materials: 1) intact and solid; 2) non-solid in poorer condition; 3) soft and rotten; and 4) very soft, rotten and easily collapse (Harmon *et al*. 1999). The samples were dried at 65^{o}C, weighed, and density calculated as dry mass divided by fresh volume. In subsequent censuses new branchfall materials were recorded.

2.2.4. Fine Root Biomass and NPP ($\boldsymbol{NPP_{\textbf{fine roots}}}$)

Fine root production was quantified using ingrowth cores following similar techniques to those successfully tested in the Amazonian forests (Metcalfe *et al*., 2007a; Metcalfe *et al*., 2007b; Metcalfe *et al*., 2008; Aragão *et al*., 2009; Girardin *et al*., 2010). The ingrowth cores were systematically installed in a 3 x 3 grid on clay and sandy loam sites in May 2008. Nine ingrowth cores made from mesh nets (mesh size: 1 cm^2) of 14 cm diameter and 40 cm height were installed to a depth of 30 cm from the soil surface in each site. The mesh nets were extracted every three months from September 2008 to October 2009. Roots were removed from the extracted soil cores manually by hand over a period of 40 minutes, which was split into 10 minutes time interval (Metcalfe *et al* 2007). Root-free soil was repacked into the mesh net and placed back into the soil. These cores were reinserted and compacted with care to replicate the natural soil conditions, horizon structure and bulk density as closely as possible. Although this approach introduced substantial disturbance to soil and roots, several studies yielded plausible outcomes with assumptions and cautions (Vogt *et al*., 1998; Hendricks *et al*., 2006; Metcalfe *et al*., 2007b; Girardin *et al*., 2010).

To estimate fine root mass, the cumulative increase in roots extracted to the first 40 minutes was used to fit a logarithmic curve which predicted root extraction rate up to 100 minutes (Metcalfe *et al*., 2007b). Fine root production was estimated as the total fine root ingrowth and scaled to a one-hectare area, with depth correction factor extrapolated up to 100 cm soil depth (Malhi *et al*., 2009). The prediction approach and depth correction is further explained in Chapter 5.

2.2.5. DIRT Experimental Plot

Soil respiration was partitioned based on treatments and manipulation established on the DIRT experimental plot. Treatments were established on 5 January 2009 on sandy loam and on 6 July 2009 on clay soil. Three PVC collars (measurement of soil collars detailed below) were installed at random points in each treatment. Figure 2.3 presents an illustration of the treatment plots established. The treatment plots established on each replicate are as follow:

1. Control (T_C): An undisturbed treatment plot with normal above-ground inputs of litterfall. Soil collars (11 cm diameter, 10 cm length) were randomly inserted to a depth of 2–5 cm from the soil surface. An additional soil collar (20 cm diameter, 11 cm length) was inserted to 4 cm depth in the soil surface for diurnal soil respiration measurement. Soil CO_2 efflux being measured represents R_s.
2. Double Litter (T_{DL}): An enriched plot with additional litter inputs from all the litter removed from the No Litter treatment (T_{NL}) and exposed to normal above-ground litter inputs thereafter. Soil collars (11 cm diameter, 10 cm length) were randomly inserted to a depth of 2–5 cm from the soil surface.

3. No Litter (T_{NL}): All existing litterfall and woody debris on the soil surface were cleared and transferred to the T_{DL} treatment plot. Subsequent above-ground inputs were excluded by using polyethylene netting. Soil collars (11 cm diameter, 11 cm length) were randomly inserted to a depth of 2–5 cm from the soil surface and covered by the netting. An additional soil collar (20 cm diameter, 11 cm length) was inserted to 4 cm depth from the soil surface for diurnal soil respiration measurement. Leaf litter and woody materials were cleared from the netting weekly to avoid any litter decomposition, which may contribute to soil respiration.

4. No Input (T_{NI}): Treatment was established with soil collars (11 cm diameter, 40 cm length) inserted to a depth of 30 cm into the soil surface to exclude ingrowth of roots and mycorrhizae. An additional soil collar (20 cm diameter, 11 cm length) was inserted to 4 cm depth from the soil surface for diurnal soil respiration measurement. All existing surface litter and roots were removed. Above-ground litter inputs were excluded using polyethylene netting, while ingrowth of roots and mycorrhizae were excluded within the soil collar.

5. Mycorrhizae (T_{Myc}): A treatment plot with three micromesh bags (36-µm pore diameter, Plastok Ltd, Birkenhead, UK) measuring 11 cm diameter and 40 cm length. Prior to installation, all existing surface litter was removed. Soil cores (11 cm diameter, 30 cm length) were carefully extracted and transferred into the micromesh bags, with minimum disturbance to the soil profile. The micromesh bags were filled with extracted soils and reinserted into the same location as the extracted soil columns. Soil collars (11 cm diameter, 10 cm length) were inserted to a depth of 2–5 cm into the mesh bags and tied with a rope to ensure a tight seal. For diurnal soil respiration measurement, fine mesh bag measuring 22 cm diameter and 20 cm length were used with soil collars (20 cm diameter, 11 cm length) inserted to 4 cm depth from the soil surface. The application of micromesh bags ensures ingrowth of mycorrhizal hyphae, but excludes ingrowth of roots (Smith and Read, 1997; Johnson *et al*., 2001; Heinemeyer *et al*., 2007; Moyano *et al*., 2007; Fenn *et al*., 2010; Nottingham *et al*., 2010).

6. No Root Undisturbed (T_{NRUD}): A treatment plot that excluded ingrowth of roots and mycorrhizal hyphae using soil collars of 11 cm diameter and 40 cm length. Soil collars were inserted at random locations to a depth of 30 cm in the soil to sever all roots and mycorhizal hyphae within the soil collars, while minimising disturbance

to the soil profile. Hence, initial soil respiration measurement may have included dead roots and hyphae in the soil. Aboveground litter inputs were included as normal. Results were not reported due to experimental failure.

7. No Root Disturbed (T_{NRD}): An additional treatment plot established as an alternative approach to exclude ingrowth of roots and mycorrhizal hyphae, with major disturbance to soil profile as a result of extraction of roots. Soil cores (11 cm diameter, 30 cm length) were extracted and all visible roots (fine and coarse) within the soil cores were removed. The resulting root-free soil was reinserted into the same location as the extracted soil column. Aboveground litterfall inputs were included as normal. Results were not reported due to experimental failure.

8. Reduced O/A Horizon ($T_{\mathrm{O/A}}$): A treatment plot constructed to remove all the existing organic layer of A- and O- horizon, but subsequently exposed to normal above-ground inputs thereafter. Soil collars (11 cm diameter, 10 cm length) were randomly inserted to a depth of 2–5 cm in the soil. Results were not reported due to experimental failure.

2.2.6. Soil Respiration

Two soil respiration measurement techniques were employed during the course of my D.Phil. study. First, soil respiration was measured using a portable Infra-Red Gas Analyser (IRGA) gas exchange system (EGM-4 and SRC-1 soil chamber, PP Systems, UK), with a custom-made adaptor to fit on soil collars (Figure 2.8). Measurement is based on a closed static chamber technique (Parkinson, 1981).

In the one-hectare plots on clay and sandy loam soils, 25 PVC plastic collars (11 cm diameter, 10 cm height) were inserted to 2–5 cm depth in the soil, ensuring a tight seal in the soil, with one each on a designated measurement point (microsite) near the centre of each subplot. The collars were installed two months prior to the initial measurement in October 2008, to minimise the effect of soil disturbance on soil respiration. Three repeated measurements were conducted on each microsite every month (typically between 08:00 h and 17:00 h) over two years between October 2008 and October 2010. Each measurement was obtained from soil collars for a maximum of 120 seconds. Soil flux was determined from the rate of CO_2 concentration increase within the closed chamber for a known period of time. A linear fit to the CO_2 concentration data proved to be adequate in all cases (typical $r^2 \geq 0.80$), with the first nine seconds of data removed due to the potential for initial disturbance associated with chamber placement on the collar. Subsequent concentration data were sometimes also removed, to a maximum of 43 seconds, if found to deviate from the linear fit.

Using the same IRGA instrument, soil respiration measurements were conducted at weekly and biweekly intervals for seven consecutive weeks and at monthly intervals thereafter in the DIRT experimental plot. Measurements began seven days after treatment installation on sandy loam (12 January 2009) and clay soil (13 July 2009), and were carried out between May 2009 and October 2010.

Together with soil respiration measurements, soil moisture, soil temperature and surface temperature were also recorded. Soil moisture was quantified down to 12 cm soil depth using a Hydrosense CS620 probe (Campbell Scientific, Australia). Air and soil temperature were recorded using a portable waterproof T-bar digital thermometer probe (Thermometers Direct, UK). Soil temperature was obtained to a depth of 10 cm in the soil, while the air temperature was recorded at < 100 cm above the soil surface.

In addition, I conducted a novel diurnal soil respiration measurement during the course of my D.Phil. study. The measurement was conducted using an automated soil CO_2

flux system (LI-8100, LI-COR Inc., Nebraska, USA), with four long-term chambers (8100-104, LI-COR, Nebraska, USA) in the DIRT experimental plot to continuously measure diurnal soil CO_2 efflux (Figure 2.9a). PVC soil collars (20 cm diameter, 11 cm length) were inserted to 4 cm depth from the soil surface on T_{C} and T_{NL}, and to 30 cm depth on the T_{NI} treatment plot. On the T_{Myc} treatment plot, similar mesh bags (36-µm pore size) of 22 cm diameter and 20 cm length (Plastok Ltd, Birkenhead, UK), filled with extracted soils, were inserted to a depth of 30 cm from the soil surface. A soil collar (20 cm diameter, 11 cm diameter) was inserted to 4 cm depth onto the mesh bags. The four long-term chambers (one for each treatment) were placed onto the designated PVC soil collars (Figure 2.9b) on the first subplot (T1), and remained in position for one week before being rotated into the second (T2) and third (T3) subplots for one week each. Within each subplot, sequential measurements rotated once every 210 seconds automatically and continuously across four treatments (T_{C}, T_{NL}, T_{NI}, and T_{Myc}) for seven days. For each treatment, soil CO_2 efflux was measured for 120 seconds. The article presented in Chapter 3 further describes the measurement procedures and provides explanation on the data analysis.

2.2.7. Partitioning of Soil Respiration

Total soil respiration (R_{s}) was partitioned into major soil respiratory sources from root (R_{root}), SOM (R_{SOM}), litter (R_{litter}), and mycorrhizae (R_{myc}) with the following equation:

$$R_{\mathrm{s}} = R_{\mathrm{litter}} + R_{\mathrm{SOM}} + R_{\mathrm{root}} + R_{\mathrm{myc}} \qquad \text{(Eq. 2.1)}$$

where each of these soil components can be estimated by taking the difference between treatments from the DIRT experimental plot using the following equations:

$$R_{\text{litter}} = T_{\text{DL}} - T_{\text{C}} \qquad \text{(Eq. 2.2)}$$

$$R_{\text{root}} = T_{\text{NL}} - T_{\text{Myc}} \qquad \text{(Eq. 2.3)}$$

$$R_{\text{myc}} = T_{\text{Myc}} - T_{\text{NI}} \qquad \text{(Eq. 2.4)}$$

$$R_{\text{SOM}} = T_{\text{NI}} \qquad \text{(Eq. 2.5)}$$

The measurements and assumptions associated with the partitioning of soil respiration are further discussed in chapters 3, 4, and 5, including data analysis.

2.2.8. Stem Respiration (R_{stem})

Stem respiration (R_{stem}) was measured using a similar portable IRGA system (EGM-4 and SRC-1 soil chamber, PP System, UK). A PVC collar measuring 11 cm diameter and of 10 cm length was sealed to each stem at 1.3 m above ground using a non-setting sealant (Figure 2.10). Collars were shaped according to the curve on the stem surface in order to provide a good seal to the stem area. Prior to installation, mosses and epiphytes were removed to provide an optimal surface area for sealing. Collar depth on each stem was recorded to estimate CO_2 efflux according to the designated volume. Field methods and equipment were adapted and modified following the RAINFOR-GEM protocol.

Measurements were conducted on the fixed collars for 18 randomly selected trees across one hectare, with DBH in the range of 13.7 to 150.7 cm on clay and 15.6 to 69.4 cm on sandy loam sites. Monthly CO_2 efflux was measured for 120 seconds on each tree during daytime (08:00 – 17:00 hours), with repetition if measurements were incomplete (< 14 seconds). Stem CO_2 efflux measurement began in September 2008 and continued until September 2009. Detailed measurements and scaling of fluxes to ecosystem-level are further discussed in Chapter 6.

Figure 2.8: Soil respiration measurement using the portable IRGA Gas Exchange System (EGM-4 and SRC-1, PP Systems, UK).

Figure 2.9: a) The LI-8100 automated soil flux system (LI-COR Inc., Nebraska, USA) and b) a long-term chamber (8100-104) in the DIRT experimental plot.

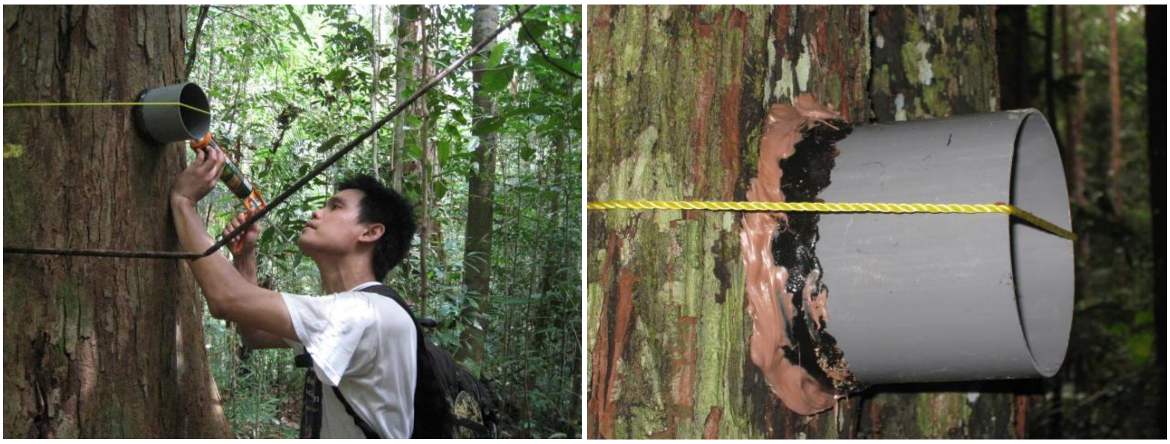

Figure 2.10: a) Sealing PVC collar to stem by LK Kho, and b) a stem collar installed

2.2.9. Validation of Measurement

The measurements as described above provided plausible methods to estimate the components of NPP and respiration. These estimates can be integrated following a bottom-up approach to quantify the comprehensive internal carbon cycle. In order to accurately estimate the C budget, these comprehensive measurements of carbon cycling were validated using two independent cross-checks. Firstly, it is assumed that the forest in Lambir is in a quasi-equilibrium condition on an annual timescale and that there is negligible inter-annual variability. Hence, the measured R_s can be validated with the following equation (see Malhi et al., 2009):

$$\text{Predicted } R_s = D_{\text{root}} + D_{\text{litterfall}} + (D_{\text{CWD}} + R_{\text{CWD}}) + R_{\text{rhizosphere}} \qquad \text{(Eq. 2.6)}$$

where D_{root} is given as root detritus for coarse and fine root NPP, $D_{\text{litterfall}}$ is given as canopy NPP, D_{CWD} is coarse woody debris detritus, R_{CWD} is coarse woody debris respiration, and $R_{\text{rhizosphere}}$ is fine roots respiration plus rhizomicrobial (including mycorrhizae and rhizodeposits). Using this approach, Malhi *et al*. (2009) found that the predicted R_s is in good agreement with the measured R_s.

The second validation method was to compare the estimated GPP from bottom-up approach measurements, as employed in my study, against those estimated from flux tower measurements (eddy covariance technique). This is necessary to test for consistency and accuracy between both the bottom-up and flux tower measurements (Luyssaert *et al*., 2009).

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Chapter 3

Chapter 3: Diurnal Variation of Soil CO_2 Efflux in a Bornean Lowland Dipterocarp Forest

Overview

Environmental factors (e.g. soil temperature, soil water content) vary temporally at different magnitudes and strongly influence variations in soil respiration. The fact that soil respiration is typically measured during daytime may mean we lack a complete understanding of its response over the diurnal cycle. This novel study presents the result from soil respiration measurement conducted over the diurnal cycle and compares it to the daytime soil respiration measurement presented in chapter 4. In addition, for the first time in a tropical forest, soil respiration is partitioned into litter, soil organic matter (SOM), roots and mycorrhizae, in order to elucidate the variation of these understudied components over 24 hours. This study partly presents the outcome of the soil respiration partitioning method employed.

Various collaborators[*] contributed to this study. The experimental design was first pioneered by Yadvinder Malhi, with contributing ideas from Luiz Aragão and Daniel Metcalfe. The meteorological data was contributed by Tomo'omi Kumagai and Tomonori Kume. Sylvester Tan provided the assistance in establishing the experimental plot and Mohd. Haniff Harun provided the instruments for measurements. The study overall (including this chapter) was supervised by Yadvinder Malhi.

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[*] Contribution Statement: experimental design: KLK, YM, LA, DM, ST; data gathering: KLK, ST; data analysis: KLK; interpretation of results: KLK,YM, LA, DM; author: KLK.

3.1. Abstract

Improved understanding of the second largest terrestrial carbon source – soil carbon dioxide (CO_2) efflux (R_s) – is essential for accurate prediction of atmospheric CO_2 levels in the future climate. However, the relative contributions of the different components of R_s and the environmental factors that regulate their diurnal variation are still poorly understood, particularly across the tropics. This study is the first attempt to explore the diurnal variation of CO_2 efflux from litter (R_{litter}), root (R_{root}), mycorrhizae (R_{myc}) and SOM (R_{SOM}) respiration. The intention is to determine their diurnal pattern and the effects from environmental drivers in a primary lowland tropical forest in Sarawak, Malaysian Borneo. The mean diurnal R_s was 9.36 ± 0.23 µmol CO_2 m^{-2} s^{-1} (mean ± standard error) measured from August 2009 to January 2010. Of this total, R_{litter} and R_{SOM} accounted for the vast majority, at about 40% and 45% respectively. Smaller but clearly discernible contributions from R_{root} and R_{myc} were detected, at around 2% and 13% of total R_s respectively. A notable feature of this study was that nighttime R_s was higher than daytime by 11%, due to nighttime enhancement of R_{litter}. Based on recent studies in Lambir, we found that the mean R_s would have been underestimated by 50% if based only on daytime measurements and not corrected for diurnal variation. Measurement of individual R_s components over the entire diurnal cycle provides novel information about the dynamic interactions between plants and soil in this critically understudied ecosystem, and highlights the major environmental drivers which will aid prediction of terrestrial carbon cycling in the face of future climate change.

3.2. Introduction

Soil CO_2 efflux (R_s) is the second largest component of the global terrestrial carbon flux (Schlesinger, 1977; Raich and Potter, 1995). Efflux of CO_2 from the forest floor surface contributes 30–80% of total ecosystem respiration in forests (Janssens *et al.*, 2001; Davidson *et al.*, 2006; Luo and Zhou, 2006), of which the largest percentage (~30% of total global forest ecosystem respiration) comes from tropical and subtropical evergreen broad-leaved forests (Raich *et al.*, 2002). The relatively higher magnitude of soil respiration in tropical forests suggests that tropical soil respiration is of global significance.

Total R_s is the combination of autotrophic respiration (root respiration) and heterotrophic respiration (soil microbes and fungi and meso- and macrofauna). The dynamics of heterotrophic components are ultimately driven by and mediated through biotic and abiotic factors such as temperature, water content, humidity, soil texture, photosynthesis, microbial community, autotrophic fungi, and aboveground substrate inputs (Hanson *et al.*, 2000; Kuzyakov, 2006; Luo and Zhou, 2006; Subke *et al.*, 2006). The relationship between R_s and soil temperature is often represented as an exponential function of temperature (Lloyd and Taylor, 1994; Rayment and Jarvis, 1997). However, it is unclear how widely applicable the exponential function between soil CO_2 efflux and temperature is in regard to describing the diurnal variation in R_s (Vargas and Allen, 2008a; Zimmermann *et al.*, 2009). In addition, studies have shown that the relationship between R_s and soil temperature is also significantly controlled by soil moisture in tropical forests (Davidson *et al.*, 2000; Schwendenmann *et al.*, 2003; Chambers *et al.*, 2004; Sotta *et al.*, 2004; Adachi *et al.*, 2006; Ohashi *et al.*, 2008). While extensive studies of the temperature sensitivity of R_s have been reported, the relationship is still confounded by several factors, mainly kinetic properties of soil organic compounds and environmental constraints (Davidson and Janssens, 2006; Bond-Lamberty and Thomson, 2010b; Subke and Bahn, 2010). Nevertheless, understanding the temperature dependency of R_s is important in terms of predicting potential feedbacks to climate change.

Soil CO_2 efflux has been extensively measured and estimated over various spatial and temporal scales in various forest ecosystems (Bond-Lamberty and Thomson, 2010a). Several studies have looked at the diurnal cycle of R_s in tropical forest regions (Meir *et al*., 1996; Kiese and Butterbach-Bahl, 2002; Sotta *et al*., 2004; Ohashi *et al*., 2008; Zanchi *et al*., 2009; Zimmermann *et al*., 2009), but none have yet demonstrated measurements over longer time scales and looked at the diurnal variation of fluxes in the components of R_s. The most common method of monitoring R_s is through manual measurements that are not conducted frequently enough to capture diurnal patterns. Furthermore, intermittent manual measurements omit significant variations in biophysical parameters (e.g. temperature, soil moisture, precipitation, photosynthesis), thus constraining estimations of long-term soil carbon dynamics (Vargas *et al*., 2010). In addition, infrequent manual measurements are based on the assumption that the magnitude of CO_2 efflux is consistent over a diurnal cycle; however, there can be substantial diurnal variation of soil CO_2 efflux (Xu and Qi, 2001; Luo and Zhou, 2006; Vargas *et al*., 2010). With these uncertainties, high time resolution measurements in tropical forest regions are imperative to determine accurate temporal (short- and long-term) CO_2 efflux from the soil, and to quantify ecosystem-scale fluxes.

The diurnal cycle of soil and litter respiration has only been investigated at one site; an Andean cloud forest by Zimmermann *et al*. (2009). To date, no studies have quantified the partitioning of R_s over a diurnal cycle time scale in a lowland tropical forest. For the first time in a lowland tropical forest, our study determines the diurnal patterns of R_s and its components (namely SOM, litter, roots and mycorrhizae) at a site in Sarawak, Malaysian Borneo. In addition, this study examines the influence of environmental factors that may drive the diurnal variation of R_s in a lowland tropical forest. The specific aims of this study are to:

1. Describe the diurnal variation of total soil respiration over time;
2. Quantify the diurnal variation of R_{litter}, R_{root}, R_{SOM}, and R_{myc} over time, and calculate their relative contribution to total R_s; and
3. Assess the sensitivity of R_s and other soil components to the daily variation of environmental factors such as soil temperature, soil moisture, rainfall, ambient air temperature, relative humidity, and solar radiation.

3.3. Materials and Methods

3.3.1. Study Site

Measurements were conducted in a stand of lowland mixed dipterocarp forest in Lambir Hills National Park (Lambir), Sarawak, Malaysia (4°12'N, 114°2'E). Lambir has the highest recorded tree diversity in the Paleotropics (Ashton and Hall, 1992; Davies and Becker, 1996; Ashton, 2005), with about 1,200 species recorded over a 52 hectare plot (Condit, 2000; Davies *et al.*, 2005). The forest in Lambir of various genera of the family Dipterocarpaceae, which covers approximately 85% of the total area. Comprehensive floristic and stand structure in Lambir plot have been described by Lee *et al*. (2002). Basal area recorded was between 35 and 53 m^2 ha^{-1} for trees ≥ 10 cm in diameter at breast height (1.3 m DBH) (Phillips *et al.*, 1994; Yamakura *et al.*, 1996) and above-ground biomass is around 520 Mg ha^{-1} (Yamakura *et al.*, 1996; Chave *et al.*, 2008). The rate of litterfall is consistent throughout the year and suggests little seasonal variation of leaf area index (LAI), which has a mean estimated annual value of 6.2 m^2 m^{-2} (Kumagai *et al.*, 2004).

Mean annual precipitation recorded in Lambir (from an 80 m canopy crane) for the period 2000–2010 was 2,630 mm. Precipitation has a strong seasonal variation, with drier months (177 mm mo^{-1}) between February and September and wetter months (300 mm mo^{-1}) between October and January. During the measurement period, there was a relatively stronger wet (January–March) and dry (April–December) season in 2009, followed by mass flowering and mast fruiting of dipterocarps (Figure 3.1). The mean annual temperature in Lambir over the years 2000 to 2009 was 25.8 ^{o}C with little seasonal variation.

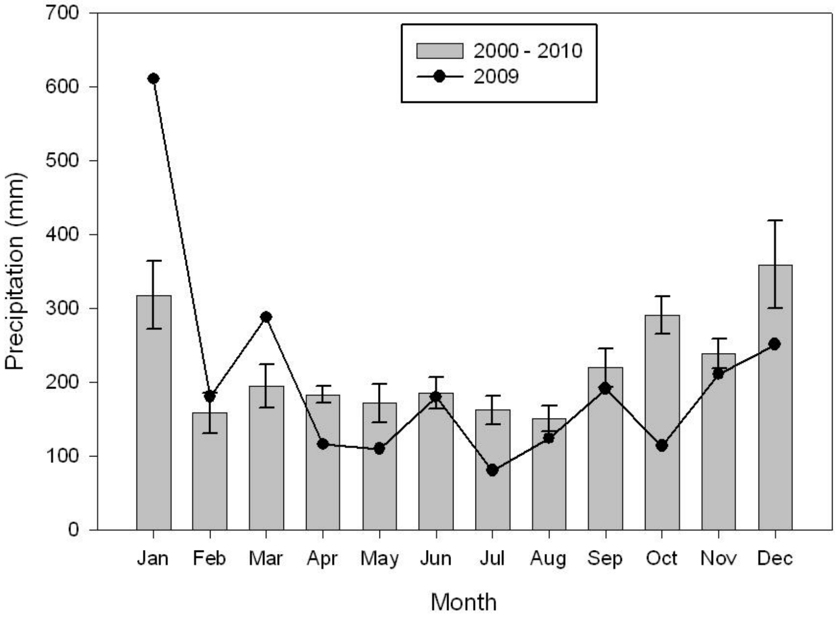

Figure 3.1: The mean monthly precipitation for the period 2000–2010 (column), and monthly precipitation for the year 2009 (line) in Lambir. Error bars indicate standard error.

The soils in Lambir are red-yellow podzolic soils in the Sarawak soil classification (Teng, 1996) or Acrisols (FAO soil taxonomy, FAO, 2006) and Ultisols (US soil taxonomy, Soil Survey Staff, 1999; Soil Survey Staff, 2006), derived mainly from shale and sandstone of the Miocene-Pliocene Lambir Formation (Watson, 1985; Ishizuka *et al.*, 1998; Baillie *et al.*, 2006). Sandstone-derived soils are humult Ultisols, with densely matted fine roots on the surface horizon, high sand content (typically 68% sand), low nutrients and low water-holding capacity. Shale-derived soils are clay-rich udult Ultisols (typically 40% sand), with a thin litter layer on the soil surface, relatively higher fertility and high water-holding capacity. Humult Ultisols are mainly found on slopes and ridges and cover about 75% of the 52-ha plot, whilst the udult Ultisols are mostly on low-lying valleys and cover about 25% (Davies *et al*., 1998). The soils and geomorphology in Lambir have previously been described in detail (Ishizuka *et al*., 1998; Baillie *et al*., 2006; Tan *et al*., 2009).

3.3.2. Experimental Design

A Detritus Input and Removal Treatment (DIRT) (Nadelhoffer *et al*., 2006; Toth *et al*., 2011) experimental plot (20 m x 20 m) was established on site with clay-rich haplic Acrisols/ udult Ultisols (28% clay, 31% silt, 41% sand) (Davies *et al*., 1998; Tan *et al*., 2009). A thin litter layer was present on the soil surface with an approximately 3.5 cm layer of litter and root mat. Soil organic carbon content was low, at less than 2%, and gradually decreased to less than 1% within 30 cm depth. Soil properties were determined at the study site and are illustrated in Table 3.1.

The DIRT plot was divided into three replicates (T1, T2, and T3) of 11 m x 5 m. The replicates and treatments were set apart with buffer zones of 2.5 m and 1 m respectively. In each replicate there were four treatment plots (2 x 2 m):

1. A Control (T_C) treatment, with R_s being measured (including the litter layer) in a PVC soil collar (20 cm diameter, 11 cm length), inserted to 4 cm depth into the soil surface.
2. A No Input (T_{NI}) treatment containing only SOM, which excluded aboveground litter input and ingrowth of roots, and mycorrhizae within 30 cm of the surface. All existing surface litter was removed, and roots were extracted. A soil collar (20 cm diameter, 40 cm length) was inserted to 30 cm depth from the soil surface.

3. A Mycorrhizal (T_{Myc}) treatment (all existing litter layer removed), enclosed by fine mesh bags (36-µm pores size) of 22 cm diameter and 20 cm length (Plastok Ltd, Birkenhead, UK) used to exclude roots but allow ingrowth of mycorrhizal hyphae (Smith and Read, 1997; Johnson *et al*., 2001; Johnson *et al*., 2002; Heinemeyer *et al*., 2007; Fenn *et al*., 2010; Nottingham *et al*., 2010), inserted to 30 cm depth from the soil surface. A soil collar (20 cm diameter, 11 cm length) was inserted to 4 cm depth onto the mesh bags.

4. A No Litter (T_{NL}) treatment (removed two days before measurement), with soil flux (without litter layer) being measured from a soil collar (20 cm diameter, 11 cm length), inserted to 4 cm depth into the soil surface.

The four treatment plots were uniformly established within the 20 x 20 m DIRT plot to accommodate for the distance to the power supply and to ensure that weekly rotation of chambers between replicates can be achieved. Given the long distance to the power supply and slightly undulating terrain within the sampling site, it was only possible to maintain the system in one position (middle of DIRT plot) and rotate the chambers weekly while maintaining little disturbance to the treatment. Replicates and treatments were confined within a small physical space, and thus provided a pseudo replicated experimental design.

Table 3.1: Soil properties on clay soils in the DIRT experimental plot, quantified by replicated sampling plots in a square of 0.5 x 0.5 m.

Soil Layer	Horizon	Depth (cm)	pH (H_2O)	Bulk Density (g cm^{-3})	C-stock (kg C m^{-2})	N (%)	Organic C (%)
Litter	L	3.5	6.2	-	1.09	0.76	20.0
Organic	O	3	4.4	0.7511	1.37	0.08	1.47
Humic	A	8	4.3	0.9044	1.65	0.07	0.83
Mineral	B1	10	4.8	0.9946	1.81	0.04	0.34
Mineral	B2	10	4.8	1.0102	1.83	0.03	0.29
Mineral	B3	10	4.9	1.0167	1.85	0.03	0.24

NB: Bulk density was determined using sampling cores of 76 mm diameter and 50 mm height. Soil samples were analysed at the Sarawak Agricultural Research Centre, Semonggok, Sarawak, Malaysia, for: pH (H_20); total organic carbon by dry combustion method at 600°C with a LECO RC-412 carbon determinator; and total N by dry combustion with a LEPO FP-528 nitrogen analyser (Chin, 2002)**.**

3.3.3. Soil CO_2 Efflux Measurement

Continuous R_s rates were measured with a Li-Cor 8100 automated closed chamber system (LI-COR Inc., Nebraska, USA), with four long-term chambers placed onto designated soil collars on the four treatment plots, which were established on 14 July 2009. Measurements started two days after installation (16 July 2009) and continued for six months until 24 January 2010. The four long-term chambers (one for each treatment) were placed onto PVC soil collars on one subplot, and remained in position for one week before being rotated into the second and third subplots for one week each (see weekly measurement routine in Supplementary Material Table S3.1). Within each subplot, sequential measurements rotated once every 210 seconds automatically and continuously across the four treatments (T_C then T_{NI} then T_{Myc} then T_{NL}) for seven days. For each treatment, soil CO_2 efflux rates were measured for 120 seconds and determined from the rate of linear CO_2 concentration increase within the closed chamber over the measurement period. Flux rates are calculated based on a linear best-fit equation using the LI-8100 File Viewer (2.0) software (LI-COR, Inc., Nebraska, USA). A linear fit to the concentration data was found adequate in all cases (typical r^2 = 0.90), with the first few seconds of data being removed if they deviated from a linear relationship. Measurement times were kept between 90 and 180 seconds in order to avoid errors in CO_2 flux estimates due to excessive build up in chamber CO_2 concentration. The long-term chamber automatically lifted away from the soil measurement point when a measurement was not in progress so as to allow free ventilation of the chamber and soil surface.

In addition, soil temperature and moisture were also recorded. Soil temperature was recorded using a Type E thermocouple probe (Omega Engineering, Inc., USA) on the soil surface (0–10 cm). The volumetric soil water contents were quantified with the ECHO EC-5 soil moisture probe (Decagon, Pullman, USA), inserted to 5 cm depth.

3.3.4. Estimation of Partitioned R_s

The partitioning of CO_2 efflux was based on the following calculation:

R_s, measured as CO_2 efflux from the T_C treatment, can be separated into four components:

$$R_S = R_{SOM} + R_{root} + R_{litter} + R_{myc} \qquad \text{(Eq. 3.1)}$$

where CO_2 efflux from soil components was derived from the four treatments established, and estimated by the following equations:

1. R_{SOM} was measured as CO_2 efflux from the T_{NI} treatment, which consists of only SOM

$$R_{SOM} = T_{NI} \qquad \text{(Eq. 3.2)}$$

2. Root respiration was estimated by:

$$R_{root} = T_{NL} - T_{Myc} \qquad \text{(Eq. 3.3)}$$

3. Litter respiration was calculated as follows:

$$R_{\text{litter}} = T_{\text{C}} - T_{\text{NL}} \qquad \text{(Eq. 3.4)}$$

4. Mycorrhizal respiration was determined as follows:

$$R_{\text{myc}} = T_{\text{Myc}} - T_{\text{NI}} \qquad \text{(Eq. 3.5)}$$

Similar methods have been successfully employed in various soil CO_2 efflux partitioning studies (see Hanson *et al.*, 2000; Kuzyakov, 2006; Subke *et al.*, 2006 for reviews).

3.3.5. Data Analysis

The soil efflux rates obtained using the LI-8100 File Viewer (2.0) software (LI-COR Inc., Nebraska, USA) were averaged into hourly mean flux rates for each day of the measurement period between August 2009 and January 2010 (Supplementary Material Table S1). The efflux rates of the soil components (i.e. R_{SOM}, R_{litter}, R_{root}, and R_{myc}) were determined based on Equation 3.1 and were averaged into hourly mean flux rates for each day of the measurement period. Data were analysed between September 2009 and January 2010 (Week 8–Week 20), which was identified as the equilibrium phase. We analysed the pattern of R_s and its soil components over daily (24 hr) cycles and the measurement period in each replicate. We used analysis of variance (ANOVA) to test for differences between measurement phases, soil treatments and soil components. Statistical outputs are reported as the test statistics (F, with degrees of freedom in subscripts) and p-value. All uncertainties were reported as standard errors and were propagated where necessary by a quadrature of absolute errors (Malhi *et al.*, 2009), with the assumptions that the uncertainties are independent and normally distributed.

Although we had replications within plot (20 x 20 m), it was impossible to establish desirable replications in such small plot, and thus yielding a pseudo replicated design (Hurlbert, 1984). However, treating the replicates as random effects allowed the generalization of the effects of fixed explanatory variables to site (Beck, 1997). In addition, days and hourly measurements were also included as random effects. Soil moisture, soil temperature, treatments were considered as fixed effects. The use of such data in statistical analyses is valid when successive dates were not treated as independent replicates (Hurlbert, 1984). We present the Markov chain Monte Carlo method (MCMC)-estimated p-values that are considered significant at $\alpha = 0.05$ level (Baayen, 2008). We used Restricted Maximum Likelihood (REML) General Linear Mixed Models (GLMM) to examine the relationship between soil CO_2 efflux and the environmental variables. We followed the guidelines from (Bolker *et al*., 2009) to fit reasonably accurate models incorporating random effects and interpreting statistical inference. Statistical analysis was conducted using R (2.13.0) statistical software (R Development Core Team, 2011) and the R packages lme4 (Bates and Maechler, 2010) and languageR (Baayen, 2009). Results are plotted using Sigmaplot (10.0) software (Systat Software Inc.).

3.4. Results

3.4.1. Experiment Establishment and Disturbance Effects

Diurnal soil fluxes measured from T_{NI}, T_C, T_{NL}, and T_{Myc} during the initial phase from July to August 2009 (Week 1–Week 7) was relatively disturbed because of installation treatments that may have disrupted soil structure and organic matter (Supplementary Material Figure S3.1). Soil CO_2 fluxes appeared to stabilise after three months of plot establishment, from September 2009 to January 2010 (Week 8–Week 20), which we termed the equilibrium phase. However, soil CO_2 fluxes were not significantly different between initial and equilibrium phases ($F_{1,14} = 3.5$, $p = 0.08$). We found significant main effects of replicates ($F_{2,14} = 51.1$, $p < 0.01$) and treatments ($F_{3,14} = 16.3$, $p < 0.01$) on the soil fluxes measured from T_{NI}, T_{C}, T_{NL}, and T_{Myc}. We also found a significant interaction of treatment and phases ($F_{3,14} = 4.2$, $p < 0.05$). Although initial phase was higher than equilibrium phase for T_{NI}, T_{NL}, and T_{Myc}, a Tukey's pairwise comparison showed that the differences were not significant for all treatments ($p < 0.05$).

We observed a progressive decline in R_{SOM}, but an increase in R_{litter} across all replicates over time (Figure 3.2), although we found no significant difference of interaction between soil components and phases ($F_{3,14} = 1.0$, $p = 0.43$). There was significant main effect of soil components ($F_{3,14} = 7.2$, $p < 0.01$) on the soil CO_2 efflux. A Tukey's pairwise comparison showed significant differences between R_{SOM} and R_{myc} ($p < 0.05$), and between R_{SOM} and R_{root} ($p < 0.01$). The trend in R_{myc} and R_{root} were variable across all three replicates throughout the measurement period (Figure 3.2), while R_{s} showed relatively consistent trend in the equilibrium phase.

3.4.2. Diurnal Variation of R_{s} and Soil Components

The mean diurnal cycles of soil CO_2 effluxes and environmental conditions are shown in Figure 3.3. There was a notable diurnal cycle in R_{s} over the 13 weeks of continuous measurement from September 2009 to January 2010 (Figure 3.3a). R_{s} was fairly constant overnight, began to decline around 08:00 h, reached a minimum around 12:00–14:00 h, and returned to nighttime values by 22:00 h, before declining slowly over the rest of the night (Figure 3.3a). This mean diurnal cycle pattern of R_{s} was observed in all three replicates (Supplementary Material Figure S3.2a, S3.2b, and S3.2c). Although there was a distinct diurnal pattern, we found no significant difference ($F_{1,14} = 0.3$, $p < 0.60$) between mid-day (10:00–15:00 h) and mid-night (22:00–03:00 h) diurnal soil fluxes. We found significant main effect of soil components ($F_{3,14} = 4.7$, $p < 0.05$) on the diurnal soil fluxes. A Tukey's pairwise comparison showed significant difference between R_{SOM} and R_{root} ($p < 0.05$).

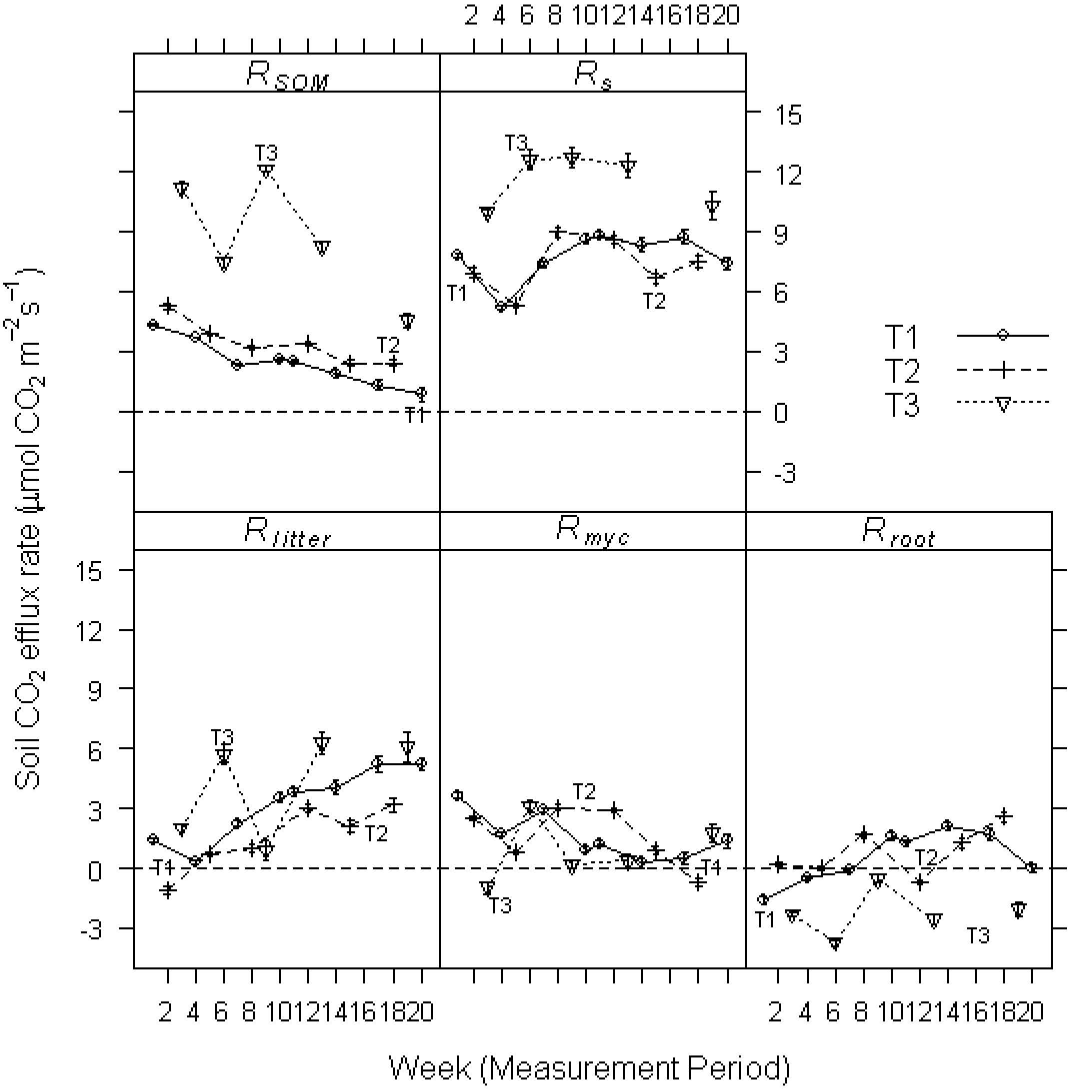

Figure 3.2: The variation of total soil CO_2 efflux (R_s), SOM (R_{SOM}), litters (R_{litter}), mycorrhizae (R_{myc}), and root (R_{root}) in each replicate of T1(○), T2 (+), and T3 (▽) from 16 July 2009 (Week 1) to 24 January 2010 (Week 20). See Supplementary Material Table S3.1 for measurement period. Each point is the hourly average in units of µmol CO_2 m^{-2} s^{-1}. Error bars are standard error of the mean.

We focus our estimation and analysis on the equilibrium phase between September 2009 and January 2010. On a daily basis, mean R_s was 9.36 ± 0.23 µmol CO_2 m^{-2} s^{-1}. R_{litter} contributed 3.71 ± 0.27 µmol CO_2 m^{-2} s^{-1} or about 40% to total R_s (Table 3.2), and showed a similar diurnal pattern to that of R_s (Figure 3.3a). R_{SOM} (4.25 ± 0.38 µmol CO_2 m^{-2} s^{-1} or 45%), R_{myc} (1.18 ± 0.24 µmol CO_2 m^{-2} s^{-1} or 13%), and R_{root} (0.22 ± 0.16 µmol CO_2 m^{-2} s^{-1} or 2%) showed the least diurnal variations (Figure 3.3a). The overall mean R_{root} may be underestimated due to an anomalous negative mean soil flux measured in T3 (Figure 3.2). Mean R_{root} would have been estimated at 1.22 ± 0.18 µmol CO_2 m^{-2} s^{-1}, if T3 was excluded.

Soil temperature averaged 24.7°C and showed a distinct mean diurnal pattern (Figure 3.3b). Soil temperature increased from a minimum at 08:00 h to a maximum at 17:00 h, before declining steadily overnight. The daily volumetric water content was very low, with mean soil moisture of 14.3%. Soil moisture increased from 11:00 h to a maximum at 17:00 h during the day, before steadily declining from 17:00 h to 00:00 h (Figure 3.3c) during the night. Soil moisture increased from a minimum at 00:00 h to 05:00 h overnight, before declining again at 08:00 h to 11:00 h (Figure 3.3c). Hence, the period of declining R_s and R_{litter} corresponded to a period of increasing soil temperature and soil moisture (Figure 3.3a).

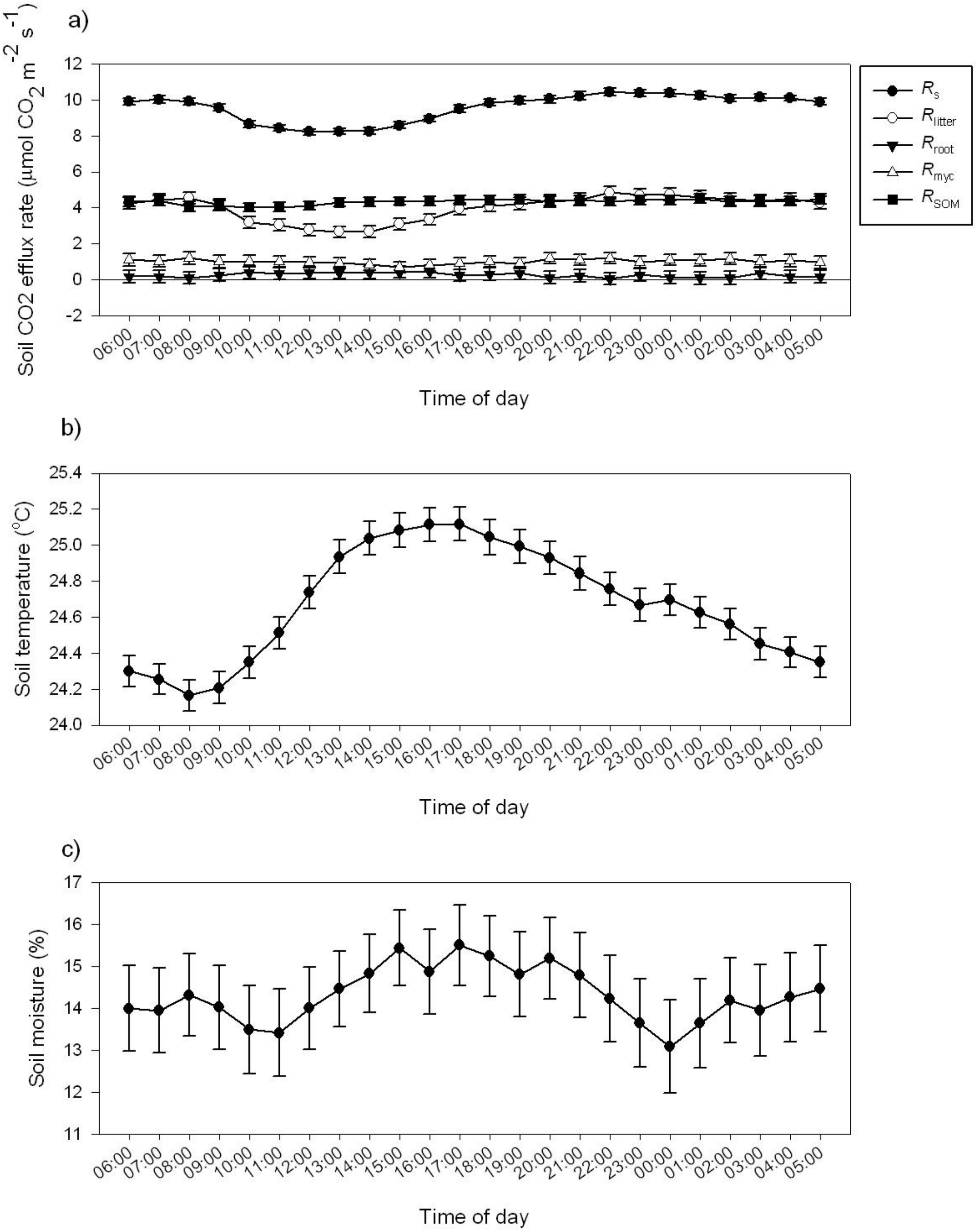

Figure 3.3: a) The mean diurnal CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) of total soil respiration (R_s: solid circle), SOM (R_{SOM}: squares), litter (R_{litter}: white circles), roots (R_{root}: solid triangle), mycorrhizae (R_{myc}: white triangle) across all three replicates. Mean diurnal cycle of b) soil temperature (^oC), and c) soil moisture (%) across all three replicates. Values are hourly averages from September 2009 to January 2010. Error bars are standard error of the mean.

Table 3.2: Mean soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for total soil respiration (R_s), SOM (R_{SOM}), litter (R_{litter}), root (R_{root}), and mycorrhizae (R_{myc}) in equilibrium phase from September 2009 (Week 8) to January 2010 (Week 20) across all replicates (T1, T2, and T3). Values are estimated based on hourly averages for each day. Data exclude Week 1 to Week 7 due to disturbance effects. Errors are reported as standard error of the mean.

	T1	**T2**	**T3**	**Mean soil efflux**	**Fraction (%)**
$\boldsymbol{R_s}$	8.39 ± 0.21	7.94 ± 0.29	11.74 ± 0.58	9.36 ± 0.23	100
$\boldsymbol{R_{SOM}}$	1.82 ± 0.17	2.89 ± 0.17	8.04 ± 1.12	4.25 ± 0.38	45.4
$\boldsymbol{R_{litter}}$	4.38 ± 0.20	2.07 ± 0.34	4.68 ± 0.70	3.71 ± 0.27	39.6
$\boldsymbol{R_{root}}$	1.30 ± 0.20	1.15 ± 0.31	-1.80 ± 0.32†	0.22 ± 0.16	2.3
$\boldsymbol{R_{myc}}$	0.89 ± 0.15	1.83 ± 0.35	0.82 ± 0.61	1.18 ± 0.24	12.6

† Mean diurnal flux of R_{root} ($T_{NL} - T_{Myc}$) were negative because mean hourly fluxes of T_{Myc} were consistently higher than T_{NL} in T3.

NB: No significant difference between means across replicates ($F_{2,6} = 0.21$, $p = 0.82$) and soil components ($F_{3,6} = 2.2$, $p = 0.19$) using two-way ANOVA model at $p < 0.05$.

3.4.3. Comparing Daytime and Nighttime Diurnal Soil CO_2 Fluxes

The most remarkable feature of the study was the daytime decrease of CO_2 fluxes from R_s, R_{litter}, R_{myc}, and R_{SOM}, contrary to what would be expected if heterotrophic respiration was positively related to soil temperature. We quantified the daytime depression by subtracting mean daytime soil CO_2 efflux from mean nighttime soil CO_2 efflux. The magnitude of nighttime soil fluxes was consistently higher than daytime fluxes of R_s and R_{litter}, with consistent daytime depression over time across all replicates within the equilibrium phase (Figure 3.4). The mean nighttime diurnal R_s (9.91 ± 0.24 µmol CO_2 m^{-2} s^{-1}) was 13% higher than daytime (8.80 ± 0.22 µmol CO_2 m^{-2} s^{-1}), although the difference was not significant ($F_{1,4} = 0.4$, $p = 0.55$). The mean amplitude of R_s was 1.11 ± 0.32 µmol CO_2 m^{-2} s^{-1} across all three replicates. Although the magnitude of nighttime R_{litter} was approximately 30% higher than daytime, there was no significant difference ($F_{1,4} = 0.6$, $p = 0.47$) and the daytime depression declined after Week 16 (Figure 3.4). The mean nighttime flux of R_{litter} was 4.19 ± 0.26 µmol CO_2 m^{-2} s^{-1}, while the daytime flux was 3.23 ± 0.28 µmol CO_2 m^{-2} s^{-1}. The amplitude of daytime depression in R_{SOM} and R_{myc} were approximately 3% and 11% respectively, while R_{root} showed no trend with time (Figure 3.4).

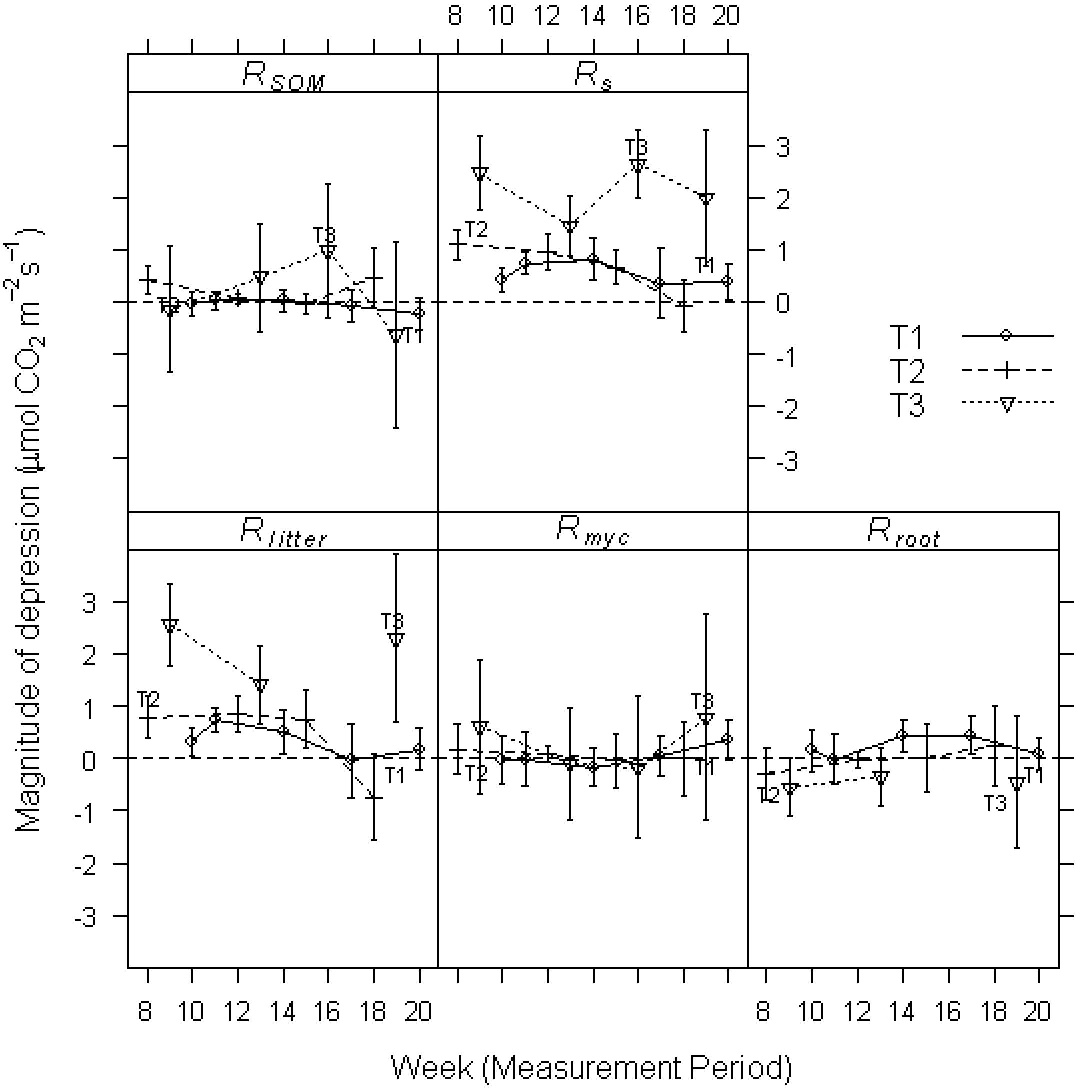

Figure 3.4: The amplitude of daytime depression during the equilibrium phase from September 2009 (Week 8) to 24 January 2010 (Week 20) for total soil respiration (R_s), litter (R_{litter}), root (R_{root}), mycorrhizae (R_{myc}), and SOM (R_{SOM}) across all replicates (T1: circles, T2: plus, and T3: triangle). Daytime depression is the difference in soil efflux between nighttime (18:00–06:00 h) and daytime (06:00–18:00 h). Positive daytime depression indicates a higher nighttime efflux magnitude while negative daytime depression indicates a higher amplitude of daytime fluxes. All fluxes are in units µmol CO_2 m^{-2} s^{-1}. Standard errors of the mean are plotted as error bars.

3.4.4. Environmental Factors Affecting Diurnal R_s and its Soil Components

Soil temperature showed a strong overall positive effect to diurnal R_s (REML GLMM: MCMC-p < 0.001) and R_{SOM} (REML GLMM: MCMC-p < 0.01), while there was a strong negative effect to R_{litter} (REML GLMM: MCMC-p < 0.01) and R_{myc} (REML GLMM: MCMC-p < 0.01). However, soil temperature did not show any effect on R_{root} (REML GLMM: MCMC-p $= 0.61$). (Supplementary Material Figure S3.3). Soil CO_2 efflux was decoupled from soil temperature between 08:00 and 12:00 h and 18:00 and 22:00 h (Figure 3.3a and 3.3b).

Soil moisture had no significant effect to diurnal R_s (REML GLMM: MCMC-p $= 0.05$) and R_{root} (REML GLMM: MCMC-p $= 0.08$). (Supplementary Material Figure S3.4). There was a strong positive effects on R_{litter} (REML GLMM: MCMC-p < 0.01) and R_{myc} (REML GLMM: MCMC-p < 0.01), while soil moisture showed a negative effect on R_{SOM} (REML GLMM: MCMC-p < 0.01).

Over daily variation, air temperature had no effect on R_s (REML GLMM: MCMC-p $= 0.14$), R_{root} (REML GLMM: MCMC-p $= 0.80$), and R_{myc} (REML GLMM: MCMC-p $= 0.76$). There was a significant negative effect of air ambient temperature on R_{litter} (REML GLMM: MCMC-p < 0.01), and a strong positive effect on R_{SOM} (REML GLMM: MCMC-p < 0.01) (Supplementary Materials Figure S3.5).

The daytime depressions (between 06:00 and 17:00 h) of R_{litter} and R_{SOM} had a significant positive effect due to air ambient temperature (REML GLMM: MCMC-p < 0.05). The daytime depression of R_{myc} had a significant negative effect from both soil temperature (REML GLMM: MCMC-p < 0.05) and moisture (REML GLMM: MCMC-p < 0.05). We did not find any effects on the daytime depressions of R_s and R_{root}.

To explicitly determine the effect of these environmental variables on daytime depressions, we related the depressions within the lowest soil CO_2 efflux period (between 10:00 and 14:00 h) to soil moisture, soil temperature, air ambient temperature, vapour pressure deficit (VPD), and solar radiation in the same period across the replicates. Daytime depression index of R_s, R_{litter} and R_{myc} did not show any significant effects to any environmental variables across all the replicates. However, air temperature showed a strong effect against R_{root} (REML GLMM: MCMC-p < 0.05) and R_{SOM} (REML GLMM: MCMC-p < 0.05) across the replicates (Supplementary Materials Figure S3.6). In addition, the daytime depression index for R_{SOM} increased with VPD (REML GLMM: MCMC-p < 0.05) (Supplementary Materials Figure S3.7).

3.5. Discussion

3.5.1. Daytime Depression of Diurnal Soil CO_2 Efflux

To our knowledge, this study is the first attempt to quantify and understand the diurnal pattern of R_s and its soil components in response to environmental drivers in a lowland tropical forest. Contrary to previous studies, our results show a consistent daytime depression in soil CO_2 efflux over six months of diurnal measurement. In tropical forests, lower and constant R_s during the night has previously been reported as opposed to higher and more variable R_s during the day (Meir *et al.*, 1996; Sotta *et al.*, 2004; Ohashi *et al.*, 2008; Zimmermann *et al.*, 2009). However, comparable daytime depressions have been observed in tropical forests elsewhere (Vargas and Allen, 2008b; Zanchi *et al.*, 2009).

In order to explain this daytime depression in soil CO_2 efflux (and in particular litter layer CO_2 efflux), we explore two hypotheses:

1) There may be daytime plant uptake of dissolved CO_2 via the transpiration stream of roots; and

2) The litter layer dries in the daytime and reduces heterotrophic respiration of this litter layer.

For hypothesis 1, CO_2 can be transported upwards to plant tissues in flowing sap by taking up soil dissolved inorganic carbon (DIC) via the roots (Levy *et al*., 1999; McGuire and Teskey, 2004; Ford *et al*., 2007; Saveyn *et al*., 2007; Teskey and McGuire, 2007). During daytime, when tree is transpiring, a large proportion of respired CO_2 is carried upwards in a xylem stream resulting in a depression. If there is a higher rate of daytime transpiration and sap flow, we would expect greater daytime depression in R_{root}. However, there was no discernible evidence of daytime depression observed in R_{root} over this period. One possible explanation for this is that the degree of acclimation of R_{root} to temperature sensitivity may have occurred rapidly (rapid changes in the demand for adenosine triphosphate (ATP)) (Atkin *et al*., 2000), resulting in lower rates and little diurnal variation observed in R_{root}, as is the case observed in this study.

With regard to hypothesis 2, another plausible reason for the daytime depression of R_{s} may be the diurnal changes in the litter environment, as R_{litter} largely drives the diurnal variation of R_{s} at this site (Figure 3.3a). Heterotrophic respiration resulting from R_{litter} is predominantly controlled by microbial activity on the soil surface. Higher VPD during daytime in our site may have caused the litter layer to dry out, and therefore caused unfavourable litter layer conditions for microbial metabolism. The soil layer, in contrast, would be more shielded from diurnal variations in litter humidity and would not be expected to show diurnal variations in respiration rates, as is the case observed here. We did not have direct measurements of the litter layer moisture content through which to validate this humidity hypothesis.

3.5.2. The Effects of Environmental Drivers to Diurnal Total R_s and Soil Components

The effect of replicates on diurnal total R_s and its soil components is relatively substantial (65%). This is largely attributed to the high spatial heterogeneity in our study site (Ohashi *et al*., 2008) and the dynamic changes in litter components (Sotta *et al*., 2004; Metcalfe *et al*., 2007). In the T3 site, soil CO_2 efflux has been showing unusual behaviour throughout the measurement period with constant potential outliers (Supplementary Material Figure S3.1). Although highly variable, the average soil CO_2 efflux measured over time shows that different locations may have different diurnal and seasonal variations (Supplementary Material Figure S3.2). These variations may have been caused by the amount of plant litter at different locations, which has been suggested to increase total R_s following an increase in plant litter input (Sayer *et al*., 2011).

It is generally acknowledged that soil respiration increases exponentially with temperature when soil moisture or other factors are not limiting (Singh and Gupta, 1977; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Kätterer *et al*., 1998; Reichstein *et al*., 2003). In this study, the strong effect between total R_s and soil temperature is comparable to similar studies over a diurnal cycle time scale (Vargas and Allen, 2008; Zanchi *et al*., 2009; Zimmermann *et al*., 2009). Soil temperature is a better predictor of total R_s at diurnal time scale mainly due to strong diurnal changes in soil temperature (Rayment and Jarvis, 1997; Bajracharya *et al*., 2000; Xu and Qi, 2001). However, daytime depression of R_s cannot be explained by soil temperature possibly due to water stress or other contributing factors. This daytime depression may be partially attributed to the strong effect of soil temperature on

R_{litter}, R_{myc} and R_{SOM}, perhaps since the changes of temperature were more closely linked to metabolic activity on the soil surface and litter layer (Sotta *et al*., 2004; Ohashi *et al*., 2008).

The apparent lack of response of total R_s to soil moisture may be attributed to very low soil moisture content over the measurement period. Soil moisture is a major controlling factor, which largely influence soil CO_2 efflux and soil temperature (Davidson *et al* 2000). Given that the soil is masked by the effect of soil moisture, it is not surprising that litter, mycorrhizae and SOM show strong effect to soil moisture. In this study, the dry period caused low variability in soil moisture, which may have led to a weak effect on soil CO_2 efflux.

3.5.3. Diurnal Total R_s and its Soil Components

Based on our other recent study in the same plot, daytime mean soil CO_2 efflux is estimated at 17.6 ± 0.8 Mg C ha^{-1} yr^{-1} over 15 months (see Chapter 4; Kho et al., *submitted* 2012). Correcting for differences in nighttime and daytime fluxes, measured in this study, we revise this estimate of mean annual R_s to 35.5 ± 0.87 Mg C ha^{-1} yr^{-1}. Therefore, mean R_s may have been underestimated by 50% if based only upon daytime measurements, as is common in many studies. Parkin and Kaspar (2004) suggested that errors of up to 60% may be computed if diurnal variations and hysteresis are not accounted for. By comparison, Zimmermann *et al*. (2009) found an overestimation of 60% if mean annual soil respiration was estimated by daytime measurement in a tropical montane cloud forest. Hence, both day- and night-time efflux for R_s and its soil components are required if one wishes to provide a complete estimate of long-term mean daily R_s rates.

Our high annual estimate agrees with similar measurements recorded in tropical forests elsewhere (Vargas and Allen, 2008b; Zanchi *et al*., 2009). Moreover, a wide fluctuation between daytime and nighttime R_s has been reported in Lambir previously, possibly due to episodic high precipitation during the day and higher rates of root respiration (Ohashi *et al.*, 2008).

Little is known about the long-term diurnal cycle of R_s and how the soil components contribute to total R_s. This study is the first attempt to report the diurnal patterns of total R_s and its underlying soil components in tropical forests. Further investigations with combinations of multiple techniques (e.g. isotopes, eddy covariance) are required in order to establish if there are any effects of environmental drivers in regard to diurnal R_s and its soil components. Given the fact that spatial heterogeneity is high and sporadic and high soil CO_2 efflux have been observed in Lambir, it is important to conduct diurnal measurement across larger spatial area.

Although we speculated that two main hypotheses may explain the daytime depression of diurnal R_s, our results should be treated with caution and further investigations are needed to validate our findings. It is possible that a combination of physical and biological processes, the dynamics of roots and rhizomorphs, and CO_2 diffusivity could be driving the daytime depression effect (Vargas and Allen, 2008a). Hence, continuous long-term measurements will be crucial in order to provide a better understanding of the mechanisms controlling diurnal patterns of R_s and its underlying soil components, as well as to accurately predict the contribution of soil CO_2 efflux in the carbon cycle.

3.5.4. Differences in IRGA system–The EGM-4 and LI-8100

In this study, we found substantial differences in soil CO_2 efflux measured using two different IRGA systems. Considering only daytime measurements between 08:00 and 17:00 h, the soil CO_2 efflux obtained using the LI-8100 automated closed chamber system (LI-COR Inc., Nebraska, USA) was significantly higher (Table 3.2, Chapter 3; Table 4.1, Chapter 4) than those obtained using a portable Infra-Red Gas Analysis (IRGA) EGM-4 system (PP Systems, UK).

There have been numerous studies to compare the methods and different systems used for soil respiration measurement (Nay *et al*., 1994; Bekku *et al*., 1997; Norman *et al*., 1997; Le Dantec *et al*., 1999; Davidson *et al*., 2002; Yim *et al*., 2002; Liang *et al*., 2004; Pumpanen *et al*., 2004). A recent study was conducted in Wayqecha, Peruvian Amazon to compare the soil CO_2 efflux using both the EGM-4 and LI-8100 systems. Measurements were made for every 5 minutes on 17 August 2009 between 12:00 and 17:00 h. The EGM-4 fluxes were approximately 5% higher than the LI-8100 [LI-8100 = 0.8593 (EGM-4) + 0.3402, r^2 = 0.64], with approximately 80% higher average standard errors (Zimmermann, *unpublished data*). In addition, Janssens *et al*. (2000) showed that the closed dynamic chamber using the EGM-4 system systematically measure the highest fluxes relative to other systems. The systematic differences detected among different systems can be corrected using correlation factors between 0.82 to 1.45 (Pumpanen *et al*., 2004; Luo and Zhou, 2006). Using these correlation factors, the soil CO_2 efflux between EGM-4 and LI-8100 in this study is in close agreement. This implies that the differences in soil CO_2 efflux observed in both the studies (Chapter 3 and Chapter 5) are not entirely due to the IRGA models used.

One possible explanation to the disparity between the IRGA systems is the frequency of measurements carried out in the course of the two studies (Chapter 3 and 4) and using different IRGA systems. Soil CO_2 efflux using the EGM-4 was obtained from a designated soil collar (11 cm diameter, 10 cm length) for 120 seconds, measured three times every month. However, the LI-8100 system measured soil CO_2 efflux from a designated soil collar (20 cm diameter, 11 cm length) for 210 seconds continuously at intervals of approximately 14 minutes over 24 hour cycle. Hence, automated soil CO_2 efflux measurements were able to capture and observe continuous short-term variation that may include rapid pulses from precipitation or microbial activity (Vargas *et al.*, 2010). Frequent occurrences due to these episodic pulses may have enhanced the release of soil CO_2 efflux over time. The range of variation measured between 08:00 and 17:00 h (equilibration period) averaged 5.31 µmol CO_2 m^{-2} s^{-1}, with the highest flux estimated at 16.2 µmol CO_2 m^{-2} s^{-1}. Similarly, this is supported by previous study in Lambir showing high spatial heterogeneity and soil CO_2 efflux varied widely in space, with extremely high fluxes over 10 µmol CO_2 m^{-2} s^{-1} (Ohashi *et al.*, 2008).

3.5.5. Mycorrhizal Treatment Design

Errors related to lateral diffusion of CO_2 can be either negligible or indeed avoided altogether. Firstly, this is evident from the observations of CO_2 efflux measured from T_{myc}, which showed a declining trend during the initial period and remained relatively stable throughout the equilibrium period (Figure S3.1). If there were lateral diffusions of CO_2, we would expect soil CO_2 efflux measured from T_{myc} to be disturbed and likely to show an increasing trend as a result of the diffused CO_2 entering the mesh bag. Furthermore, mycorrhizal respiration in this study accounts for approximately 12% of total soil respiration, which is comparable to a recent study using a similar mesh bag method (Nottingham *et al.*, 2010).

Secondly, the differences in CO_2 concentration between the outside and inside of the mesh bags can be partially overcome by estimating R_{myc} as a fraction of $R_{\mathrm{myc}} + R_{\mathrm{rhizo}}$. The theoretical proportion (1/x) of R_{myc} or R_{rhizo} diffusing into the treatment cores can be cancelled out, and the relationship remains constant even if there is lateral diffusion of CO_2 into the treatment cores, assuming that the proportional diffusion is equal in all cases (Moyano *et al.*, 2008).

Although we have been able to partition the extraradical mycelia, mycorrhizae respiration may be underestimated (Nottingham *et al.*, 2010). This is partly because measurements of CO_2 efflux capture only the ingrowth of hyphae or mycelia within the mesh bags and therefore do not include the mycorrhizae biomass that is in the roots. Ectomycorrhizal biomass is present in all dipterocarp trees (Singh, 1966; de Alwis and Abeynayake, 1980; Alexander and Högberg, 1986; Lee, 1990; Peay *et al.*, 2010) and may comprise up to 20% of root weight (Smith and Read, 1997). Our study provides significant insights into the source of CO_2 efflux from the mycorrhizae component in a lowland dipterocarp forest, and thus shows that mycorrhizal fungi represent an important source of soil respiration. However, further information is needed for a fuller understanding of mycorrhizae respiration in regard to the community composition of mycorrhizae and the entire soil fungal flora.

3.6. Conclusion

There was a notable diurnal variation in R_s caused by R_litter, with a daytime depression. The nighttime soil CO_2 efflux in this study was higher than daytime. R_SOM appeared to be the largest contributor to R_s, followed by contributions from R_litter, R_myc, and R_root,. There was no significant relationship between diurnal soil CO_2 efflux and soil temperature. In addition, soil moisture and solar radiation did not fully explain the diurnal variation of R_s and the soil components. This study highlights the importance of long-term day- and night-time efflux for R_s and its components to shed light on mean daily rates and model soil CO_2 efflux over spatial and temporal patterns.

3.7. Acknowledgement

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3.9. Supplementary Material

Table S3.1: The dates for weekly measurement routine of three replicates (T1, T2, and T3) in DIRT experimental plot.

Measurement week	Date	Subplot
1	16–19 Jul 2009	T1
2	20–24 Jul 2009	T2
3	29 Jul–2 Aug 2009	T3
4	3–9 Aug 2009	T1
5	10–16 Aug 2009	T2
6	17–23 Aug 2009	T3
7	24–30 Aug 2009	T1
8	31 Aug–6 Sep 2009	T2
9	7–12 Sep 2009	T3
10	14–20 Sep 2009	T1
11	12–18 Oct 2009	T1
12	19–23 Oct 2009	T2
13	26 Oct–1 Nov 2009	T3
14	2–7 Nov 2009	T1
15	9–15 Nov 2009	T2
16	16–22 Nov 2009	T3
17	23–29 Nov 2009	T1
18	30 Nov–2 Dec 2009	T2
19	11–17 Jan 2010	T3
20	18–24 Jan 2010	T1

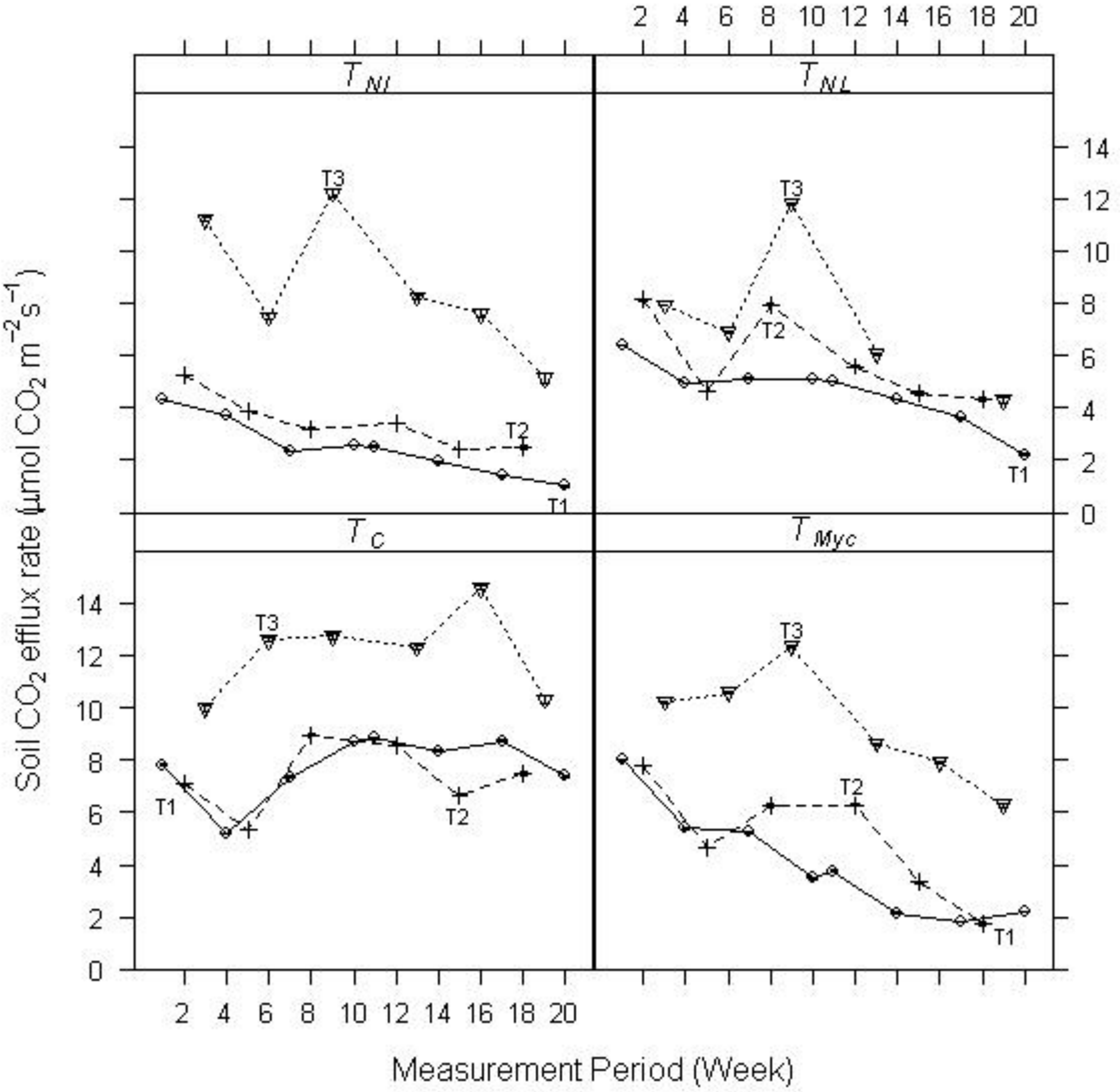

Figure S3.1: Soil CO_2 efflux of all treatments of control (T_c), mycorrhizal (T_{myc}), no input (T_{NI}), and no litter (T_{NL}) for each replicates (T1, T2, and T3) over 20 weeks from July 2009 (Week 1) to January 2010 (Week 20). Each point is the average diurnal soil CO_2 efflux of a measurement period. Standard errors of the mean are plotted as error bars.

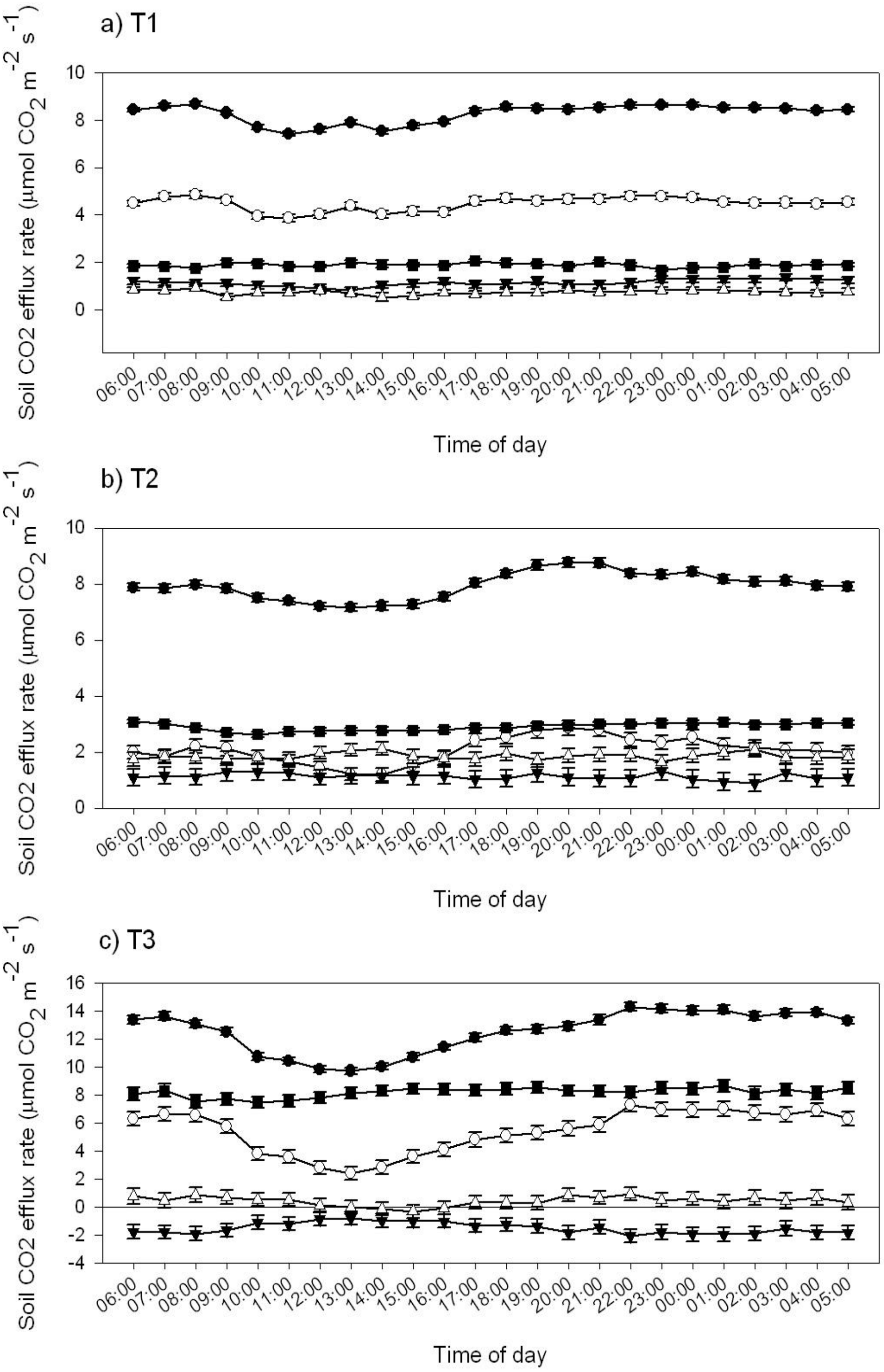

Figure S3.2: Diurnal variation of soil respiration across all replicates of a) T1, b) T2, and c) T3 in DIRT experimental plot from 31 August 2009 (Week 8) to 24 January 2010 (Week 20). Solid circles denote R_{s}, squares are R_{SOM}, white circles are R_{litter}, white triangles are R_{myc}, and the solid triangle denotes R_{root}. Standard errors of the mean are plotted as error bars.

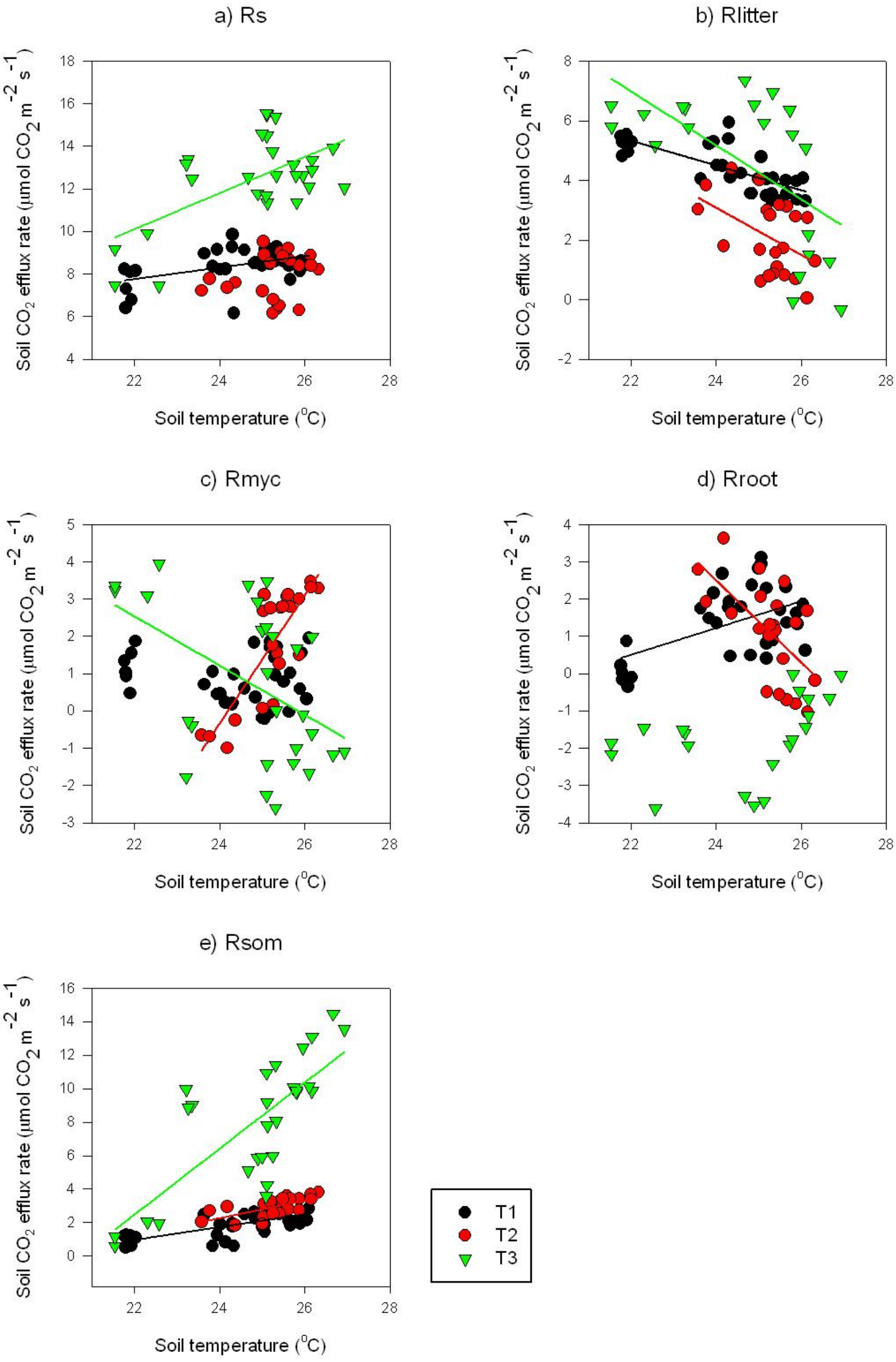

Figure S3.3: Relationship between mean daily soil CO_2 efflux of a) total soil respiration (R_s), b) litter (R_{litter}), c) root (R_{root}), d) soil organic matter (R_{SOM}), and e) mycorrhizae (R_{myc}) against soil temperature (°C) from 31 August 2009 (Week 8) to 24 January 2010 (Week 20) across all replicates. Each point is the mean daily soil CO_2 efflux over the measurement period. Least square regression lines were shown for those relationships which were significant ($p < 0.05$).

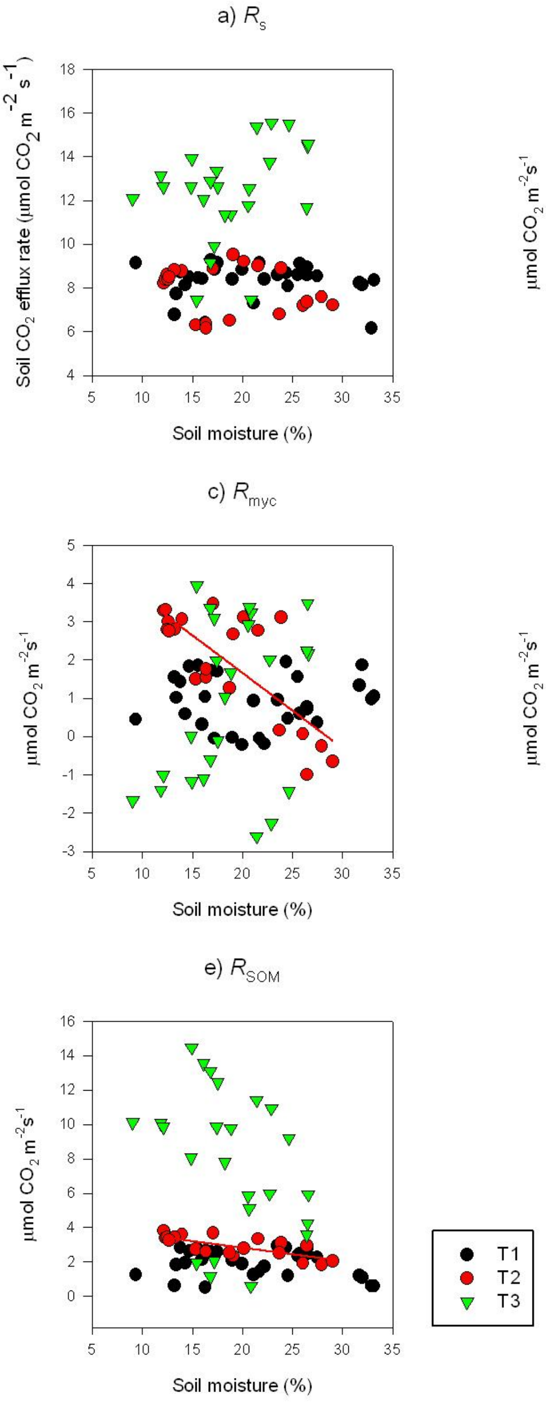

Figure S3.4: Relationship between mean daily soil CO_2 efflux of a) total soil respiration (R_s), b) litter (R_{litter}), c) root (R_{root}), d) soil organic matter (R_{SOM}), and e) mycorrhizae (R_{myc}) against soil moisture (%) from 31 August 2009 (Week 8) to 24 January 2010 (Week 20) across all replicates. Each point is the mean daily soil CO_2 efflux over the measurement period. Least square regression lines were shown for those relationships which were significant ($p < 0.05$).

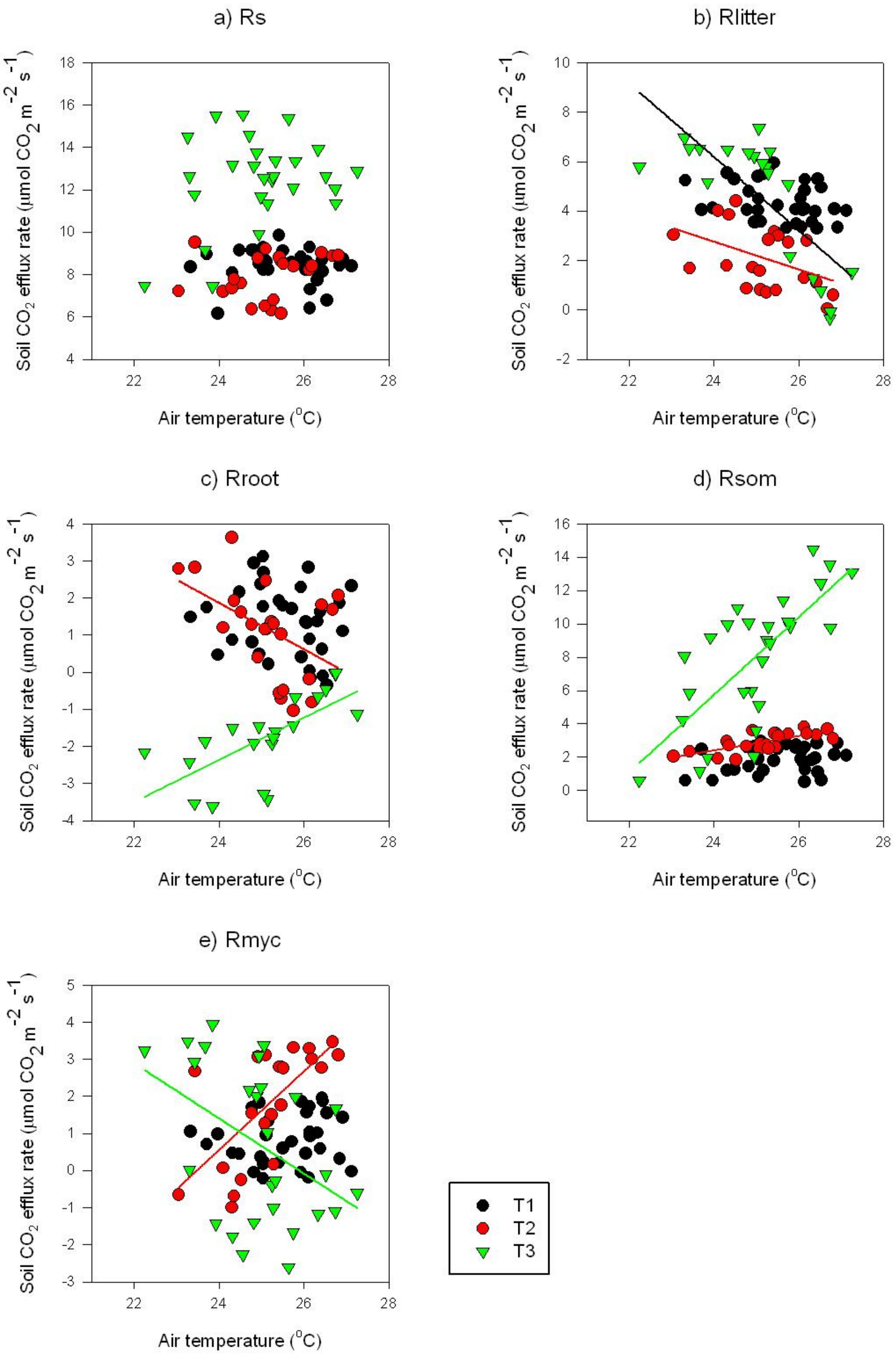

Figure S3.5: Relationship between mean daily soil CO$_2$ efflux of a) total soil respiration (R_s), b) litter (R_{litter}), c) root (R_{root}), d) soil organic matter (R_{SOM}), and e) mycorrhizae (R_{myc}) against air ambient temperature (^{o}C) from 31 August 2009 (Week 8) to 24 January 2010 (Week 20) across all replicates. Each point is the mean daily soil CO$_2$ efflux over the measurement period. Least square regression lines were shown for those relationships which were significant ($p < 0.05$).

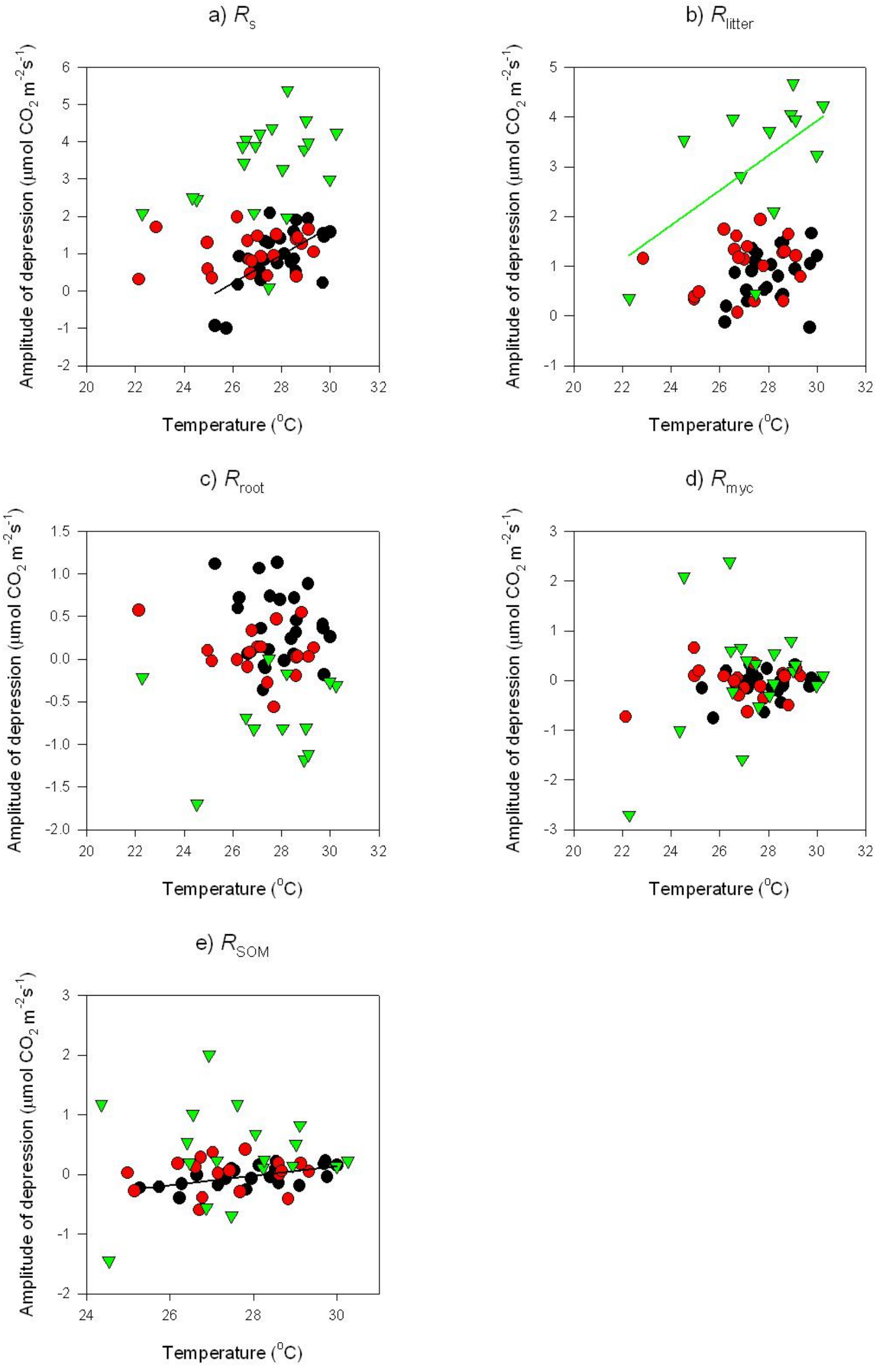

Figure S3.6: The daytime depression (10:00–14:00 h) of a) total soil respiration (R_s), b) litter (R_{litter}), c) root (R_{root}), d) soil organic matter (R_{SOM}), and e) mycorrhizae (R_{myc}) against air ambient temperature (°C) from 31 August 2009 (Week 8) to 24 January 2010 (Week 20) across all replicates. Each point is the mean daily daytime depression (nighttime flux subtract daytime flux between 10:00 and 14:00 h) over the measurement period. Least square regression lines were shown for those relationships which were significant (p <0.05).

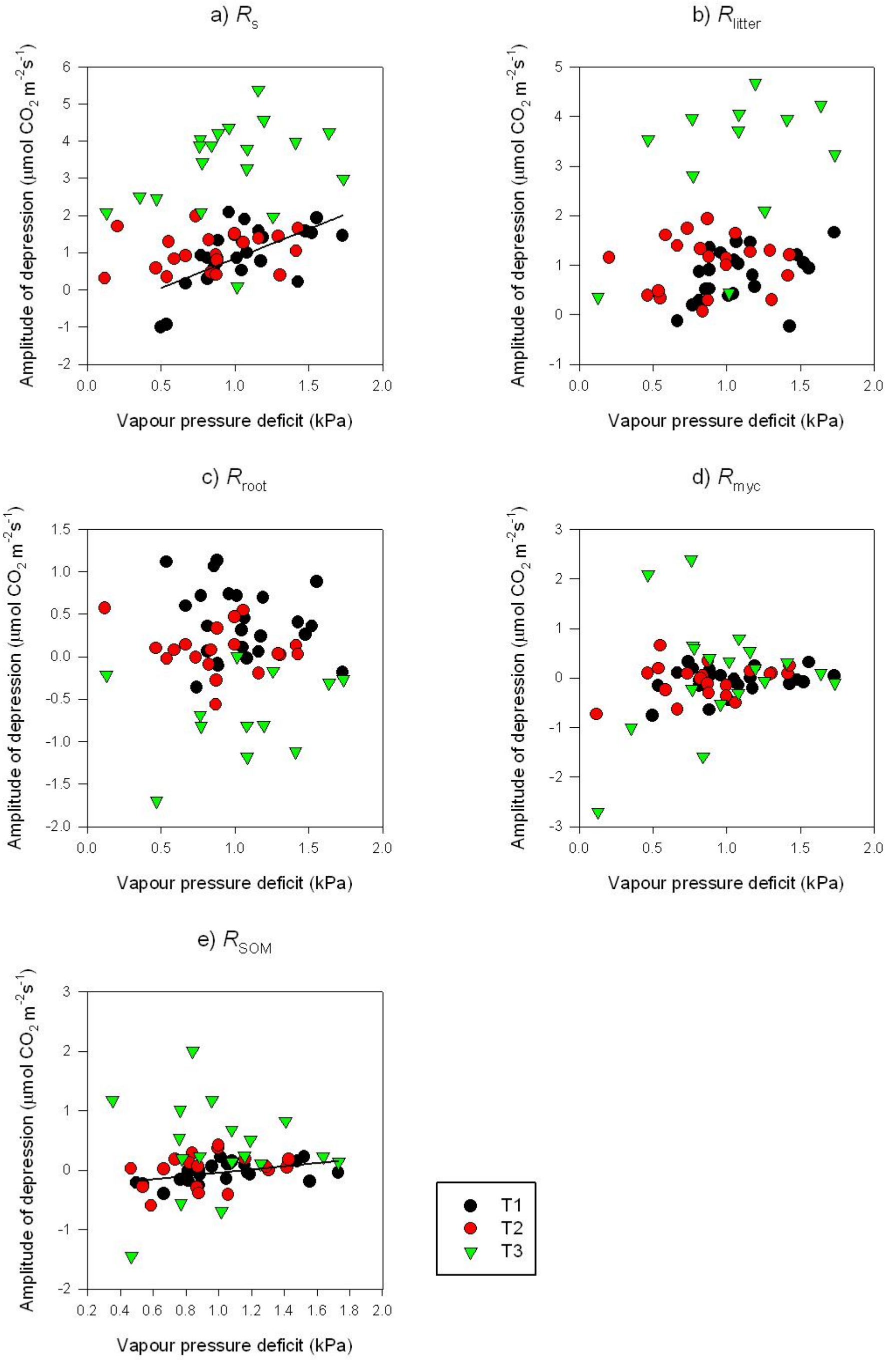

Figure S3.7: The daytime depression (10:00–14:00 h) of a) total soil respiration (R_s), b) litter (R_{litter}), c) root (R_{root}), d) soil organic matter (R_{SOM}), and e) mycorrhizae (R_{myc}) against vapour pressure deficit (VPD) (kPa) from 31 August 2009 (Week 8) to 24 January 2010 (Week 20) across all replicates. Each point is the mean daily daytime depression (nighttime flux subtract daytime flux between 10:00 and 14:00 h) over the measurement period. Least square regression lines were shown for those relationships which were significant ($p < 0.05$).

Chapter 4

Chapter 4: Magnitude and Seasonal Variation of the Components of Soil CO_2 Efflux in a Lowland Tropical Forest in Borneo

Overview

This study presents the magnitude and seasonal variation of soil respiration in a lowland dipterocarp forest. In addition, this study seeks to understand how soil respiration is partitioned into litter, soil organic matter (SOM), roots and mycorrhizae, and how these components vary over the seasonal cycle. Using the soil respiration partitioning method, this study is able to examine the variation in each soil component over the seasonal cycle and their response to environmental factors.

Various collaborators* made this study possible. The experimental design was contributed by Yadvinder Malhi, and later supported by Daniel Metcalfe. Sylvester Tan provided field assistance and Mohd. Haniff Harun provided the instruments for field measurements. Tomo'omi Kumagai and Tomonori Kume provided meteorological data from Lambir.

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* Contribution Statement: experimental design: KLK, YM, LA, ST; data gathering: KLK, ST; data analysis: KLK; interpretation of results: KLK, YM, LA, DM; paper writing: KLK.

4.1. Abstract

Soil carbon dioxide (CO_2) efflux (R_s) constitutes the second largest terrestrial CO_2 source but the behaviour and relative contribution of different soil components to R_s remain uncertain. The partitioning of soil into litter, root, mycorrhizae, and SOM respiration is crucial in aiding our understanding of how these underlying soil components are driving total R_s over space and time. In previous studies, a wide range of methods have been used to partition total R_s, but these studies have mainly focused on temperate ecosystems whilst tropical forests have received relatively little attention. We examined patterns of R_s and its soil components on two soil types in a Bornean lowland dipterocarp forest, determining the responses to environmental factors. The mean annual R_s varied between 11.2 and 14.6 Mg C ha^{-1} yr^{-1}, with distinct seasonal patterns and spatial differences on clay and sandy loam over the two years of observation. Across both sites, mean annual R_s was partitioned into 6.1 ± 0.3 Mg C ha^{-1}yr^{-1} (mean ± standard error) from SOM (R_{SOM}), 2.8 ± 0.4 Mg C ha^{-1} yr^{-1} from roots (R_{root}), 2.6 ± 0.4 Mg C ha^{-1}yr^{-1} from litter (R_{litter}), and 1.5 ± 0.3 Mg C ha^{-1}yr^{-1} from mycorrhizae (R_{myc}). Heterotrophic respiration (R_h) – including litter, SOM, and mycorrhizae components, accounted for 78% of total R_s and was mainly derived from SOM and litter. By comparison, a relatively minor portion of R_s was autotrophic (R_a) in origin. Monthly mean R_s was negatively correlated with soil moisture, but increased exponentially with soil surface temperature. Litter respiration showed a significant positive relationship. In multiple linear regression, soil moisture explained 66% of total R_s in the one-hectare plot, but showed a relatively weak effect on R_{litter}, R_{SOM} and R_{myc}. This information improves our understanding of the underlying factors determining spatial and temporal variation in R_s within an important but acutely understudied biome.

4.2. Introduction

Soil carbon dioxide (CO_2) efflux (R_s) accounts for a large proportion of total biosphere respiration and is the second largest terrestrial carbon flux (Schlesinger, 1977; Raich and Potter, 1995; Davidson *et al*., 2006; Luo and Zhou, 2006). Two-thirds of this flux comes from tropical and subtropical forests (Raich *et al*., 2002). In addition, R_s is sensitive to environmental factors and these interactions are critical for regulating the global carbon balance (Raich and Schlesinger, 1992; Davidson and Janssens, 2006). Therefore, even a small shift in R_s across tropical ecosystems could have a major impact on the global carbon cycle and hence the rate of climate change (Jenkinson *et al*., 1991; Davidson and Janssens, 2006).

Total R_s is derived from autotrophic respiration (R_a) by roots and heterotrophic respiration (R_h) by microbes that decompose surface organic litter, root tissues and exudates, SOM, and mycorrhizal fungi. These sources of soil CO_2 efflux exhibit different patterns of spatial and temporal variation, and respond differently to environmental drivers such as temperature, water and light availability. Studies have shown that these soil components are driven by microbial activities and influenced by soil environmental factors such as soil temperature, water content, pH, and other biophysical characteristics (Schlesinger, 1977; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Raich *et al*., 2002).

The partitioning of R_s into R_a and R_h has received considerable attention, as the responses of these soil components are important for understanding the underlying soil processes that contribute to total R_s and their sensitivity to environmental changes, which have significant implications for plant–soil interactions and ecosystem carbon cycling. To date, numerous partitioning methods such as non-direct (modeling, mass-balance, subtraction, and root mass regression), non-isotopic (component integration, root exclusion, and substrate-induced respiration), and isotopic techniques have been applied and evaluated to estimate the contribution of soil components to total R_s (Hanson *et al*., 2000; Kuzyakov, 2006; Subke *et al*., 2006). However, the interactions of R_s and its soil components with environmental factors are still uncertain and data limited (Kuzyakov, 2006; Metcalfe *et al*., 2007; Heinemeyer *et al*., 2011; Kuzyakov, 2011). Furthermore, most advances in soil partitioning methods have been established in temperate and boreal forests or grasslands (see Hanson *et al*., 2000; Subke *et al*., 2006 for review), with relatively few studies conducted in tropical forests (Ogawa, 1978; Nakane, 1980; Trumbore *et al*., 1995; Li *et al*., 2004; Silver *et al*., 2005; Metcalfe *et al*., 2007). Silver *et al*. (2005) examined root efflux in a lowland moist Amazonian forest using both trenching and mass-balance approaches, finding that both approaches yielded similar estimates. In the Southeast Asian region, Nakane (1980) used the mass-balance approach to determine that R_h contributed about 50% of total R_s. In addition, recent studies in the Amazon have found mean annual heterotrophic contribution in the range of 30–52% of R_s (Metcalfe *et al*., 2007; Zimmermann *et al*., 2010).

The principal objective of this study is to quantify total R_s and partition its components (from surface organic litter, roots, mycorrhizae and SOM), on sandy loam and clay soils in a lowland dipterocarp forest located in Lambir Hills National Park in Sarawak, Malaysian Borneo. In addition, we examined the temporal variability of total R_s and its individual components, exploring correlations amongst our partitioned CO_2 flux data and environmental factors such as soil temperature and soil moisture. Specifically, we addressed the following scientific questions:

1. What is the mean annual flux from R_s and which environmental factors control its temporal variation?

2. How is total R_s divided into component fluxes (litter respiration, soil organic respiration, root and mycorrhizal respiration), how do these components vary seasonally, and which environmental factors control this variation?

3. Are there any significant differences in R_s and its components between the clay and sandy loam sites?

4.3. Materials and Methods

4.3.1. Study Site

This study was carried out in a lowland Bornean mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4^{o} 12’ N, 114^{o} 2’ E). Lambir is dominated by various genera of the family Dipterocarpaceae, and has the highest recorded tree diversity in the Paleotropics (Ashton and Hall, 1992; Davies and Becker, 1996; Palmiotto *et al*., 2004). Approximately 1,200 tree species were recorded over a 52 hectare forest dynamics plot in Lambir (Condit, 2000; Davies *et al*., 2005). A comprehensive description of its floristics and stand structure was presented by Lee *et al*. (2002). The basal area of trees > 10 cm diameter at breast height is between 35 and 53 m^2 ha^{-1} (Phillips *et al*., 1994; Yamakura *et al*., 1996) and above-ground biomass is approximately 260 Mg C ha^{-1} (Yamakura *et al*., 1996; Chave *et al*., 2008). These values are much higher than those typically reported from South American or African tropical forests (Malhi *et al*., 2006; Lewis *et al*., 2009), reflecting the tall stature and large diameter of the Southeast Asian rainforest trees. The rate of litterfall is consistent throughout the year and suggests little seasonal variation of leaf area index (LAI), with a mean estimated annual value of 6.2 m^2 m^{-2} (Kumagai *et al*., 2004). The dipterocarp species which dominate the forest have mass flowering events which occur periodically, including during our measurement period (Kettle *et al*., 2011).

Lambir received approximately 2,630 mm of mean annual precipitation (recorded from an 80 m canopy crane) for the period 2000–2010, with a modest seasonal pattern. Over the 10 years between 2000 and 2010, drier months (mean 172 mm mo^{-1}) were recorded between February and August, while the wetter months (mean 285 mm mo^{-1}) were recorded between September and January. During the measurement period, the rainfall pattern differed between 2009 and 2010. The period between April to October was relatively dry in 2009 (161 mm mo^{-1}) compared to 2010 (263 mm mo^{-1}). The mean annual temperature in Lambir for the period 2000–2009 was 25.9 ^{o}C, with little diurnal or seasonal variation.

The soils and geomorphology of Lambir have been previously described in detail (Ishizuka *et al*., 1998; Baillie *et al*., 2006; Tan *et al*., 2009). The soils in Lambir are red-yellow podzolic soils based on the Sarawak soil classification (Teng, 1996), or classified as Acrisols (FAO, 2006) and Udults (Soil Survey Staff, 2006). The soils are derived mainly from sandstone sandy loam and shale-derived clay soils of the Miocene-Pliocene Lambir Formation (Watson, 1985; Ishizuka *et al*., 1998). Sandstone-derived soils are humult Ultisols (Soil Survey Staff, 2006), with densely matted fine roots on the surface horizon, high sand content (typically 68% sand), low nutrients and low water-holding capacity (Ashton and Hall, 1992; Davies *et al*., 1998). Shale-derived soils are clay-rich udult Ultisols (Soil Survey Staff, 2006) (typically 40% sand), with a thin litter layer on the soil surface, relatively higher fertility and high water-holding capacity (Davies *et al*., 1998; Davies *et al*., 2005). Humult Ultisols are mainly found on slopes and ridges and cover about 75% of the 52-ha forest dynamics plot, whilst the udult Ultisols are mostly on low-lying valleys and cover the remaining 25% or so (Davies *et al*., 1998).

4.3.2. Soil CO_2 Efflux Partitioning Method

We established two Detritus Input and Removal Treatment (DIRT) (Sulzman *et al*., 2005; Nadelhoffer *et al*., 2006; Fekete *et al*., 2011) experimental plots (20 m x 20 m) on contrasting soil types: the clay-rich udult Ultisol (27% clay, 34% silt, 40% sand) and sandy humult Ultisols (15% clay, 16% silt, 68% sand) (Tan *et al*., 2009). Each DIRT plot was divided into three 11 m x 5 m subplots (T1, T2, and T3) as replicates, and then further divided into eight 2 m x 2 m as treatment plots. Three PVC soil collars (measurement of soil collars detailed below) were installed at random points in each treatment plot. The treatments were established on 5 January 2009 on the sandy humult Ultisol (the sandy loam site), and on 6 July 2009 on the clay udult Ultisol (the clay site).

Partitioning of soil CO_2 efflux was determined from the following treatments:

1. A Control (T_C) treatment, with R_s being measured (including the surface organic litter layer) in undisturbed conditions and with normal above-ground inputs of litterfall in three soil collars (11 cm diameter, 10 cm length) that were inserted to a depth of 2–5 cm from the soil surface at random locations (Figure 4.1).
2. A No Litter (T_{NL}) treatment, which excluded all above-ground inputs of litterfall and woody debris to the soil surface using polyethylene netting. Soil CO_2 efflux was measured from soil collars (11 cm diameter, 10 cm length) randomly inserted to a depth of 2–5 cm from the soil surface (Figure 4.1). Leaf litter and woody debris were cleared from the netting weekly to avoid litter decomposition that may contribute to soil respiration.
3. A Double Litter (T_{DL}) treatment, which was enriched with the litter removed from the T_{NL} treatment, and exposed to normal above-ground litter inputs. Soil CO_2 efflux was

measured in soil collars (11 cm diameter, 10 cm length) randomly inserted to a depth of 2–5 cm from the soil surface (Figure 4.1). The effects of doubled litter inputs on soil carbon are likely to introduce a priming effect that may accelerate SOM turnover and increase respiratory activity.

4. A No Input (T_{NI}) treatment was established with soil collars (11 cm diameter, 40 cm length) inserted to a depth of 30 cm into the soil surface to exclude ingrowth of roots and mycorrhizae (Figure 4.1). All existing surface litter and roots were removed. The disturbance and removal of fine roots is likely to have caused a disturbance effect, which we evaluated in the weeks following installation.
5. A Mycorrhizae (T_{Myc}) treatment constructed using three mesh bags (36-µm pore diameter, Plastok Ltd, Birkenhead, UK) of 11 cm diameter and 40 cm length (Figure 4.1). The mesh bags have been successfully used to exclude roots but allow ingrowth of mycorrhizal hyphae in various ecosystems (Smith and Read, 1997; Heinemeyer *et al.*, 2007; Moyano *et al.*, 2007; Fenn *et al.*, 2010; Nottingham *et al.*, 2010). Prior to installation, all existing surface litter was removed. Soil cores (11 cm diameter, 30 cm length) were carefully extracted and transferred into the micromesh bags, with minimal disturbance to the soil profile. The micromesh bags filled with soils were reinserted into the same location of extracted soil columns, and soil collars (11 cm diameter, 10 cm diameter) were inserted to a depth of 2–5 cm in the mesh bags.

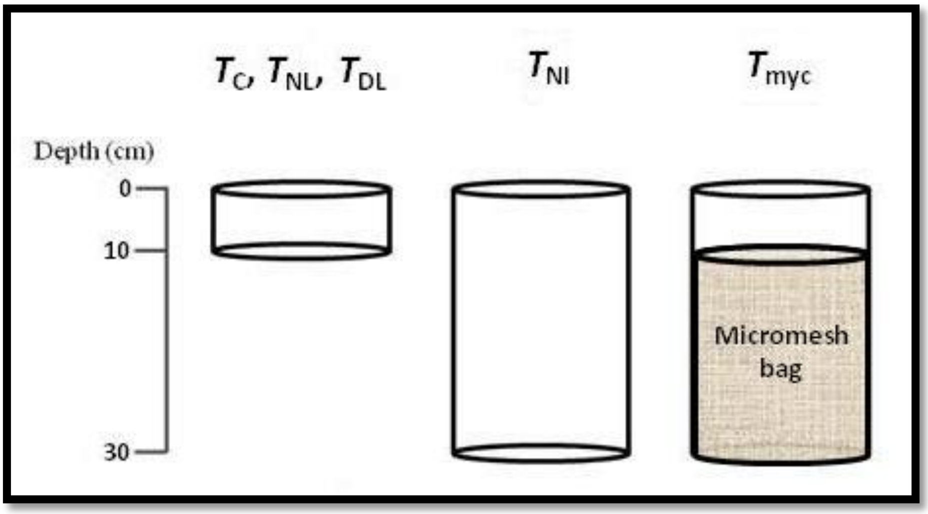


Figure 4.1: The soil collars were made from PVC. Diameter of collars were 11 cm, with 10 cm length for Control (T_C), No Litter (T_{NL}), and Double Litter (T_{DL}) treatments, 30 cm length for No Input (T_{NI}) treatment, and 10 cm length extended/covered with 36 µm mesh bags for Mycorrhizae (T_{Myc}) treatment.

The treatments to exclude any ingrowth into soil collars of T_{NI} guaranteed that roots and mycorrhizae were effectively excluded using PVC soil collars of 40 cm length. Soil collars were inserted to a depth of 30 cm in the soil because the majority of fine roots occur within the uppermost 30 cm soil layer, with this layer also being the main source of root and microbial respiration (Cavelier, 1992; Silver *et al*., 2000; Veldkamp *et al*., 2003; Silver *et al*., 2005).

4.3.3. Measurement of Soil CO_2 Efflux

Soil CO_2 efflux was measured using a portable Infra-Red Gas Analysis (IRGA) system (EGM-4 and SRC-1 soil chamber, PP Systems, UK), with a custom-made adaptor to fit on soil collars. Each measurement was obtained from soil collars of each treatment plot for a maximum of 120 seconds. Soil flux was determined from the rate of CO_2 concentration increase within the closed chamber for a known period of time. A linear fit to the CO_2 concentration data proved to be adequate in all cases (typical $r^2 \geq 0.80$), with the first nine seconds of data removed due to the potential for initial disturbance associated with chamber placement on the collar. Subsequent concentration data were sometimes also removed, to a maximum of 43 seconds, if found to deviate from the linear fit.

Measurements were conducted at weekly and biweekly intervals for seven consecutive weeks and at monthly intervals thereafter. Measurements commenced seven days after treatment installation on 12 January 2009 in sandy loam, and on 13 July 2009 in clay soils. A total of 72 measurements were obtained from each interval.

Together with soil CO_2 efflux measurements, soil moisture, soil temperature and surface temperature were also recorded. Soil moisture was quantified down to 12 cm soil depth using a Hydrosense CS620 probe (Campbell Scientific, Australia). Air and soil temperature were recorded using a portable waterproof T-bar digital thermometer probe (Thermometers Direct, UK). Soil temperature was obtained to a depth of 10 cm in the soil, while the air temperature was recorded at < 100 cm above the soil surface.

4.3.4. Estimation of Total R_s and CO_2 Efflux from Soil Components

Total R_s was partitioned into the major soil components: roots (R_{root}), SOM (R_{SOM}), surface litters (R_{litter}), and mycorrhizae (R_{myc}), with the following expression:

$$R_s = R_{litter} + R_{SOM} + R_{root} + R_{myc} \qquad \text{(Eq. 4.1)}$$

where each component of soil CO_2 efflux was calculated by taking the differences between treatments in each subplot based on the following equations:

1. Litter respiration was calculated as follows:

$$R_{litter} = T_{DL} - T_C \qquad \text{(Eq. 4.2)}$$

2. Root respiration was calculated as follows:

$$R_{\mathrm{root}} = T_{\mathrm{NL}} - T_{\mathrm{Myc}} \quad \text{(Eq. 4.3)}$$

3. Mycorrhizae respiration was determined as follows:

$$R_{\mathrm{myc}} = T_{\mathrm{Myc}} - T_{\mathrm{NI}} \quad \text{(Eq. 4.4)}$$

4. Respiration of SOM was measured directly from T_{NI} treatment

$$R_{\mathrm{som}} = T_{\mathrm{NI}} \quad \text{(Eq. 4.5)}$$

Monthly average soil components such as R_{litter}, R_{root}, R_{SOM}, and R_{myc} were estimated based on the additional equations for each subplot on sandy loam and clay soils, over the period May 2009 to October 2010. Measurements were made initially at weekly intervals (seven weeks) and at monthly intervals from May 2009 to October 2010. Though the data were analysed, the early period data (12 January–2 March 2009 for sand, 13 July–31 August 2009 for clay) were not used in annual budgets (but are displayed in the figures) because of evident post-installation disturbance effects. Total annual R_s was calculated by multiplying the monthly average value of daily flux of two consecutive months by the time interval between the consecutive months, then summing these values over the year.

4.3.5. Soil CO_2 Efflux Measurement in the One-Hectare Plot

In addition to soil CO_2 efflux measurements on the DIRT experimental plots, we also measured R_s in a larger one-hectare plot on both clay and sandy loam (the DIRT site was located just outside the larger plot). The plot was divided into 25 subplots (20m x 20m) on each clay and sandy loam site, with a designated measurement point (microsite) near the centre of each subplot. Using the same IRGA instrument (EGM-4 and SRC-1, PP Systems, UK) and procedures, we took three repeat measurements on each microsite, once a month. Monthly R_s over the one-hectare plot was calculated based on the average CO_2 efflux of each microsite. Monthly measurements of R_s were conducted over two years from October 2008 to October 2010. Measurements were conducted during daytime between 08:00 h and 17:00 h.

4.3.6. Data Analysis

Student's t-tests were used to explore differences between the clay and sandy loam sites. A two-way analysis of variance (ANOVA) was used to determine spatial and temporal differences in the soil component CO_2 fluxes. We used linear and non-linear regressions to explore the relationship between environmental parameters such as soil temperature, soil water content, and air temperature to total R_s and its component fluxes. In addition, stepwise multiple regression analysis was used to explore the causes of variation in total R_s and its component fluxes. Data were log-transformed where necessary and outliers were removed using Grubbs's test.

All uncertainties were reported as standard errors and, where necessary, propagated by quadrature of absolute errors for addition/subtraction, and quadrature of proportional errors for division/multiplication (Malhi *et al*., 2009), with the assumptions that the uncertainties are independent and normally distributed. Statistical analysis was conducted using R (version 2.13.0) statistical software (R Development Core Team), and the results were plotted using SigmaPlot 10.0 software (Systat Software, Inc.).

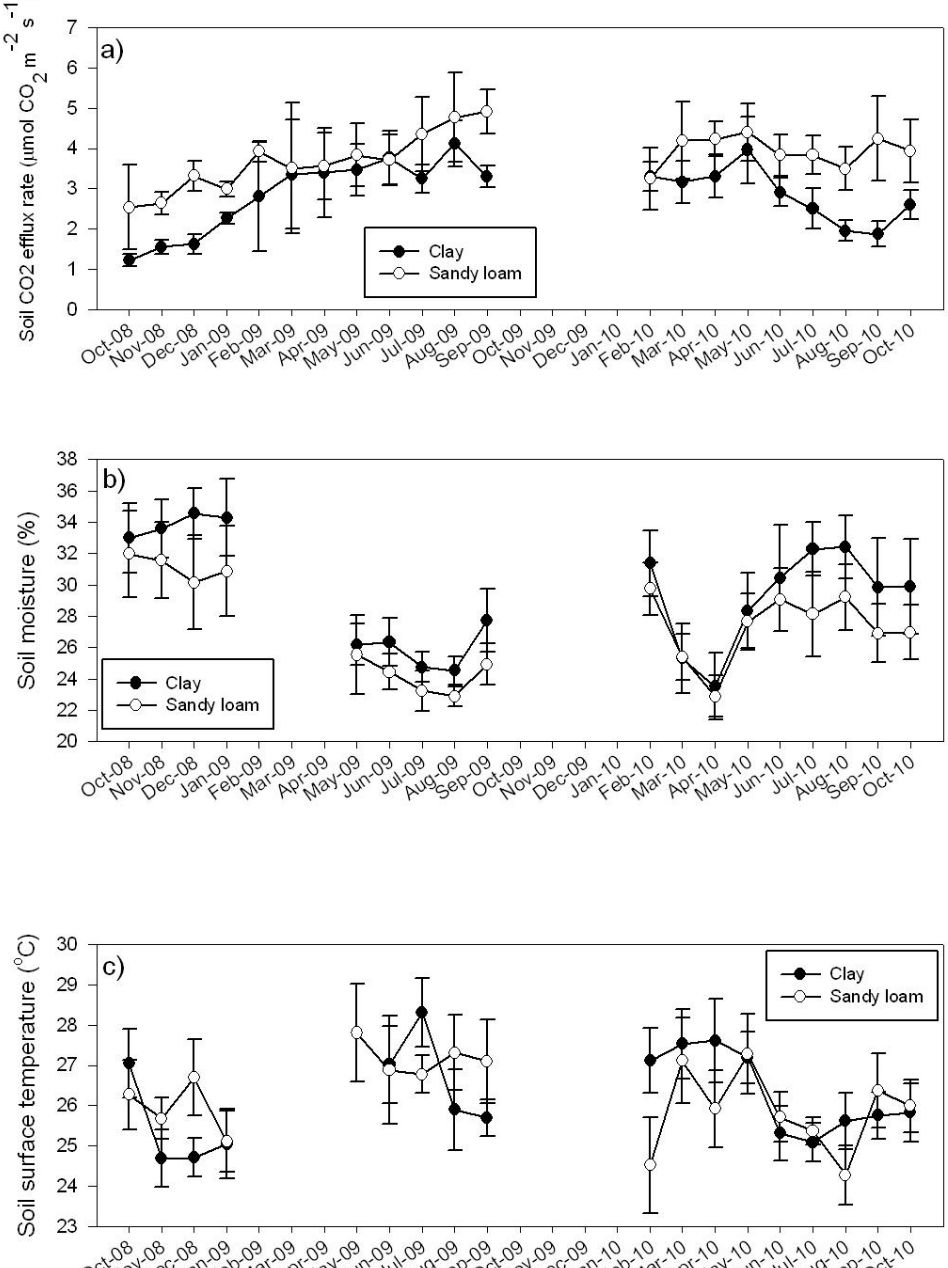
4.4. Results

4.4.1. Temporal Variation of Total R_s on Clay and Sandy Loam in the One-Hectare Plot

We first focus on recorded patterns of total soil CO_2 efflux from the 25 points on each one-hectare plot. There was a notable seasonal pattern observed over two years of monthly measurement on both sandy loam and clay sites. R_s gradually increased in the first year from October 2008 to September 2009 (Figure 4.2a), while soil moisture declined over the same period (Figure 4.2b). R_s progressively declined from May to September 2010, while soil moisture increased from April to August 2010 due to the wetter months and decreasing solar radiation during that measurement period (Figure 4.2d). In addition, there was a brief decline in soil surface temperature from May to August 2010 (Figure 4.2c).

4.4.2. The Effect of Environmental Factors on R_s across Sandy Loam and Clay in the One-Hectare Plot

We next explore the relationship between total R_s (averaged across the 25 microsites) and environmental factors (soil moisture, soil surface temperature and solar radiation). Total R_s showed a significant decrease with increasing soil water content on both sandy loam (r^2 = 0.71, $p < 0.001$) and clay (r^2 = 0.62, $p < 0.001$) (Figure 4.3a). R_s also showed a significant exponential increase with soil surface temperature (< 100 cm below soil surface) on both clay (r^2 = 0.24, p < 0.05) and sandy loam (r^2 = 0.28, $p < 0.05$) (Figure 4.3b). Soil temperature at 10 cm did not show any clear significant relationship to the monthly variation of R_s. When a minimum adequate multiple regression model was developed, soil moisture contributed most strongly to the variation of monthly R_s over the two years of measurement across clay and sandy loam (r^2 = 0.66, $p < 0.001$), with soil surface temperature and soil temperature unable to significantly explain the residual variance ($p > 0.05$). This suggests that soil moisture is the most important of the factors measured in this study for controlling the seasonal variation in R_s, but, rather unexpectedly, R_s declines with increasing soil moisture.



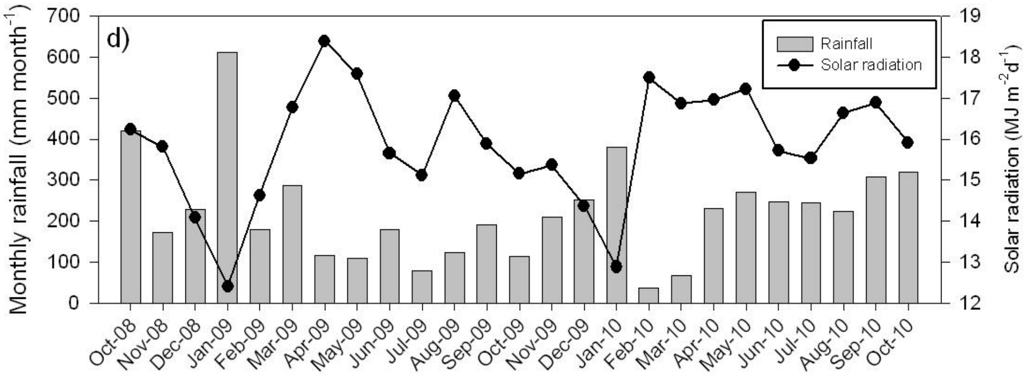


Figure 4.2: a) Mean total soil CO_2 efflux (R_s), b) soil moisture (%), c) soil surface temperature (^oC), and d) monthly rainfall (mm mo^{-1}) and solar radiation (MJ m^{-2} d^{-1}) on sandy loam (white circles) and clay (solid circles) from October 2008 to October 2010. Each point is the monthly average value (n = 25) on clay and sandy loam. All fluxes are in units of µmol CO_2 m^{-2} s^{-1}.

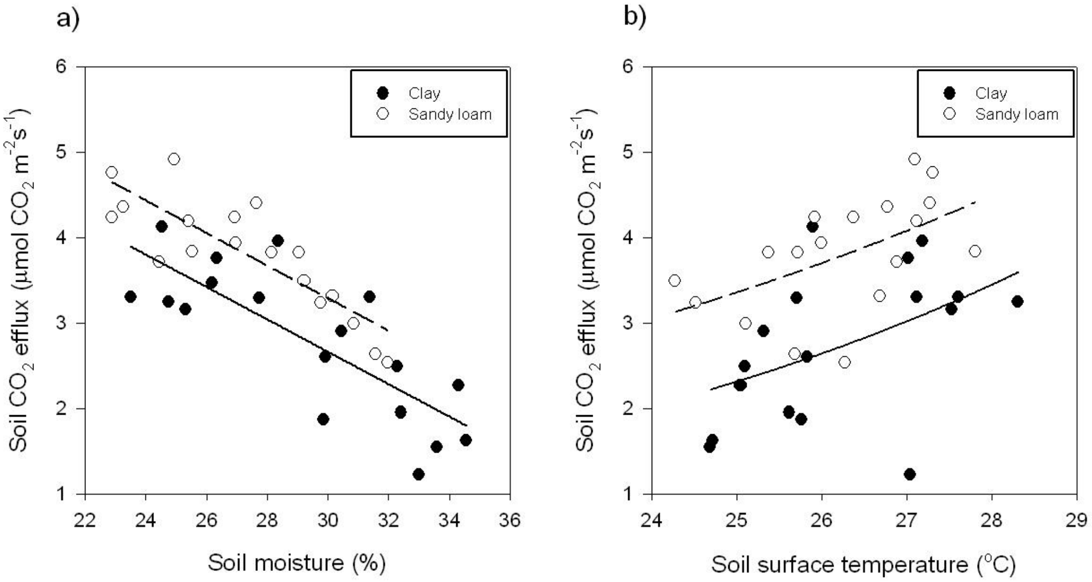


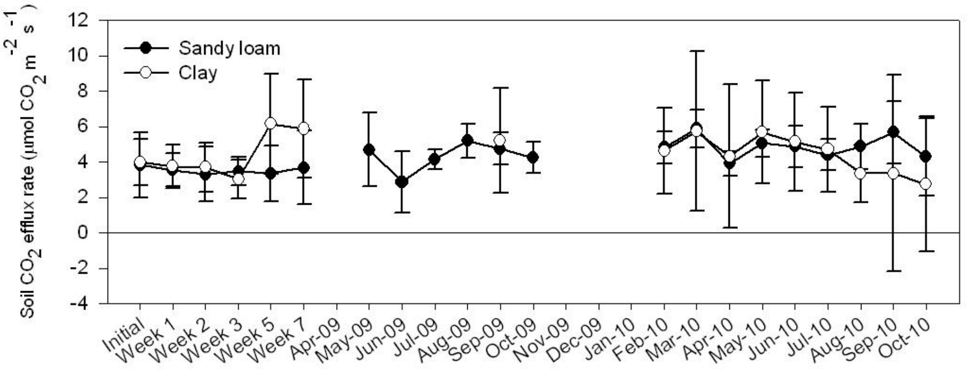
Figure 4.3: Relationship between the R_s and a) soil moisture (%), b) soil surface temperature (^{o}C) across sandy loam (white circle) and clay sites (solid circle) in the one-hectare plot from October 2008 to October 2010. Each point represents monthly average R_s on clay and sandy loam sites (n = 18). Least squares regression lines for sandy loam (broken line) and clay (solid line) are plotted at $p < 0.05$.

4.4.3. Temporal Variation of Total R_s and its Soil Components over the DIRT Experimental Plot

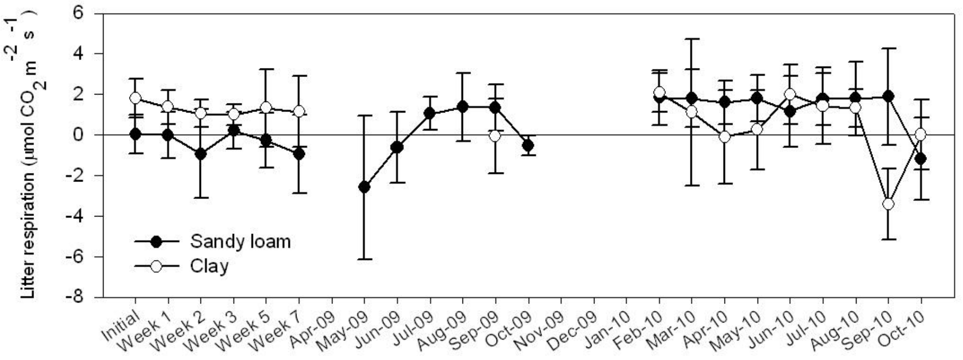
We next focus on the DIRT experiments to explore how total R_s is partitioned into components, and whether seasonal variation in any particular components dominates any overall seasonality in R_s. Mean total R_s on the DIRT plots showed little variation between sandy loam and clay soils from January 2009 to October 2010 (Figure 4.4a). However, there was a progressive decrease in total R_s observed on clay during the wetter months and from May to October 2010 (Figure 4.4a). This coincided with significantly higher mean soil moisture in 2010 (mean = 24.3%) than in 2009 (mean = 23.0%, t = 8.73, $p < 0.05$) (Figure 4.2b), probably because of the relatively higher rainfall recorded in 2010 (Figure 4.2d). Based on a subset of data between April to October in 2009 (drier months) and 2010 (wetter months) on the sandy loam, in which contrasting wetter and drier months were observed during the measurement period (Figure 4.2d), there was no significant difference (t = 0.77, $p = 0.45$, d.f. = 29.7) in R_s between drier and wetter months. In addition, soil temperature progressively declined during the same period from April to October

The partitioned soil components such as R_{litter}, R_{SOM}, R_{root} and R_{myc} respiration showed no clear seasonal pattern across sandy loam and clay over time (Figure 4.4b–4.4e). However, there was a brief decline in R_{root} and R_s, from May to September 2010 (Figure 4.4c and 4.4a). This suggests that seasonal variation in R_s could be driven by root respiration when water is not a limiting factor (Figure 4.5b).

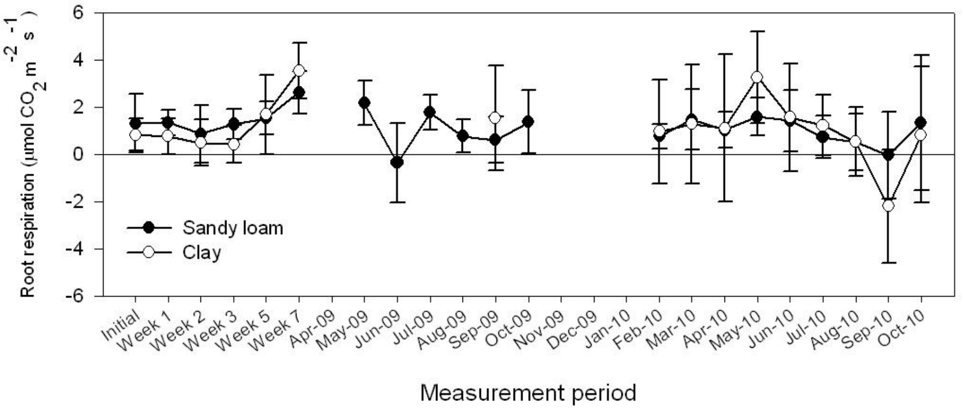
a) Total R_s



b) R_{litter}



c) R_{root}



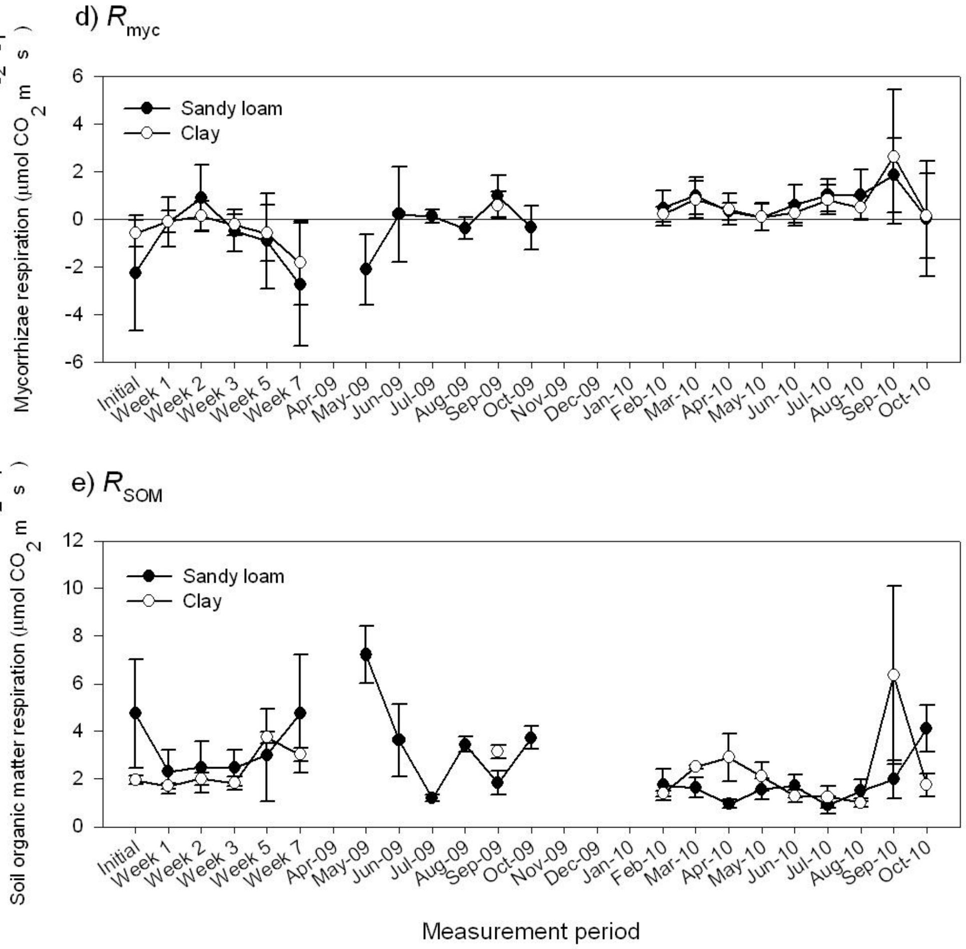
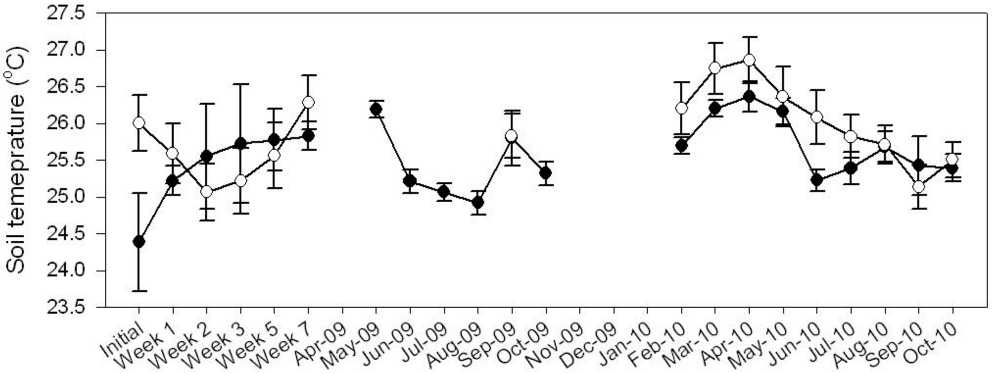
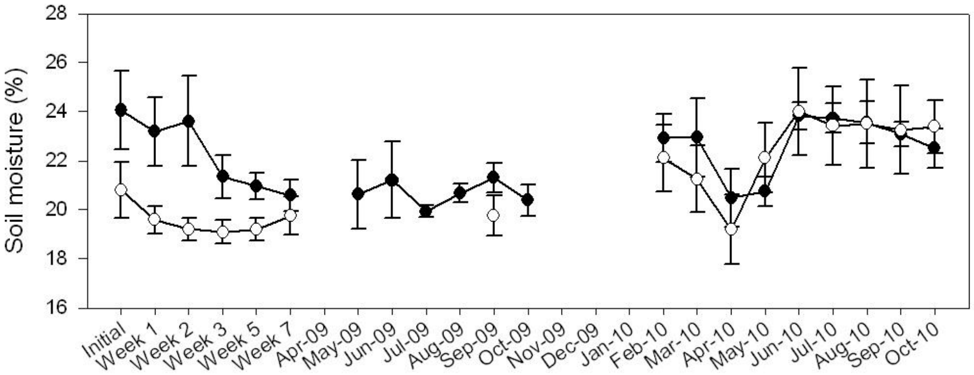


Figure 4.4: Average CO_2 efflux of a) total soil respiration (R_s), b) litter (R_{litter}), c) root (R_{root}), d) mycorrhizae (R_{myc}), and e) SOM (R_{SOM}) on both sandy loam (solid circles) and clay soil (white circles) in DIRT plot from January 2009 to October 2010. Each point is the average value across three replicates of T1, T2, and T3. Initial indicates post-treatment (14 days) soil respiration rate. Measurements were conducted on 8 January 2009 in sandy loam, while measurements on clay soils started on 15 July 2009. All fluxes are in units of µmol CO_2 m^{-2} s^{-1}. Standard errors of the mean are plotted as error bars.

a) Soil temperature



b) Soil moisture



c) Soil surface temperature

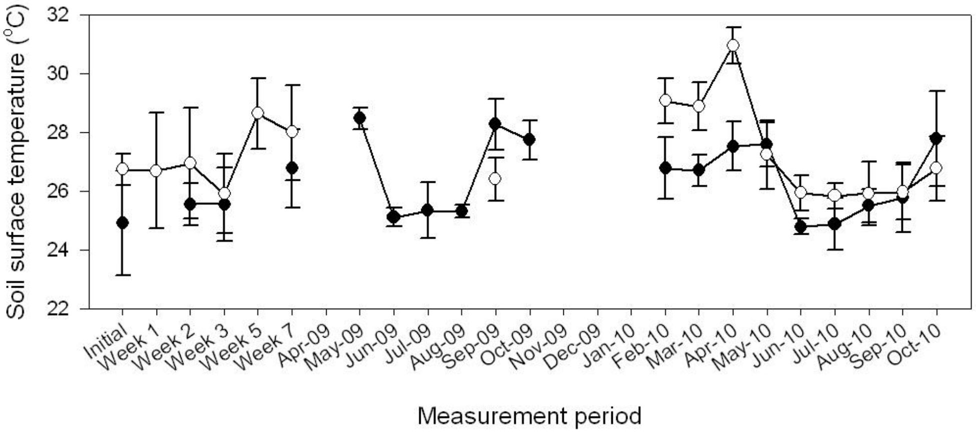


Figure 4.5: a) Soil temperature, b) soil moisture, and c) soil surface temperature on sandy loam (solid circles) and clay (white circles) sites in DIRT plot from January 2009 to October 2010. Error bars denote standard deviations around the mean.

The soil components showed variable flux patterns from January to August 2009, indicating that the effect of disturbance could persist up to nine months after installation. Fluxes of soil components appeared stable in the following year from February to October 2010. R_{litter}, R_{myc}, and R_{SOM} showed considerable month-to-month variation, with numerous outliers (Figure 4.4b, 4.4d, and 4.4e). In particular, R_{myc} on the clay site appears particularly problematic with frequent negative values. This is because unusually high fluxes were consistently measured on the T_{myc} treatment across all three replicates (especially T3), suggesting that the clay soil is particularly vulnerable to the disturbance introduced by installing the mycorrhizal treatment. In contrast, the R_{myc} at the sandy loam site seemed stable and plausible. In the absence of alternative estimates of R_{myc} and the clear impossibility of negative mean values, we decided to apply the value of R_{myc} measured at the sandy loam site to the clay site. R_{root} (clay) was then calculated as R_{rhizo} (clay) - R_{myc} (sandy loam), where R_{rhizo} is given as the sum of R_{myc} (clay) and R_{root} (sandy loam). Mean R_{myc} values from the sandy site were 1.9 ± 0.2 Mg C $\mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$, about 11% of R_s.

The mean value of R_s in the DIRT plots was 17.7 ± 0.2 Mg C $\mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ on clay and 18.1 ± 0.2 Mg C $\mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ on sandy loam, compared to whole-hectare plot values of 11.2 ± 0.2 Mg C ha^{-1}yr-1 on clay and 14.6 ± 0.2 Mg C $\mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ on sandy loam over two years of measurement (Table 4.1). Hence the DIRT experiment treatments may be at sample locations with soil CO_2 fluxes substantially higher than the hectare mean values.

Table 4.1: Annual total R_s and the contribution of litter, root, mycorrhizae and SOM to total R_s on sandy loam and clay from August 2009 to October 2010. Values are means ± standard error. All fluxes are in units Mg C ha^{-1} yr^{-1}

	Clay	**Sandy loam**	**Mean percentage clay (%)**	**Mean percentage sandy loam (%)**	**Clay (hectare-level)**	**Sandy loam (hectare-level)**
R_s (one-hectare)	11.2 ± 0.2	14.6 ± 0.2				
R_s	17.6 ± 0.8	18.1 ± 0.2			11.2 ± 0.2	14.6 ± 0.2
R_{litter}	2.5 ± 0.5	4.4 ± 0.3	14.2 ± 2.9	24.3 ± 1.7	1.6 ± 0.3	3.5 ± 0.2
R_{root}	4.0 ± 0.5†	3.7 ± 0.2	22.7 ± 3.0	20.4 ± 1.1	2.5 ± 0.4	3.0 ± 0.2
R_{myc}	2.2 ± 0.3‡	1.9 ± 0.2	12.5 ± 1.8	10.5 ± 1.1	1.4 ± 0.2	1.5 ± 0.2
R_{SOM}	8.9 ± 0.3	8.1 ± 0.1	50.6 ± 2.9	44.8 ± 0.7	5.7 ± 0.5	6.5 ± 0.1
R_{rhizo}	6.3 ± 0.4	5.6 ± 0.2	35.8 ± 2.8	30.9 ± 1.2	4.0 ± 0.4	4.5 ± 0.2

†value corrected by $R_{root} = R_{rhizo} - R_{myc\ (sandy\ loam)}$, where $R_{rhizo} = R_{myc\ (clay)} + R_{root\ (sandy\ loam)}$, and $R_{myc\ (sandy\ loam)}$ values from sandy loam were used because of unstable T_{myc} obtained on clay

‡R_{myc} on clay is corrected with R_{myc} values from sandy loam site

4.4.4. Effects of Soil Water Content and Soil Temperature on Total R_s and its Soil Components

We next explore seasonal variation in the components of soil respiration DIRT partitioning plots, in order to determine which components of soil respiration drive seasonal variation in total soil respiration. We examined correlations between all components of R_s and three environmental variables: soil temperature, soil moisture and solar radiation. The regressions against soil temperature were exponential based on the theoretical justifications provided by Lloyd and Taylor (1994), and linear against moisture and solar radiation in the absence of any *a priori* theoretical expectation.

In contrast to the whole-hectare analysis above, no significant relationship was found between R_s in the DIRT plots and soil moisture, but an exponential positive relationship was found with soil temperature on the clay site ($r^2 = 0.25$, $p < 0.01$) (Figure 4.6a) from January 2009 to October 2010. Based on a minimum adequate multiple regression model, soil temperature significantly contributed to the variation of total R_s on the sandy loam site, but could only explain 21% of the variation in R_s ($r^2 = 0.21$, $p < 0.01$).

At the clay site, two components of soil respiration did show a relationship with soil moisture: R_{litter} respiration showed a positive relationship ($r^2 = 0.13$, $p < 0.05$; Figure 4.7a) and R_{SOM} a negative relationship ($r^2 = 0.23$, $p < 0.01$; Figure 4.7b). At the sandy loam site, R_{litter} again increased with soil moisture ($r^2 = 0.16$, $p < 0.05$; Figure 4.7a), as did R_{myc} ($r^2 = 0.17$, $p < 0.01$; Figure 4.7b). In addition, the multiple regression model suggested that the variations in R_{litter}, R_{SOM} and R_{myc} were mainly driven by soil moisture on the sandy loam and clay sites ($p < 0.05$). However, the low coefficient of determination ($r^2 < 0.25$) observed in these interactions probably reflects the small sample size, rather than the absence of any strong effect on total R_s, R_{litter} and R_{SOM}. In the sandy loam soil, we found that R_{SOM} was highly correlated with soil moisture, soil temperature and soil surface temperature ($r^2 = 0.46$, $p < 0.001$), given by $R_{\text{SOM}} = 16.3477 + 0.3227(\text{soil moisture}) - 1.6529(\text{soil temperature}) + 0.7808(\text{soil surface temperature})$.

There was a significant relationship between solar radiation and R_{litter} ($r^2 = 0.43$, $p < 0.05$) on the clay site (Figure 4.8), but no relationship between solar radiation and soil and root respiration fluxes.

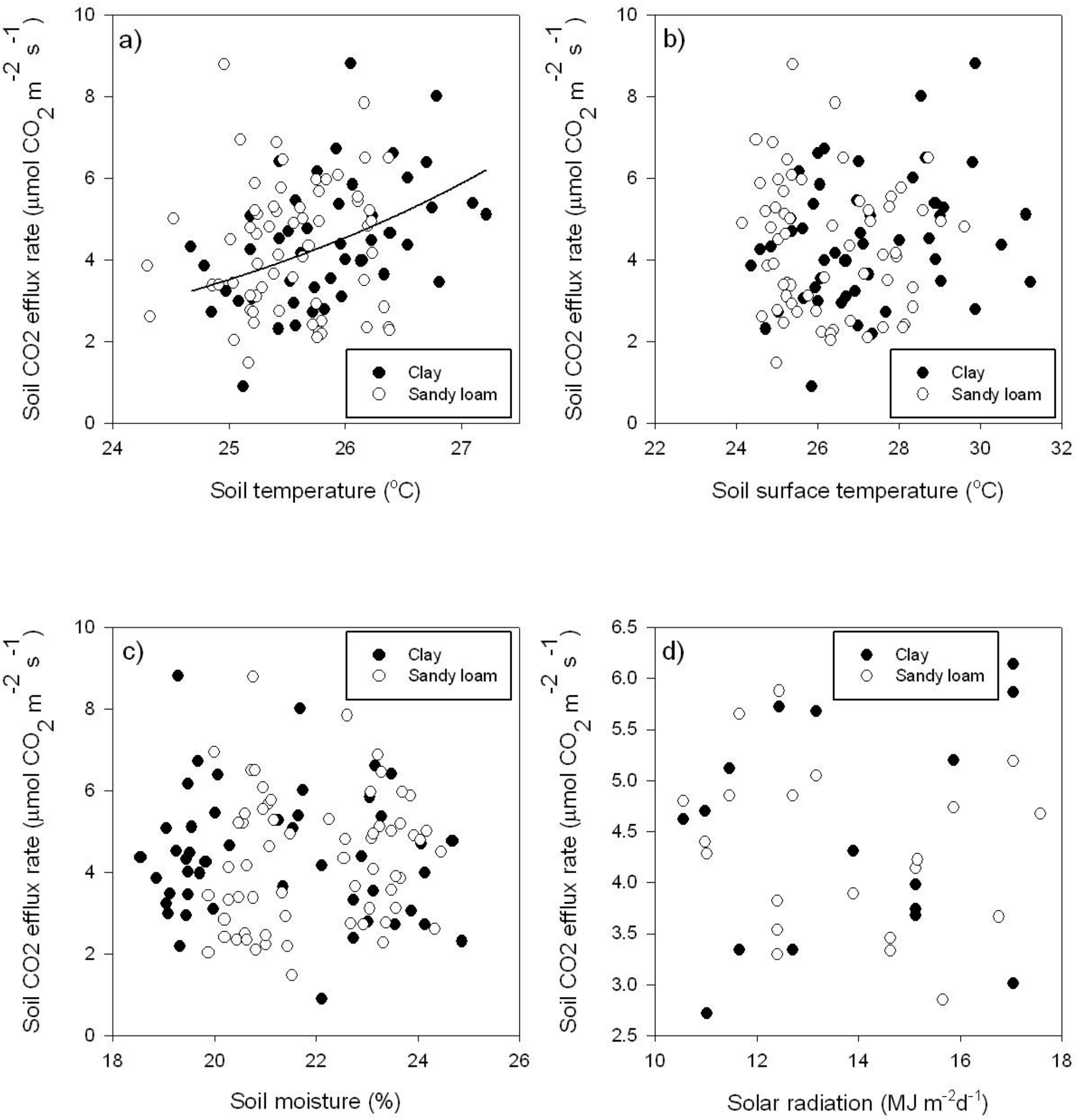


Figure 4.6: Relationship between monthly soil CO$_2$ efflux (R_s) over DIRT experimental plot and a) soil temperature (°C), b) soil surface temperature (°C), c) soil moisture (%), and d) solar radiation (MJ m^{-2} d^{-1}) across sandy loam (white circle) and clay (solid circle) sites from January 2009 to October 2010. Each point is the monthly average soil efflux of three replicates in T1, T2, and T3. The least squares regression line for the clay site (solid line) is plotted at $p < 0.05$.

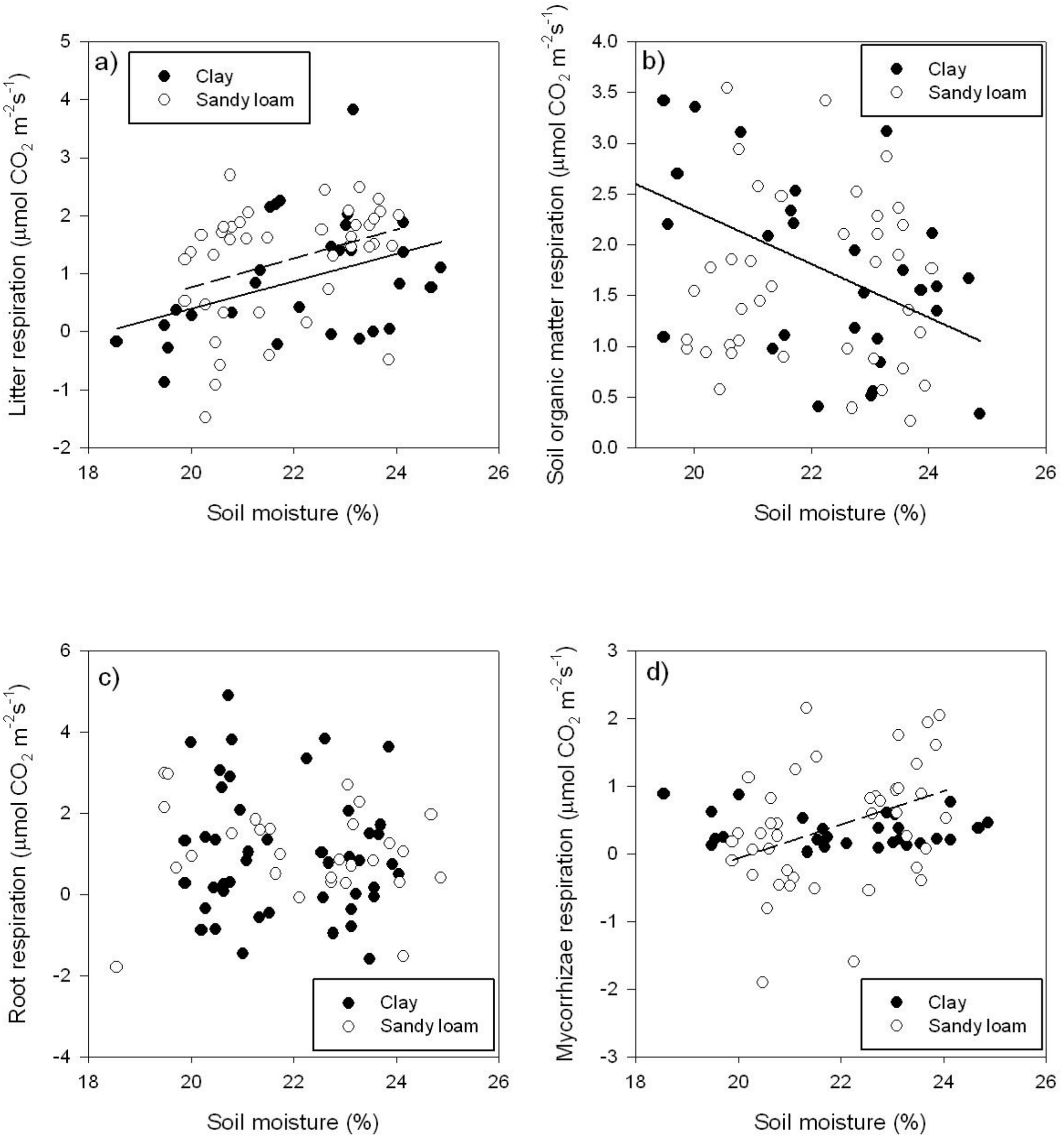


Figure 4.7: Relationship between soil moisture (%) and a) litter respiration (R_{litter}), b) SOM (R_{SOM}) respiration, c) root (R_{root}) respiration, and d) mycorrhizae (R_{myc}) respiration across sandy loam and clay sites in DIRT plot from August 2009 to October 2010. Each point is the monthly average value of three replicates in T1, T2, and T3. The least squares regression lines for the clay site (solid line) and sandy loam site are plotted at $p < 0.05$.

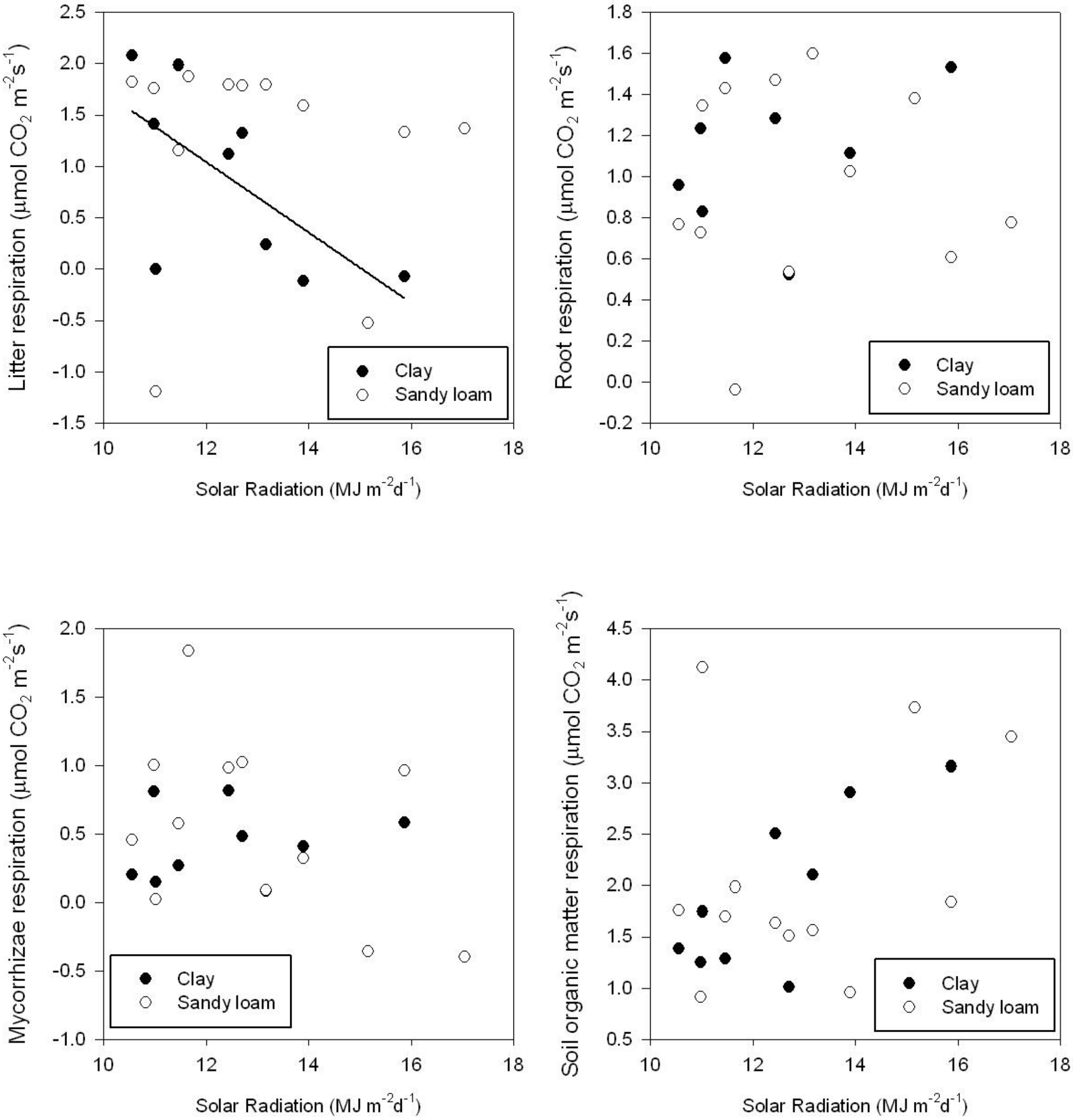


Figure 4.8: Relationship between solar radiation (MJ m^{-2} d^{-1}) and a) litter respiration (R_{litter}), b) root (R_{root}) respiration, c) mycorrhizae (R_{myc}) respiration, and d) SOM (R_{SOM}) across sandy loam and clay sites in DIRT plot from August 2009 to October 2010. Each point is the monthly average value of three replicates in T1, T2, and T3.

4.4.5. Mean Partitioning of Soil Respiration and its Components

In the one-hectare plots, R_s on clay (2.84 ± 0.12 μmol CO_2 m^{-2} s^{-1}) was significantly lower than on the sandy loam site (3.78 ± 0.17 μmol CO_2 m^{-2} s^{-1}, t = 6.817, $p < 0.05$, d.f. = 956.4) from October 2008 to October 2010. The mean annual R_s over one hectare was 11.2 ± 0.2 Mg C ha^{-1} yr^{-1} on clay and 14.6 ± 0.2 Mg C ha^{-1} yr^{-1} on sandy loam over the two years of measurement (Table 4.1)

In the DIRT experimental plots, the average total R_s on clay soil of 4.47 ± 1.10 μmol CO_2 $m^{-2}s^{-1}$ was not significantly different from the sandy loam of 4.82 ± 0.35 μmol CO_2 m^{-2} s^{-1} (t = 0.91, p = 0.36, d.f. = 59.1) from August 2009 to October 2010. However, there was significant variation in within-plot measurements among T1, T2, and T3 replicates in each of the sandy loam and clay soils ($p < 0.01$), indicating that there could be a large spatial heterogeneity. In both cases, the R_s fluxes in the DIRT plots were significantly higher than the mean fluxes observed over the corresponding one-hectare plot.

Soil components such as R_{litter}, R_{root}, R_{myc}, and R_{SOM} were not significantly different (p = 0.49) between the sandy loam and clay sites, with estimated mean CO_2 efflux of 1.83 ± 0.38 μmol CO_2 m^{-2} s^{-1}, 0.99 ± 0.41 μmol CO_2 m^{-2} s^{-1} and 0.59 ± 0.24 μmol CO_2 m^{-2} s^{-1} and 2.23 ± 0.22 μmol CO_2 $m^{-2}s^{-1}$ respectively. Moreover, R_{myc} and R_{root} together contributed 1.59 ± 0.33 μmol CO_2 m^{-2} s^{-1} to total R_s across clay and sandy loam sites. The mean annual flux of soil components scaled to one hectare on clay and sandy loam (clay/sandy loam) was 5.6 ± 0.5/6.5 ± 0.1 Mg C ha^{-1} yr^{-1} for SOM, 1.6 ± 0.3/3.5 ± 0.2 Mg C ha^{-1} yr^{-1} for litter, 1.4 ± 0.2/1.5 ± 0.2 Mg C ha^{-1} yr^{-1} for mycorrhizae, and 2.6 ± 0.4/3.0 ± 0.2 Mg C ha^{-1} yr^{-1} for roots (Table 4.1).

4.5. Discussion

4.5.1. Annual total R_s and the Respiration of Soil Components

We quantified the annual total R_s and the contribution of soil components in a lowland dipterocarp forest in Borneo. Our mean annual R_s is relatively lower than previous studies in the Southeast Asia region (Hashimoto *et al*., 2004; Adachi *et al*., 2006; Ohashi *et al*., 2008; Katayama *et al*., 2009), but within the range expected for tropical forests (Bond-Lamberty and Thomson, 2010).

R_h contributed approximately 77% to annual R_s across sandy loam and clay sites. This is within the range estimated by varying partitioning methods recently reviewed across the tropical forests (Subke *et al*., 2006). The majority of R_h was derived from surface organic litter, SOM and mycorrhizae, with each component contributing approximately 24%, 61%, and 15% to total R_h respectively. In our study, R_{litter} shows a relatively higher contribution to annual R_s than has been reported in tropical forests elsewhere (e.g. Chambers *et al*., 2004; Sayer *et al*., 2007; Sayer *et al*., 2011), but agrees with an earlier study undertaken in the Pasoh Forest Reserve (Nakane, 1980). By comparison, Metcalfe *et al*. (2007) estimated a much lower contribution of annual litter respiration (6–13%) at an Amazon rainforest site with a much more pronounced dry season.

Higher annual R_s is typically associated with declining R_h/R_s because greater above-ground gross primary productivity increases R_s due to increased allocation of assimilated C to R_a (Subke *et al*., 2006). We found that the proportion of R_{root}, approximately 22% of total R_s, is relatively lower than typical estimates (40–60%) in tropical forests (Nakane, 1980; Trumbore *et al*., 1995; Hanson *et al*., 2000; Chambers *et al*., 2004; Metcalfe *et al*., 2007).

4.5.2. The Effects of Environmental Factors on Rs and Soil Components

In the one-hectare study site, total R_s is negatively correlated with, and well explained by, soil water content (Figure 4.3). Higher soil moisture may have decreased CO_2 efflux due to water-filled pores that reduce gas diffusivity. Suppressed R_s at high soil moisture levels can also potentially be explained by reduced soil aeration that may inhibit the respiratory sources for aerobic microbial activity (Davidson *et al*., 2000; Schwendenmann *et al*., 2003; Adachi *et al*., 2006). In addition, larger soil porosity typically present in sandy loam soil may potentially reduce the rate of this gas diffusivity. The rate of diffusion is higher on sandy loam than on clay, as observed from the slope in Figure 4.3a. This implies that the spatial variation and physico-chemical properties of the soil mediate R_s responses to soil water content (Sotta *et al*., 2006; Hashimoto *et al*., 2007; Takahashi *et al*., 2011).

In the DIRT plot, the responses to soil water content are different among all soil components (Figure 4.7). Our results show that higher soil moisture significantly increases R_{litter}. This relationship is also observed for R_{myc} on clay, indicating higher CO_2 efflux due to an increase in microbial activity associated with fine roots. Our interpretation that higher soil moisture may inhibit microbial activity due to decreased gas diffusivity is further supported by the negative relationship between R_{SOM} and soil moisture on the sandy loam.

There have been many reviews showing that R_s increases exponentially with soil temperature when soil water content and other environmental factors are not limiting (Singh and Gupta, 1977; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Raich *et al*., 2002; Reichstein *et al*., 2003; Bond-Lamberty and Thomson, 2010). In our study, we have found very low dependence of total R_s on soil temperature (< 10%). Hence, the relationship between R_s and soil temperature may be confounded by other environmental factors when assessing seasonal long-term measurements (Metcalfe *et al*., 2007), particularly in tropical forests where the magnitude of temperature variation is usually relatively slight.

4.5.3. The Partitioning of Soil CO_2 Efflux

Partitioning soil CO_2 efflux is challenging and different approaches are likely to reflect different effects and show different magnitudes. Our partitioning approach is more comprehensive in that we accounted for mycorrhizal respiration, which is rarely quantified in tropical forests. The partitioning of R_s using various treatments may have introduced large disturbances to the soil system. To address this issue, we allow the DIRT plot to stabilise and recover from treatment manipulation. The response of CO_2 efflux from soil components was variable during initial observation (the first 2–3 months), but showed a stable pattern thereafter. Furthermore, it has been shown that the response of soil CO_2 efflux may take up to one year to stabilise depending on the season of the experimental set up and soil moisture (Sayer *et al*., 2007). Similar approaches have been used in the temperate deciduous and coniferous forests (Nadelhoffer *et al*., 2006). Therefore, long-term repeated measurements are needed to clearly define the equilibration stage and estimate accurate contributions of soil components. There include additional observations and sampling such as litter decomposition (Sayer *et al*., 2006).

4.6. Conclusion

Our results shed light on the partitioning of soil CO_2 efflux in a lowland tropical forest. There was a notable seasonal variation, with an increase in soil CO_2 efflux when soil moisture declines. R_s and R_{litter} are mainly driven by soil water content. We have shown that the annual R_s are driven by R_h, mainly contributed by SOM and litter respiration. The allocation to R_a was relatively low. Our approach to quantifying the partitioning of soil CO_2 efflux is comprehensive and allows plausible estimation of respiration from soil components. Further work, applying this approach at other tropical sites and over longer timescales, will help to build a more comprehensive picture of the role of this understudied biome in the global carbon cycle.

4.7. Acknowledgement

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Chapter 5

Chapter 5: Annual Budget and Seasonal Variation of Above- and Below-Ground Net Primary Productivity in a Lowland Dipterocarp Forest in Borneo

Overview

It is well recognised that there is a lack of data on the productivity of tropical forests, particularly in regard to Asian forests. This chapter provides information on the above- and below-ground net primary productivity (NPP) for forest plot on two contrasting soil types. This is the first attempt to determine the annual budget for all components of NPP in a lowland Asian tropical forest. A similar methodological approach has been employed to that widely used in Amazonian forests, so as to directly compare the findings with similar observations from Amazonian forests. In addition, the paper explores the seasonal variation of each NPP component in order to understand how allocation of NPP may shift over time, as well as if the variation may be driven by particular environmental factors. This contributes to our understanding of tropical forest productivity, which plays a critical role in the global carbon cycle and ecosystem functioning.

This study was conducted with the support of the Center for Tropical Forest Science (CTFS), which provided the census data. Various collaborators[*] contributed to this study: Tomo'omi Kumagai and Tomonori Kume provided the meteorological data; Hiroko Kurokawa provided the herbivory data; Sylvester Tan assisted in establishing the experimental design; and Mohd. Haniff Harun provided various instruments for measurements. The study overall and this chapter in particular were supervised by Yadvinder Malhi.

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[*] Contribution Statement: experimental design: KLK, YM, ST, MHH; data gathering: KLK, ST; data analysis: KLK; interpretation of results: KLK, YM; paper writing: KLK.

5.1. Abstract

Tropical forests are thought to have amongst the highest values of NPP on Earth, but comprehensive data on NPP have rarely been collected for tropical forests, especially outside of the Neotropics. In addition, almost nothing is known about any seasonal variation of NPP in the aseasonal climate of parts of the tropics. In this study, we quantify above- and below-ground NPP, along with additional environmental factors over a 1–2 year period in a lowland dipterocarp forest in Borneo, on two one-hectare plots at Lambir Hills National Park, Sarawak, Malaysia. The site is characterised by high annual rainfall and typically there is no month of the year when the forest is under water stress. We estimated the total NPP to be 15.82 ± 0.90 Mg C ha^{-1} yr^{-1} (mean ± standard error) for a forest plot on clay soil and 12.85 ± 0.69 Mg C ha^{-1} yr^{-1} for a forest plot on sandy loam soils. Of this productivity, the allocation to above-ground NPP is 81.7 ± 6.7/80.5 ± 6.0% and to below-ground NPP is 18.3 ± 3.7/19.5 ± 2.6% on clay and sandy loam respectively. The litterfall ($NPP_{\text{litterfall}}$) and above-ground coarse wood (NPP_{ACW}) contributed the largest fractions of the total NPP. Fine root productivity ($NPP_{\text{fine roots}}$) shows stronger seasonal variation relative to other components of NPP. There is evidence suggesting inter-annual variation in $NPP_{\text{fine roots}}$, leaf flush, litterfall and NPP_{ACW}. The seasonal allocation of NPP shows a strong variation and contrasting shifts between clay and sandy loam. Following the wetter period on the clay site, productivity increases and there is increased allocation to NPP_{ACW} and reproductive materials on clay. In contrast, on the sandy loam soils NPP is higher in the less wet season, with large proportions invested in leaves and reproductive materials. This is the first attempt to develop a complete seasonal allocation profile to clearly understand how the biomass of a tropical forest is allocated to the various components of NPP over the seasonal cycle. The study highlights the marked seasonality of a tropical forest even under largely aseasonal environmental conditions, as well as illuminating the effect of contrasting seasonality on contrasting soil types.

5.2. Introduction

The magnitude and dynamics of the allocation of NPP in various tissues and organic structures in plants are essential characteristics of forest ecosystem ecology but have rarely been well-quantified for tropical forests (Malhi *et al*., 2011; Malhi, 2012). Tropical forests are amongst the most productive ecosystems on Earth and have been estimated to account for approximately one-third of the global terrestrial net NPP (Melillo *et al*., 1993; Field *et al*., 1998; Grace *et al*., 2001). In addition, tropical forests play an important role in the exchange of carbon with the atmosphere, as well as in the overall carbon balance of the terrestrial biosphere.

NPP is the net production of biomass used by plants to produce various organic structures including leaves, wood, reproductive materials, roots, root exudation, and volatile organic compounds (Roy *et al*., 2001). Quantifying the biomass components that contribute to total NPP is difficult and confounded by challenging methodologies (Clark *et al*., 2001b). Hence, most studies have typically investigated components that are easily measured, such as above-ground coarse wood productivity or litterfall (Proctor *et al*., 1983; Clark *et al*., 2001b; Chave *et al*., 2008; Malhi *et al*., 2011). There are very few studies on below-ground biomass and productivity (Yoda, 1978; Green *et al*., 2005; Fisher *et al*., 2007; Niiyama *et al*., 2010), in particular in conjunction with above-ground productivity data, and it is often estimated as some fixed proportion of the above-ground biomass (Clark *et al*., 2001a). As such, it is difficult to generate a reliable estimation of the carbon budget for tropical forests (Kira, 1978; Chambers *et al*., 2004; Luyssaert *et al*., 2007; Malhi *et al*., 2009; Tan *et al*., 2010; Adachi *et al*., 2011). In recent years, a larger and more comprehensive dataset on tropical forest NPP has begun to emerge for the Andes-Amazon region (Chambers *et al*., 2004; Aragão *et al*., 2009; Girardin *et al*., 2010). However, estimation of NPP, and in particularly the allocation of

NPP, is still very limited in tropical forests elsewhere, such as in Africa or Asia (Malhi *et al*., 2011; Malhi, 2012).

The dipterocarp-dominated forests of Southeast Asia are well recognised for their richly diverse and relatively tall trees (Ashton, 1964; Whitmore, 1984; Ashton and Hall, 1992; Ashton, 2005), with very high above-ground biomass (Proctor *et al*., 1983; Yamakura *et al*., 1986; Yamakura *et al*., 1996; Paoli *et al*., 2008). On the island of Borneo, above-ground biomass in lowland dipterocarp forest is typically 60% more than in Amazonian forests (Slik, 2006). A considerable number of studies have estimated above-ground wood biomass for dipterocarp forests at several sites in Borneo (Proctor *et al*., 1983; Yamakura *et al*., 1986; Yamakura *et al*., 1996; Basuki *et al*., 2009; Kenzo *et al*., 2009; Morel *et al*., 2011; Saner *et al*., 2012), and others have done the same for litterfall (Proctor, 1984; Burghouts *et al*., 1992; Burghouts *et al*., 1994). However, studies of the components of NPP are rare in regard to Borneo (Kitayama and Aiba, 2002; Paoli and Curran, 2007) and generally scarce in Southeast Asia (Ogino *et al*., 1967; Yoneda *et al*., 1977; Kira, 1978; Hertel *et al*., 2009). Hence, quantification and understanding of productivity, its allocation, and their response to climate is imperative in a lowland dipterocarp forest. Moreover, to our knowledge no studies have examined the seasonality of NPP, a topic of particular interest in the generally aseasonal climate of Borneo.

So, the overall aim of this study is to quantify above- and below-ground NPP and develop a better understanding of the allocation of NPP and its seasonal variation in a Bornean lowland tropical forest. The specific research questions addressed in this study are as follows:

a) What is the above- and below-ground productivity, and how is it partitioned into wood material, leaves, flowers, fruits, fine roots and coarse roots in a lowland dipterocarp forest in Borneo?
b) What is the seasonal variation in the components of above-ground NPP and below-ground NPP, and how are these related to environmental factors?
c) What is the overall allocation of NPP at this site, and how does it vary between the sand and clay sites?

5.3. Materials and Methods

5.3.1. Study Site

This study was carried out in the 52-ha forest dynamics plot in Lambir Hills National Park, Sarawak, Malaysia (4^o 12’ N, 114^o 2’ E), which is part of the Center for Tropical Forest Science (CTFS) global network of large plots (Condit, 1995; Lee *et al*., 2004). Within the 52-ha plot, we established two one-hectare research plots (100 m x 100 m), one each on clay and sandy loam soils. The one-hectare plot was further divided into 25 subplots measuring 20 x 20 m. Lambir is an exceptionally diverse lowland mixed dipterocarp forest, with the highest recorded tree diversity in the Paleotropics (Phillips *et al*., 1994; Davies and Becker, 1996; Lee *et al*., 2002; Ashton, 2005). The Euphorbiaceae and Dipterocarpaceae are the most species-rich families at the site. The dipterocarp species have mass flowering events which occur periodically, including during our measurement period (Kettle *et al*., 2011). A comprehensive description of floristic and stand structure has been presented by Lee *et al*. (2002). The 52-ha forest dynamics plot was established in 1992 (Yamakura *et al*., 1995). All trees ≥ 1 cm in diameter at breast height (1.3 m, DBH) were mapped, identified to species, and their DBH measured following standard methods (Condit, 1998). The census was repeated in 1997 and every five years thereafter.

The soils in Lambir range from sandstone sandy loam to shale-derived clay. From this gradient, four soil types have been identified in order of increasing fertility and moisture: sandy loam, loam, fine loam, and clay based on soils clustering (Davies *et al*., 2005). The sandstone-derived soils are humult Ultisols (Soil Survey Staff, 2006), with densely matted fine roots on the surface horizon, high sand content (typically 68% sand), low nutrients and low water-holding capacity (Ashton and Hall, 1992; Davies *et al*., 1998). The shale-derived soils are clay-rich udult Ultisols (Soil Survey Staff, 2006) (typically 40% sand), with a thin litter layer on the soil surface, relatively higher fertility and high water-holding capacity (Davies *et al*., 1998; Davies *et al*., 2005). Davies *et al*. (1998) showed that sandstone-derived soils typically occur on slopes and ridges, while the shale-derived soils are mostly in low-lying gullies. The altitude difference between the highest point and the lowest point is approximately 150 m, with steep, undulating and complex bisected topography (Yamakura *et al*., 1995). The soils and geomorphology of Lambir have been previously described in detail (Watson, 1985; Ishizuka *et al*., 1998; Baillie *et al*., 2006; Tan *et al*., 2009).

To measure the main components in regard to NPP, we broadly used the protocols developed by the RAINFOR-GEM network, which are described in detail in a manual (available at http://gem.tropicalforests.ox.ac.uk/, Global Ecosystems Monitoring Network (GEM)) and which will facilitate direct comparison with new NPP data emerging from the African and Amazonian tropics.

5.3.2. Estimate of Above-Ground NPP (NPP_{AG})

Wood Density and Tree Height

Wood-specific gravity was determined for the most common species based on locally-measured wood density of 11 tree species (King *et al*., 2006) and five tree species of soil specialists and generalists (Heineman *et al*., 2011), all of which was assessed at the Lambir site. In addition, other values of wood density measured in this region (Borneo and West Malaysia) were included: 12 species from Kuala Belalong, Brunei (Osunkoya *et al*., 2007); four species from East Kalimantan, Indonesia (Basuki *et al*., 2009); 70 species from West Kalimantan, Indonesia (Suzuki, 1999); three species from the Pasoh Forest Reserve, Peninsular Malaysia (King *et al*., 2006); and three species from secondary forest near Lambir (Kenzo *et al*., 2009). For the remaining species, we used the average wood density of each individual species in a global wood density dataset (Chave *et al*., 2009; Zanne *et al*., 2009). Where data on wood density were not available for a particular tree species or an unidentified species (but genus or family known), we determined the average density to genus or family level. For unknown tree species and those unlisted in the global dataset (32 species), we used the Lambir average value of 0.64 g cm^{-3} (King *et al*., 2006).

Tree heights were derived from locally measured height data for clay and sandy loam sites in Lambir (King *et al*., 2009). Given that the tree species distribution in Lambir was edaphically biased to different soil types (Palmiotto *et al*., 2004; Davies *et al*., 2005; Russo *et al*., 2005), tree species were determined and assigned into clay (29 trees) and sandy loam (49 trees) respectively. Regression analysis was employed to explore the relationship between tree heights and DBH. The relationship between tree height and DBH was well-described by a quadratic regression on both clay ($r^2 = 0.98$, $p < 0.001$) and sandy loam ($r^2 = 0.97$, $p < 0.001$). The best-fit equations are as follow:

$$\text{Tree height (clay)} = -0.0029\left(\text{DBH}^2\right) + 0.7636(\text{DBH}) + 4.7529 \qquad \text{(Eq. 5.1)}$$

$$\text{Tree height (sandy loam)} = -0.0034\left(\text{DBH}^2\right) + 0.7679(\text{DBH}) + 4.6880 \qquad \text{(Eq. 5.2)}$$

where tree height was in metres, and DBH was in centimetres. Next, we applied this regression equation to the trees on clay and sandy loam sites.

Above-ground Coarse Wood NPP (NPP_{ACW})

Multiple tree censuses from sandy loam and clay sites were used to determine plot-level above-ground coarse woody biomass and fluxes. Four censuses over five-yearly intervals have been conducted by the CTFS following a standard protocol (Condit, 1998) on all trees > 1 cm DBH since 1992. All trees were identified to species (Lee *et al.*, 2005). Using these tree censuses from both the one-hectare clay and sandy loam sites, we determined the growth rate for all existing trees. We also separately estimated the growth and recruitment of only trees > 10 cm DBH, for comparability with other studies.

We assessed above-ground coarse woody biomass as a function of DBH and wood-specific gravity for each tree using an allometric equation for moist tropical forest stands (Chave *et al.*, 2005):

$$AGB = 0.0509 \times \rho \times DBH^2 \times H \qquad \text{(Eq. 5.3)}$$

where AGB is above-ground dry biomass (kg), ρ is the oven-dry wood specific gravity (g cm^{-3}), DBH is diameter at breast height, 1.3 m (cm), and H is height (m). The above-ground coarse wood productivity (NPP_{ACW}) was then estimated based on the change in woody biomass between census intervals. Biomass values were converted by assuming that dry-stem biomass has a carbon content of 47.4% (Martin and Thomas, 2011), based on a study in Panama which is the first to account for the volatile carbon lost when wood is dried.

Several allometric equations for estimating biomass in tropical dipterocarp forests have been developed in the Southeast Asian region (Kato *et al.*, 1978; Yamakura *et al.*, 1986; Basuki *et al.*, 2009; Kenzo *et al.*, 2009). Here we employed the allometric equation by Chave *et al.* (2005), which incorporates wood density and height data, to directly compare with similar studies conducted at several Amazonian forest sites. In addition, recent studies in Amazonia and Borneo showed that wood-specific density is important in seeking to produce accurate estimates and capture the spatial variation of above-ground biomass at a regional scale (Baker *et al*., 2004; Chave *et al*., 2005; Malhi *et al*., 2006; Slik, 2006; Slik *et al*., 2010).

To capture seasonal variation of NPP_{ACW}, we installed dendrometer bands on trees (≥ 10 cm DBH) and approximately 20 randomly selected fast-growing trees (≥ 10 cm DBH) on both clay and sandy loam sites. Monthly (for fast-growing trees) and three-monthly (all trees > 10 cm DBH) increments from dendrometer bands were recorded from June 2009 to September 2010. The dendrometers were installed in July 2008 (all subplots on sandy loam and 10 subplots on clay) and February 2009 (15 subplots on clay), but the first 10 and three months of data were not used to allow the dendrometer to settle onto the trees. The dataset was carefully checked for irregularities (e.g. measurement errors) and obviously erroneous data points were linearly interpolated. Dendrometer increments in each month were added to the initial DBH, which was measured prior to dendrometer installation, in order to estimate monthly diameter. Woody biomass was calculated using Equation 5.3 and biomass growth rates were determined by taking the difference in biomass between months. Monthly woody growth rates for all trees were estimated from the monthly growth rates for fast-growing trees, scaled to match the three-monthly growth rates measured by the wider dendrometer dataset. As the dendrometer trees did not include all the trees (≥ 10 cm DBH) in the one-hectare plot on clay (36 trees not included) and sandy loam (61 trees not included) sites, we scaled the monthly biomass increment by a scaling factor (1.22 on clay and 1.08 on sandy loam) based on the ratio of biomass growth of all trees over that of dendrometer trees, as determined from the long-term census data.

Furthermore, we tried to account for any moisture-related seasonal cycle that may be caused by bark or hydraulic expansion during wet periods and contraction during dry periods. We did this by separating live trees with very low growth rates ($NPP_{\mathrm{ACW}} < 0.05$ kg tree^{-1} day^{-1}) on clay (n = 124 trees) and sandy loam (n = 197 trees) and estimated annual seasonal growth for distinctively growing trees, calculating the mean seasonal growth cycle of these trees and subtracting this cycle from all other trees. In this wet, broadly aseasonal forest, the seasonal cycle was very small. The mean seasonal NPP due to moisture expansion effects was calculated at 0.001 Mg C ha^{-1} yr^{-1} on clay and 0.003 Mg C ha^{-1} yr^{-1} on sandy loam, making this effect negligible.

Litterfall NPP ($NPP_{\text{litterfall}}$)

Litterfall collection over a long-term steady state (typically one year or more) contributes to canopy production, but exclude canopy herbivory and in-canopy decay or trapped leaves. Dead organic material (woody material < 2 cm diameter) was collected from litter traps measuring 0.25 m^2 (0.5 x 0.5 m) installed at one metre above the ground in the middle of each 20 x 20 m subplot on both clay and sandy loam sites (25 traps in each plot in total). Collection took place from July 2008 to August 2009. Litterfall was collected every 14 days to minimise in-trap decomposition, oven-dried at 80^{o}C to constant weight, and weighed immediately after removal from the oven. The litter was separated into: i) leaves; ii) branches; twigs and woody tissue; iii) fruits, flowers and seeds; and iv) undefined fine debris. Biomass values were converted by assuming that dry-stem biomass has a carbon content of 50% (Kenzo *et al*., 2003).

Seasonal Leaf Productivity

Canopy productivity estimated from litterfall over annual or longer-term timescales may not capture the seasonal variability in leaf production because litterfall reflects the timing of canopy biomass loss rather than biomass gain. To determine the seasonal variation of leaf productivity, we combined the litterfall dataset with data on changes in leaf area index (LAI) and mean values of specific leaf area (SLA) based on the following equation (Doughty and Goulden, 2008):

$$\text{Leaf production} = \frac{\text{dLAI}}{\text{SLA}} + \text{leaf litterfall} \qquad \text{(Eq. 5.4)}$$

where leaf production is in g m^{-2}, dLAI is the change in LAI (m^2 m^{-2}) between months, SLA is the mean SLA (m^2 g^{-1}), and leaf litterfall is g m^{-2}.

We determined LAI by recording canopy hemispherical images using a digital camera (Nikon Coolpix 990) and a hemispherical lens (Nikon FC-E8 fisheye converter) near the centre of each of the 25 subplots across the one-hectare clay and sandy loam sites. Twenty images were recorded at one metre above the soil surface during overcast conditions in the early morning (06:30–08:00 h). LAI data were collected every month from August 2009 to May 2010. Monthly canopy hemispherical images were analysed using the CAN-EYE software (available at www4.paca.inra.fr/can-eye, Demarez *et al.*, 2008; Weiss, 2012).

Mean SLA was estimated by collecting sub-samples of leaf from 11 specialist dominant tree species on sandy loam and five specialist dominant tree species on clay. Fresh leaf samples collected were scanned, and the leaf areas were analysed using image analysis software available at http://rsb.info.nih.gov/ij/, ImageJ). The samples were then oven-dried to constant mass. SLA is the fresh leaf area divided by the dry mass of leaf.

Branch Turnover NPP (NPP$_{\text{branch turnover}}$*)*

The turnover of branches (branch growth and shedding not associated with tree death) can be a significant component of NPP but is rarely measured. To assess branch turnover, we conducted censuses every three months between August 2009 and July 2010. Fallen coarse woody materials (woody material > 2 cm diameter, including bark) were collected from four 100 m x 1 m transects established along the boundary within each one hectare plot. Initial collection of coarse woody materials was considered as dead wood stock rather than production of new branch material. Branches that were easily lifted were cut to only include the transect-crossing component, removed and weighed directly. Heavier and larger branches that could not be removed were recorded for dimensions (diameter, height, and length), and were allocated a wood density value based on their decomposition stage. In subsequent censuses, new branchfall material was noted. Care was taken to discard any branchfall associated with tree mortality, as that component is already included in the mortality data and whole-tree allometric equation.

NPP Lost to Leaf Herbivory ($NPP_{\text{herbivory}}$)

Foliar herbivory alters nutrient cycles and carbon inputs in the terrestrial ecosystems, and hence influences the feedback to above- and below-ground productivity (Bardgett and Wardle, 2003). Although leaf herbivory contributes a substantial fraction of losses (Coley and Barone, 1996), $NPP_{\text{herbivory}}$ is often unaccounted for in tropical forests (Clark *et al*., 2001b). In this study, we did not directly quantify herbivory for canopy leaves. We adopted an average herbivory rate of 0.0135% per day according to synchronous and continuous leafing patterns across 40 tree species in Lambir (Kurokawa and Nakashizuka, 2008). This involved measuring the percentage loss in area for each leaf sampled from the canopy and comparing the damaged leaf area (evidence of leaf being eaten) to the intact leaf shape from scanned images. The herbivory rate for each tree was estimated based on accumulated damage by the life span of the leaf to correct for potential underestimation (Kurokawa and Nakashizuka, 2008). Hence, the production lost to leaf herbivory was calculated by multiplying NPP_{leaf} by the herbivory rate. Given that this estimation may be associated with substantial sampling uncertainty and varies between canopy and understory level, we assigned a 50% error to the multiplying factor.

5.3.3. Estimate of Below-Ground NPP (NPP_{BG})

Coarse Root NPP ($NPP_{\text{coarse roots}}$)

Coarse root productivity is the least measured and estimated woody biomass component because it is difficult to sample large biomass below the stem without destructive sampling of trees. To estimate coarse root biomass, we used an allometric equation for coarse root biomass developed from a large-scale root excavation study in the Pasoh Forest Reserve in Peninsular Malaysia (Niiyama *et al*., 2010), a similar lowland dipterocarp forest to our study site:

$$\text{Dry mass coarse root}(\text{tree} \geq 2.5 \text{ cm DBH}) = 0.023 \times \text{DBH}^{2.59} \qquad \text{(Eq. 5.5)}$$

$$\text{Dry mass coarse root}(\text{tree} < 2.5 \text{ cm DBH}) = 0.079 \times \text{DBH}^{1.04} \qquad \text{(Eq. 5.6)}$$

where coarse roots per tree is in kg (coarse root in Equation 5.5 corrected for lost roots), and DBH is in centimetres. Because there is some uncertainty surrounding coarse root measurement, the allometric model, and variations between sites, we assign an error of 40% and propagate this through our calculations.

Fine Roots NPP ($NPP_{\text{fine roots}}$)

Production of fine roots was quantified using ingrowth cores, which were systematically installed in a 3 x 3 grid on each site in May 2008. Nine ingrowth cores made from mesh nets (mesh size: 1 cm^2) of 14 cm diameter and 40 cm height were installed to 30 cm in each site. The mesh nets were extracted every three months from September 2008 to October 2009, with new ones being installed at the same time. Roots were removed manually from the extracted soil cores in four 10-minute time steps (Metcalfe *et al*., 2007). Root-free soil was repacked into the mesh net and placed back into the soil. These cores were reinserted and compacted with care to replicate the natural soil conditions, horizon structure and bulk density as closely as possible. We fitted a logarithmic curve to the first 40 minutes of extracted root and predicted cumulative root mass up to 100 minutes (Metcalfe *et al.*, 2007). On average, an additional 38% and 49% of fine root mass on clay and sandy loam soils was collected in each ingrowth cores, which is comparable to the prediction put forward by Metcalfe *et al.* (2007). Fine production was estimated by scaling to a one-hectare area.

Given that fine roots production was estimated between 0 and 30 cm from the soil surface, we corrected the estimation up to 100 cm depth to reduce the discrepancies in fine root production measured from different soil depths. The depth correction applied here assumed that the ratio of fine root to coarse root biomass was invariant with depth, and fine root productivity per unit of fine root biomass was invariant (Malhi *et al.*, 2009). Following a similar approach to that employed by Malhi *et al.* (2009), the correction factor was calculated using the root profile biomass in the Pasoh Forest Reserve (Yoda, 1978). We extrapolated the root biomass up to 100 cm based on the following equation (Yoda, 1978):

$$W_R = W_{R0} \exp\left(-\varepsilon z\right) \qquad \text{(Eq. 5.7)}$$

where W_R is the dry mass of fine roots in Mg ha^{-1} cm^{-1}, W_{R0} is the biomass density of fine root at surface soil given as a constant value at 1.5 Mg ha^{-1} cm^{-1}, ε is given as constant of 0.073, and z is the soil depth in centimetres. Hence, the correction factor for soil depth between 30 cm and 100 cm was 1.125.

5.3.4. Statistical and Error Analysis

We analysed the data in this study to determine NPP components and allocations for above- and below-ground biomass over time. Using the monthly estimates, we plotted the results to look for seasonal variations. The student's t-test was used to compare differences in the annual and monthly mean between the clay and sandy loam sites. Statistical analysis was conducted using R statistical software (version 2.13.0; R Development Core Team) and the results were plotted using SigmaPlot 10.0 (Systat Software, Inc.).

We presented mean estimates with standard deviations (SD; reported as mean ± SD) and standard errors (SE; reported as mean ± SE). The propagation of errors were based on the quadrature of absolute errors for addition/subtraction and the quadrature of proportional errors for fractions (as in Aragão *et al.*, 2009; Malhi *et al.*, 2009), with the assumption that the uncertainties are independent and normally distributed.

5.4. Results

5.4.1. Meteorology

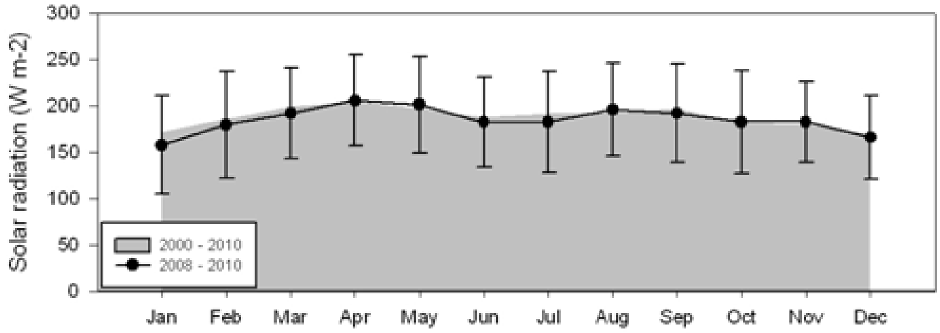
We analysed meteorological data for the two periods 2000–2010 (a context period) and 2008–2010 (the measurement period) (from an 80 m canopy crane approximately 3 km away from our study site). Lambir is characterised by little seasonality in climate (Kumagai *et al.*, 2005). The strongest seasonality is manifested in terms of rainfall, with a strong wet season associated with the north-eastern Monsoon from September to January, and a drier season from February to August (Figure 5.1c). However, even the drier season has mean monthly rainfall around 150 mm mo^{-1}, well above the 100 mm mo^{-1} typically transpiring from forest canopies (Fisher *et al.*, 2007), indicating that the site does not experience water stress at any time of the year. It should be noted, however, that the region does experience strong *El*-Niño associated droughts about once per decade (Walsh and Newbery, 1999; Malhi and Wright, 2004). Total mean annual precipitation over the 10-year period was 2,630 mm, and over the three-year observation period was 2,694 mm. The other meteorological variables show moderate seasonality associated with the precipitation seasonality. In the very wet season, solar radiation is slightly lower (Figure 5.1a), relative humidity is slightly higher (Figure

5.1b), and air temperature is 1–2 ºC cooler. Soil moisture, sampled once per month, shows little coherent variation over the year, as would be expected from a wet site where the time since the last rain event is probably the biggest influence on measured values. Mean annual solar radiation is 187.3 ± 12.6 W m^{-2} (mean ± SD), mean annual relative humidity is 86.5 ± 1.6%, and mean annual air temperature (on the 80 m crane, ground level will be about 0.4 ºC warmer) is 25.9 ± 0.3 ºC. Over our measurement period, soil moisture was significantly higher on clay (mean = 29.5 ± 2.2 %) than on sandy loam (mean = 27.4 ± 2.1%).

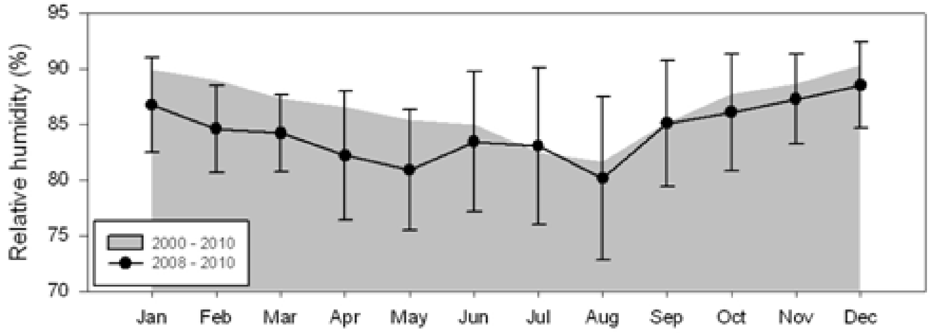
5.4.2. Forest Structure and Biomass

The average wood density was 0.61 ± 0.11 g cm^{-3} (mean ± SD) on clay and 0.61 ± 0.11 g cm^{-3} on sandy loam. The mean height of trees (≥ 10 cm DBH) estimated following the most recent census (2008) was 19.6 ± 0.4 m (mean ± SE) on the clay site and 19.6 ± 0.3 m on the sandy loam site. The mean height of canopy trees (≥ 40 cm DBH) was 40.0 ± 1.0 m on clay and 37.7 ± 0.6 m on sandy loam. This is substantially higher than the mean heights of 20–25 m for similar trees greater than 40 cm DBH reported for humid Amazonian forests (e.g. Farfan-Amezquita et al., *submitted* 2012). Height was not significantly different between the clay and sandy loam sites (t = 0.37, p-value = 0.71, t-test).

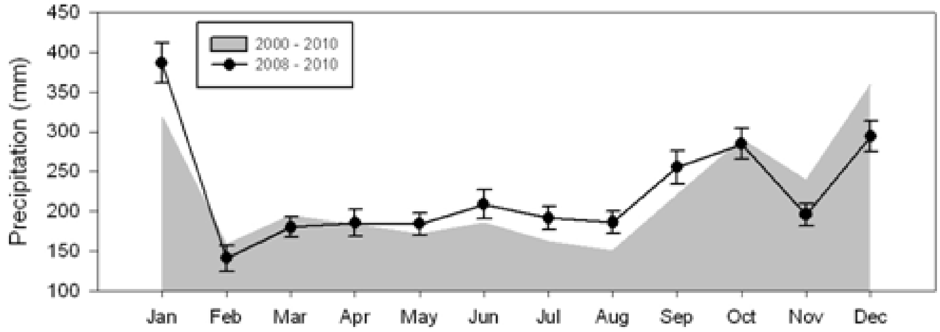
a) Solar radiation



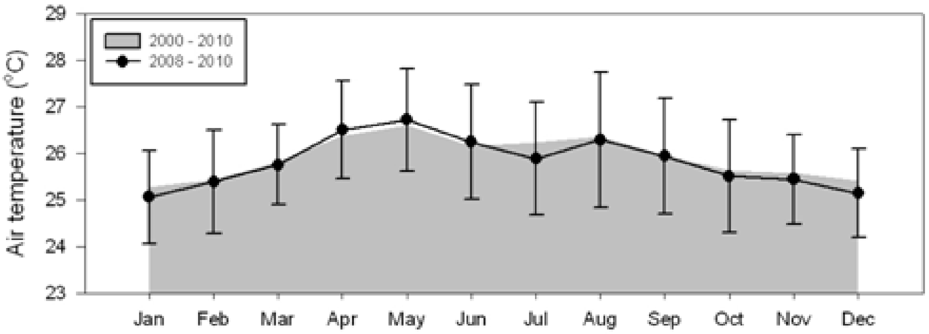
b) Relative humidity



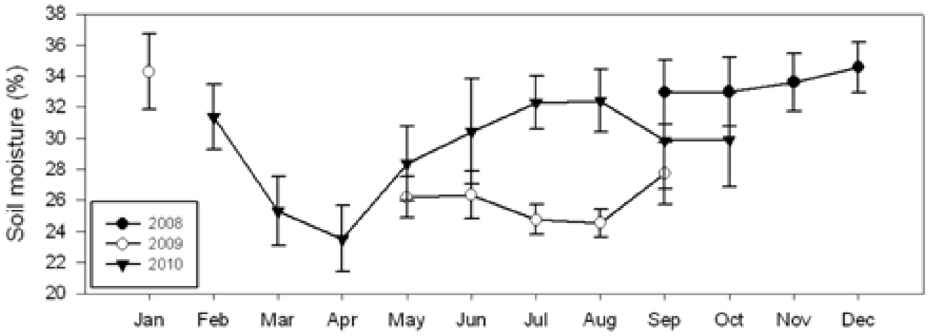
c) Precipitation



d) Air temperature



e) Soil moisture on clay



f) Soil moisture on sandy loam

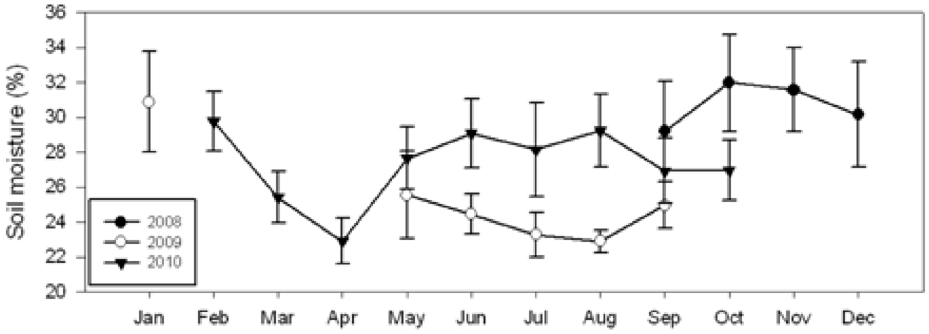


Figure 5.1: Monthly mean a) solar radiation (W m^{-2}), b) relative humidity (%), c) precipitation (mm), d) air temperature (^{o}C), and soil moisture (%) on e) clay and f) sandy loam in Lambir (meteorological data from canopy crane) over observation period between 2008 and 2010. Shaded area is meteorological data between 2000 and 2010. Each point of soil moisture (e and f) is the average of point measurements obtained from both clay and sandy loam sites (*n* = 25) from September 2008 to October 2010. Errors are plotted as standard deviation of the mean.

The average above-ground coarse woody biomass (trees ≥ 10 cm DBH) between 1992 and 2008 was 210.4 Mg C ha^{-1} on the clay site and 254.5 Mg C ha^{-1} on the sandy loam site (Table 5.1). For smaller trees (< 10 cm DBH), the mean value was 6.9 Mg C ha^{-1} on clay and 8.5 Mg C ha^{-1} on sandy loam. For larger trees (≥ 40 cm DBH) the mean value was 165.3 Mg C ha^{-1} on clay and 179.9 Mg C ha^{-1} on sandy loam. The number of trees (> 10 cm DBH) on clay (429 stems ha^{-1}) was substantially lower than on sandy loam (642 stems ha^{-1}). Looking at the longer-term data, we can see that above-ground coarse woody biomass (trees ≥ 10 cm DBH) showed moderate variation, with a notable decline (19.9 Mg C ha^{-1}) on the sandy loam site over the period 1997–2003, which may be associated with the strong 1997/1998 *El*-Niño drought (Figure 5.2). The clay site showed a smaller variation in overall biomass.

Table 5.1: Above-ground coarse wood biomass for all trees on clay and sandy loam sites between 1992 and 2008

	Mean above-ground coarse wood biomass (Mg C ha^{-1})				
	1992	**1997**	**2003**	**2008**	**Average**
Clay	215.5	199.0	207.8	219.2	210.4
Sandy loam	253.0	264.0	244.1	256.7	254.5

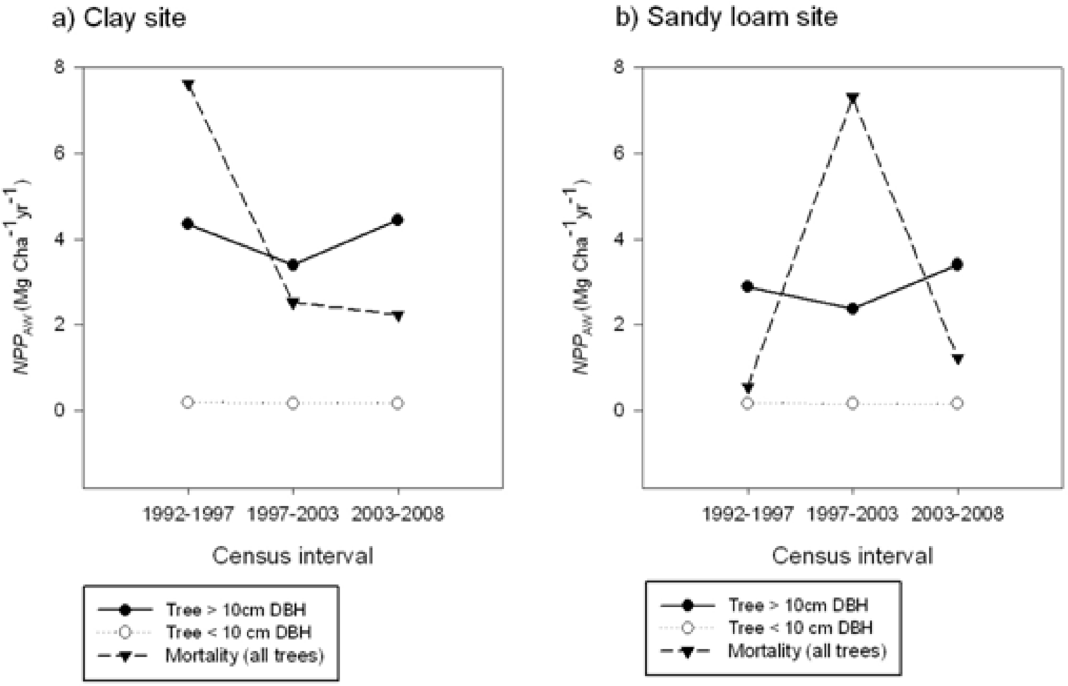


Figure 5.2: The mean growth for trees greater than 10 cm diameter breast height (DBH) (solid circle), less than 10 cm (open circle), and mortality for all trees (solid triangle) on a) clay, and b) sandy loam soils over three census intervals between 1992 and 2008.

5.4.3. Above-Ground Coarse Wood NPP (NPP_{ACW}) and Seasonal Pattern

Over the long term, the mean woody growth of trees (> 10 cm DBH) was 4.06 ± 0.41 Mg C ha^{-1} yr^{-1} on the clay site and 2.89 ± 0.29 Mg C ha^{-1} yr^{-1} on the sandy loam site. For smaller tress (< 10 cm DBH) it was 0.18 ± 0.02 Mg C ha^{-1} yr^{-1} on clay and 0.17 ± 0.02 Mg C ha^{-1} yr^{-1} on the sandy loam site (Table 5.2). Consequently, the total NPP_{ACW} was 4.24 ± 0.42 Mg C ha^{-1} yr^{-1} and 3.05 ± 0.31 Mg C ha^{-1} yr^{-1} on clay and sandy loam respectively. Dividing the above-ground biomass by the NPP_{ACW}, we calculated the mean carbon residence time to be 51 years on clay and 86 years on sandy loam.

Table 5.2: Summary of the total annual average net primary productivity (NPP) for above- and below-ground components on both the one-hectare clay and sandy loam sites. All fluxes are reported in Mg C ha^{-1} yr^{-1}. Reported errors are the sample standard error of the mean.

	Clay		Sandy loam	
	Mean	Standard error	Mean	Standard error
$NPP_{\mathrm{ACW}\ (\geq 10\ \mathrm{cm\ DBH})}$	4.06	0.41	2.89	0.29
$NPP_{\mathrm{ACW}\ (< 10\ \mathrm{cm\ DBH})}$	0.18	0.02	0.17	0.02
$NPP_{\mathrm{litterfall}}$	7.89	0.43	5.99	0.46
NPP_{leaves}	5.52	0.37	4.35	0.29
NPP_{twigs}[1]	1.39	0.17	0.70	0.11
NPP_{reprod}[2]	0.25	0.06	0.47	0.10
NPP_{debris}	0.73	0.11	0.47	0.06
$NPP_{\mathrm{herbivory}}$	0.27	0.14	0.21	0.11
$NPP_{\mathrm{branch\ turnover}}$[3]	0.53	0.09	1.08	0.11
$NPP_{\mathrm{coarse\ roots}}$	0.93	0.37	0.65	0.26
$NPP_{\mathrm{fine\ roots}}$	1.96	0.55	1.86	0.30
NPP_{AG}	12.93	0.61	10.34	0.57
NPP_{BG}	2.89	0.67	2.51	0.40
NPP_{Total}	15.82	0.90	12.85	0.69

[1] woody material < 2 cm diameter

[2] reproductive materials (e.g. flowers, fruits, seeds)

[3] woody material > 2 cm diameter, including fallen stem and bark

Key: NPP_{ACW}, above-ground coarse wood NPP; $NPP_{\mathrm{litterfall}}$, litterfall NPP; NPP_{leaves}, leaves NPP, NPP_{twigs}, twigs NPP, NPP_{reprod}, reproductive materials NPP, NPP_{debris}, undefined fine debris; $NPP_{\mathrm{herbivory}}$, NPP lost to leaf herbivory; $NPP_{\mathrm{branch\ turnover}}$, branch turnover NPP, $NPP_{\mathrm{coarse\ roots}}$, coarse roots NPP, $NPP_{\mathrm{fine\ roots}}$, fine roots NPP, NPP_{AG}, above-ground NPP, NPP_{BG}, below-ground NPP.

Over the 15-month measurement period, we found little evidence of seasonality in growth rates. In fact, the signal appeared dominated by inter-annual variability, with higher growth rates in the 2010 drier season (June to September) than in the equivalent 2009 season (Figure 5.3). The mean monthly NPP_{ACW} based on the dendrometers was 0.33 ± 0.01 Mg C ha^{-1} mo^{-1} on clay and 0.25 ± 0.02 Mg C ha^{-1} mo^{-1} on sandy loam. In summary, the clay soil plot is characterised as a plot with relatively low biomass, more small trees, and high growth rates and tree turnover rates. The sandy soil plot has high biomass, more medium and large trees, slower growth rates and slower tree turnover.

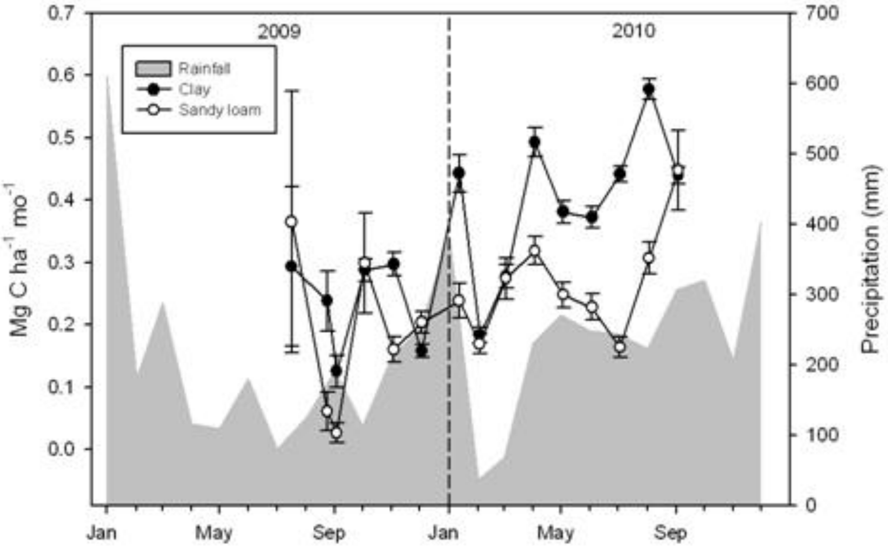


Figure 5.3: The monthly above-ground coarse wood NPP for all trees (> 10 cm DBH) measured using dendrometer on clay and sandy loam sites between June 2009 and September 2010. Each point is the average monthly growth scaled up using three-monthly dendrometer data and based on growth rates estimated from the monthly dendrometer data for fast-growing trees. Shaded area is the monthly rainfall from 2009 to 2010.

5.4.4. Seasonal Variation of Litterfall NPP ($NPP_{\text{litterfall}}$)

The litterfall NPP ($NPP_{\text{litterfall}}$) was 7.89 ± 0.43 Mg C ha^{-1} yr^{-1} on clay and 5.99 ± 0.46 Mg C ha^{-1} yr^{-1} on sandy loam (Table 5.2). The fractions of litterfall (clay/sandy loam) were partitioned into 70.0 ± 6.0/72.6 ± 7.4% leaves, 17.6 ± 2.4/11.7 ± 2.0% twigs, 3.2 ± 0.8/7.8 ± 1.8% reproductive materials, and 9.3 ± 1.5/7.8 ± 1.2% of undefined fine debris.

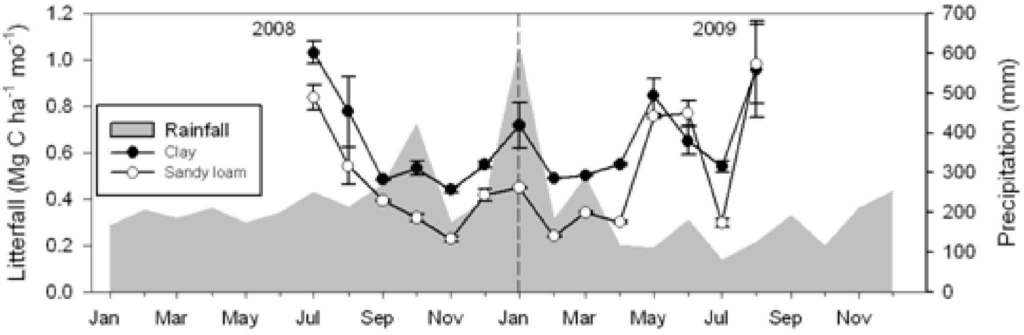
Litterfall and leaves presented some evidence of seasonality, with higher rates typically during the drier period on both clay and sandy loam (Figure 5.4a and 5.4b). Given that litterfall collection was at a different period and incomplete for a full-year cycle, the evidence of seasonal variation may be tentative. However, there were contrasting trends between both years from July to August, suggesting some effects due to the mass flowering of dipterocarps that occurred in June 2009 (Figure 5.4a and 5.4b). The NPP_{reprod}, NPP_{twigs}, and NPP_{debris} showed very little seasonal and inter-annual variation, with several periodic peaks on both the clay and sandy loam sites (Figure 5.4c, 5.4d and 5.4e). Similar seasonality in litterfall rates was observed in northern Borneo, with no apparent relationship to dry and wetter months (Burghouts *et al*., 1992; Saner *et al*., 2012).

5.4.5. Seasonal Pattern of Leaf Production

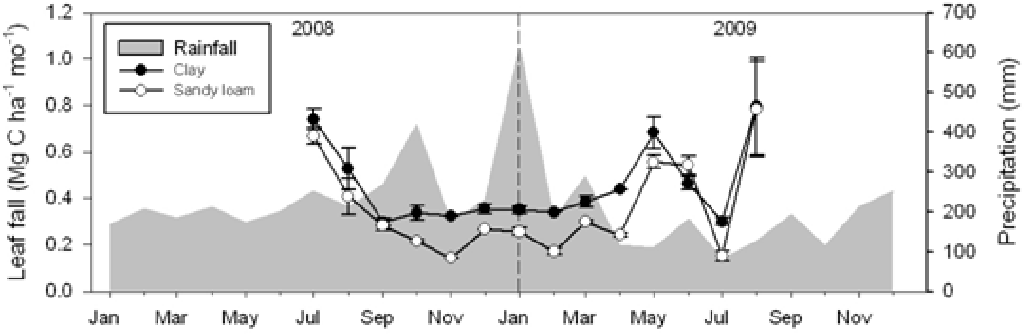
The means of LAI recorded from August 2009 to May 2010 were 5.2 $m^2\ m^{-2}$ on clay and 5.6 $m^2\ m^{-2}$ on sandy loam. LAI decreased over time on the clay site, but showed no overall trend in regard to the sandy loam site (Figure 5.5a). We determined SLA based on dominant species, with DBH in the range of 1.0 to 80.0 cm and tree height between 6.0 and 44.0 m on clay and sandy loam sites. The mean SLA was $14.8 \pm 1.8\ m^2\ kg^{-1}$ on clay and $8.1 \pm 0.3\ m^2\ kg^{-1}$ on sandy loam. This is comparable to previous reported SLA with similar species and heights (Yoda, 1983; Osada *et al*., 2003; Paoli, 2006).

Using monthly changes in the LAI (dLAI) and the estimated SLA for dominant species for both sites, we estimated the seasonal variation in leaf production from August 2009 to May 2010. Since our litterfall collection period did not fully coincide with LAI image recording, we substituted leaf litterfall data between September and December 2009 with data from September to December 2008 and assumed that there was little variation in the leaf fall between 2008 and 2009 ($t = 141$, $p > 0.05$). There was no evidence of a seasonal pattern in leaf flush or leaf fall at the clay site. At the sandy loam site, there was a suggestion of higher leaf production in the drier–wet transition (August–December). However, with the lack of concurrence of LAI and leaf fall data, such evidence should be regarded as tentative.

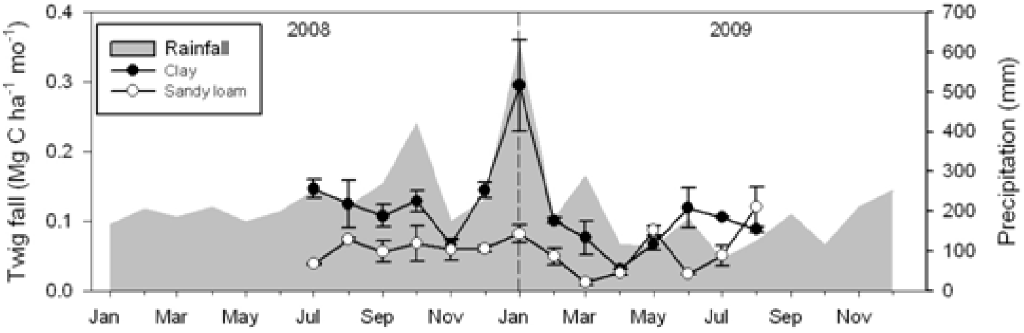
a) $NPP_{\text{litterfall}}$



b) $NPP_{\text{leaf fall}}$



c) $NPP_{\text{twig fall}}$



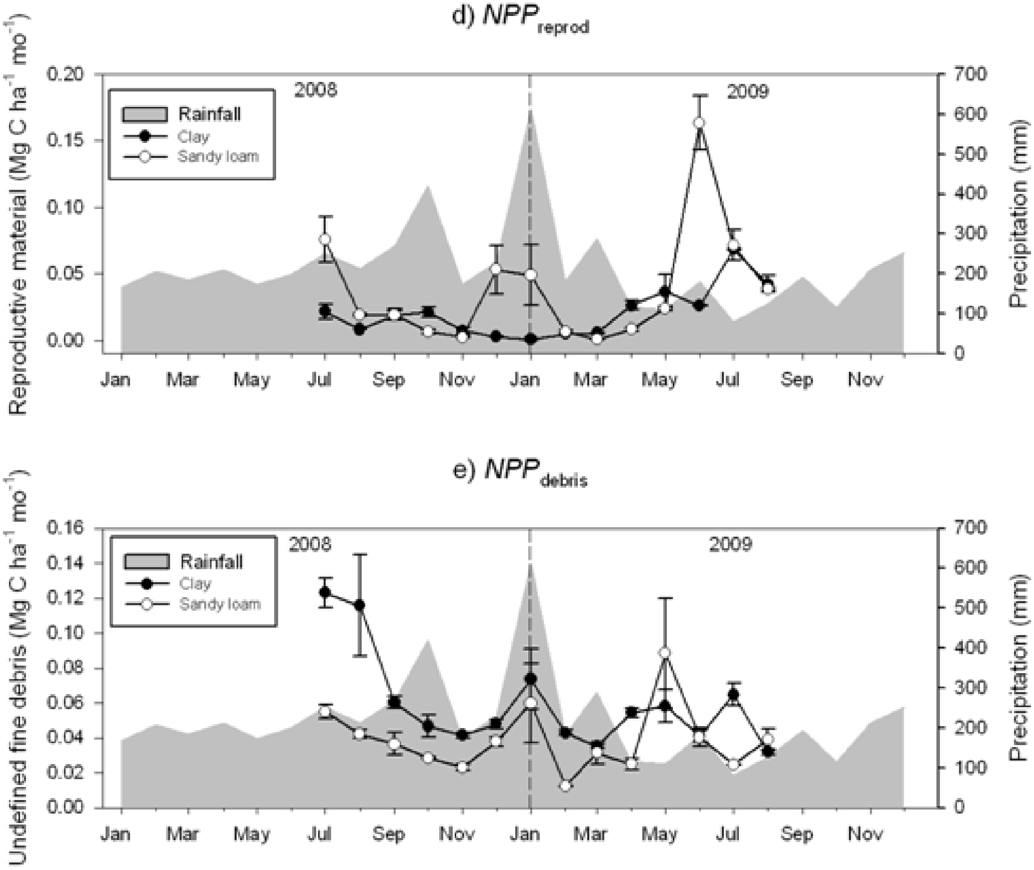


Figure 5.4: The seasonal variation of monthly NPP for a) litterfall ($NPP_{\text{litterfall}}$), b) leaf (NPP_{leaves}), c) twigs (NPP_{twigs}), d) reproductive materials (NPP_{reprod}), and undefined fine debris (NPP_{debris}) on clay and sandy loam sites between 2008 and 2009. Monthly rainfall (mm) is the shaded plot area from January 2008 to December 2009. Each point is the average litterfall collections ($n = 2$) per month. Errors are plotted as the standard error of the mean.

5.4.6. Branch turnover NPP ($NPP_{\text{branch turnover}}$)

The branch turnover NPP for woody material (> 2 cm diameter) was significantly higher on the sandy loam site (1.08 ± 0.11 Mg C ha^{-1} yr^{-1}) (mean ± SE) than on the clay site (0.53 ± 0.09 Mg C ha^{-1} yr^{-1}) ($t = 2.8$, $p < 0.05$) (Table 5.2). Branch turnover showed little seasonality over time on both clay and sandy loam sites (Figure 5.6). However, there was a sharp peak in June 2010 on the clay site to a value of 2.28 ± 0.14 Mg C ha^{-1} mo^{-1}, when a large tree caused substantial damage to adjacent trees and branches over a large area. In the absence of a longer data-collection period, this single event has a disproportionate effect on our estimated NPP.

When this event is included in the clay site, $NPP_{\text{branch turnover}}$ is 2.16 ± 0.14 Mg C ha^{-1} yr^{-1}. However, when it is replaced with an average value from the rest of the period the $NPP_{\text{branch turnover}}$ is 0.53 ± 0.09 Mg C ha^{-1} yr^{-1}. For our overall calculations, we decided that the latter value was the better estimate of mean long-term branch turnover.

5.4.7. NPP Lost to Leaf Herbivory ($NPP_{\text{herbivory}}$)

The NPP lost to leaf herbivory was 0.27 ± 0.14 Mg C ha^{-1} yr^{-1} on clay and 0.21 ± 0.11 Mg C ha^{-1} yr^{-1} on sandy loam. Our estimated levels of $NPP_{\text{herbivory}}$ were relatively higher than the earlier study in Pasoh, which was estimated based on caterpillar frass droppings (Kira 1978).

5.1.1. Coarse root net primary productivity ($NPP_{\text{coarse roots}}$)

The average coarse root biomass was 48.5 Mg C ha^{-1} on the clay and 57.6 Mg C ha^{-1} on the sandy loam sites. This was calculated using coarse root allometry derived for Pasoh, and the ratio of coarse root over above-ground coarse wood biomass was 0.22 on both clay and sandy loam. This is comparable to the general ratio value of 0.21 applied in the Amazonian forests (Malhi *et al.*, 2009). Using multiple censuses, we estimate $NPP_{\text{coarse roots}}$ to be 0.93 ± 0.37 Mg C ha^{-1} yr^{-1} on clay and 0.65 ± 0.26 Mg C ha^{-1} yr^{-1} on sandy loam (Table 5.2). Similarly, the ratio of $NPP_{\text{coarse roots}}$ to NPP_{ACW} was 0.22 on clay and 0.21 on sandy loam.

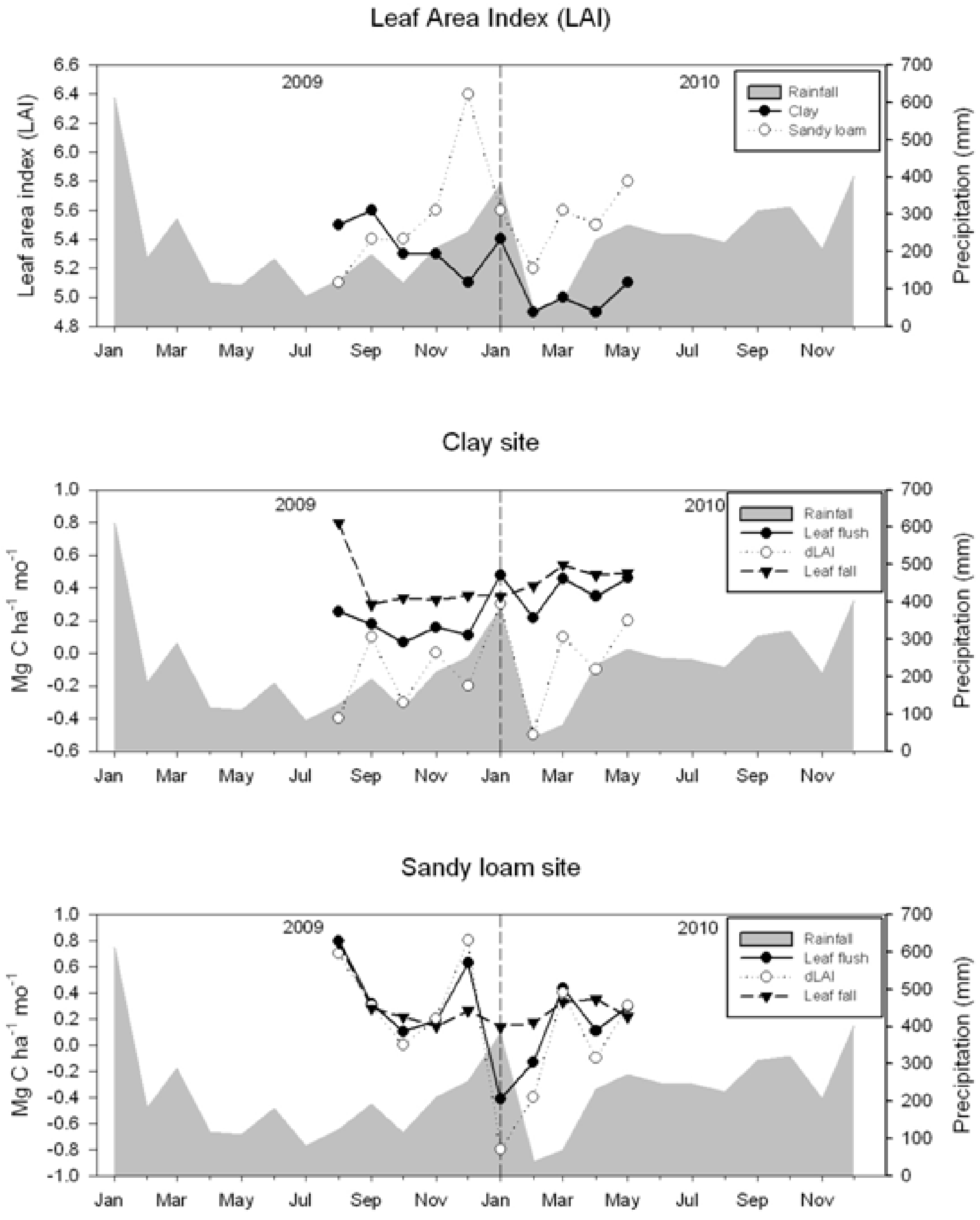


Figure 5.5: Seasonal variation of a) LAI, b) monthly leaf fall and production on clay, and c) monthly leaf fall and production on sandy loam from August 2009 to May 2010. Substituted data between September 2009 and December 2009 is based on the rate of leaf fall from September 2008 to December 2008, since data for the later period was unavailable. Shaded area is the monthly rainfall from 2009 to 2010.

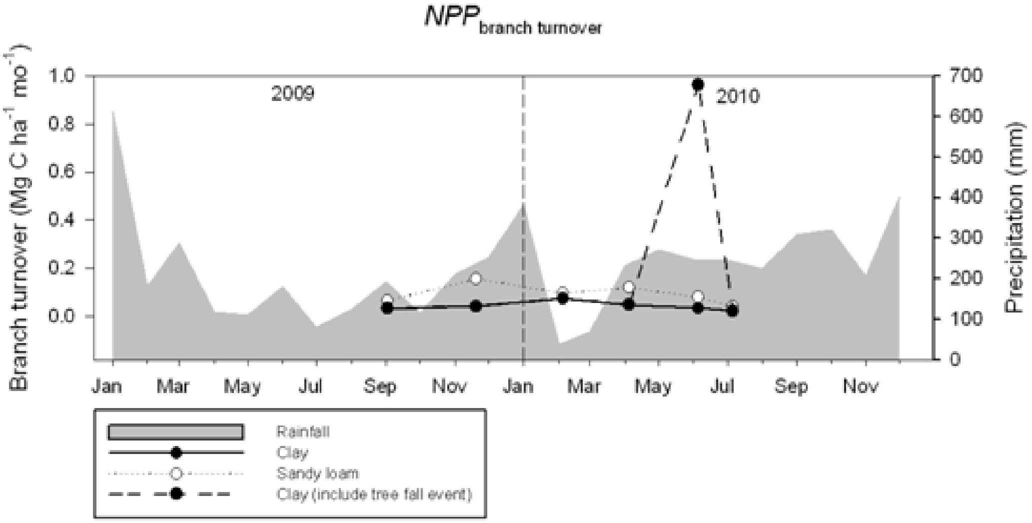


Figure 5.6: Monthly *NPP*branch turnover on clay and sandy loam sites from August 2009 to July 2010. The monthly *NPP*branch turnover for a particular large tree fall event in May 2009 along a sampling transect on the clay site is plotted with dashed line.

5.1.2. Fine Roots NPP (*NPP*fine roots)

To our knowledge, this is the first attempt to quantify fine root NPP in a lowland dipterocarp forest. Fine root production was 1.74 ± 0.49 Mg C ha^{-1} yr^{-1} on clay and 1.65 ± 0.27 Mg C ha^{-1} yr^{-1} on sandy loam following cumulative prediction up to 100 minutes. Using the depth correction factor, *NPP*fine root was 1.96 ± 0.55 Mg C ha^{-1} yr^{-1} on clay and 1.86 ± 0.30 Mg C ha^{-1} yr^{-1} on sandy loam sites (Table 5.2). Fine root production was higher towards the wetter period between late July and December 2008, and declined during the drier period between March and September 2009 (Figure 5.7). The values in September 2008 and September 2009 were significantly different, indicating substantial inter-annual variability.

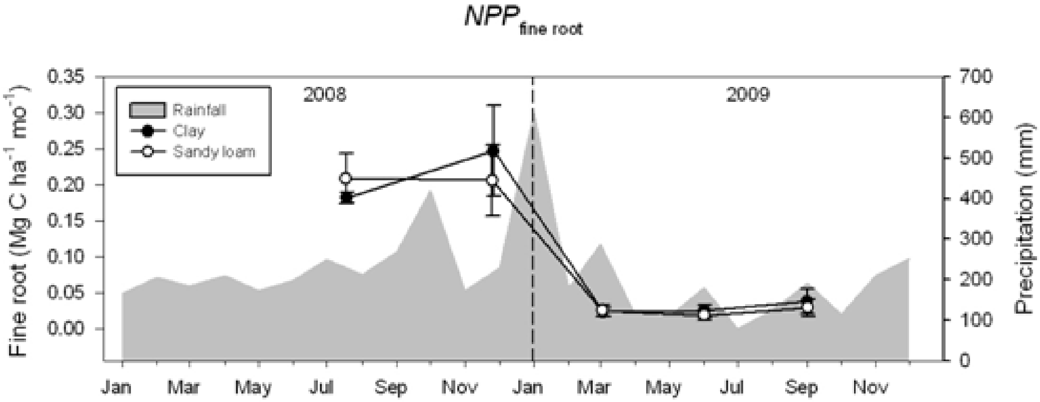


Figure 5.7: Seasonal pattern for fine root NPP ($NPP_{\text{fine roots}}$) on clay and sandy loam sites between September 2008 and October 2009. Three-monthly $NPP_{\text{fine roots}}$ is estimated based on the logarithmic curve to predict for extraction of fine root mass beyond 40 minutes (10-min time step extraction method). Each point is the average $NPP_{\text{fine roots}}$ from nine ingrowth cores. Errors are plotted as the standard error of the mean.

5.1.3. Allocation of NPP

By summing up the components described above, we estimated the total NPP (NPP_{Total}) to be 15.82 ± 0.90 Mg C ha^{-1} yr^{-1} on the clay site and 12.85 ± 0.69 Mg C ha^{-1} yr^{-1} on the sandy loam site (Table 5.2). Above-ground NPP was 12.93 ± 0.61 Mg C ha^{-1} yr^{-1} on clay and 10.34 ± 0.57 Mg C ha^{-1} yr^{-1} on sandy loam. Below-ground NPP was 2.89 ± 0.67 Mg C ha^{-1} yr^{-1} on clay and 2.51 ± 0.40 Mg C ha^{-1} yr^{-1} on sandy loam. The above-ground productivity contributed 81.7 ± 6.0% and 80.5 ± 6.0% of the total NPP on the clay and sandy loam sites respectively.

Out of the NPP_{Total}, $NPP_{\text{litterfall}}$ contributed the largest fraction of 49.9 ± 3.9% and 46.6 ± 4.9% on clay and sandy loam respectively. This is followed by above-ground coarse wood productivity of 26.8 ± 3.0% on clay and 23.8 ± 2.6% on sandy loam. Fine root NPP contributed between 12.4 ± 3.6% and 14.5 ± 2.5%, while coarse root contributed approximately 5.9 ± 2.4% on clay and 5.1 ± 2.0% on sandy loam. Hence, NPP_{BG} contributed 18.3 ± 4.3% and 19.5 ± 3.3% of total NPP. The NPP on the clay site was consistently higher than on the sandy loam site, with significantly higher values in regard to the productivity of woody biomass, leaves, twigs, and litter debris. Only reproductive NPP was higher on the sandy site, and there was no significant difference in fine root NPP between the sites.

5.2. Discussion

5.2.1. Seasonal Variation of the Allocation of NPP

We found moderate evidence of seasonality in the budget and allocation of NPP, but some evidence of strong inter-annual variation in the components of NPP. In addition, the allocation of NPP in this forest is inherently different between soil types, and may be different to tropical forests elsewhere.

In this study, we have made several assumptions in order to capture a complete picture of seasonality in relation to the components of NPP. Given that the seasonal productivity of twigs, branch and smaller trees are not available, we have assumed that these terms are proportional following the same seasonal cycle of NPP_{ACW} (>10 cm DBH). Hence, seasonal production is multiplied by the ratios of the annual production of these terms (Table 5.2). On the other hand, we have assumed that NPP_{reprod} equals the measured loss of flowers, fruits, and seeds because these components probably have a canopy lifetime of less than three months.

Figure 5.8 illustrates the seasonal proportion and fraction of NPP components. This quantification is the first attempt to explore the variation of NPP components and the allocation over the seasonal cycle for a Paleotropical lowland forest. Clay and sandy loam sites show contrasting productivity patterns over the year. For the first half of the year on the clay site, the NPP increases to a high of approximately 1.3 Mg C ha^{-1} mo^{-1} (April–June) following the wetter period. Productivity progressively declines to approximately 0.7 Mg C ha^{-1} mo^{-1} (October–December) in the second half of the year, which is typically at the end of the drier period (Figure 5.8a). The wetter conditions on clay may have provided favourable conditions on this soil and tropical clay substrates tend to have higher nutrient retention and hence encourage higher production. This is supported by previous studies that reported higher productivity and allocation for tropical forests on high soil fertility (Russo *et al*., 2005; Paoli and Curran, 2007; Aragão *et al*., 2009; Cleveland *et al*., 2011; Vicca *et al*., 2012). On the sandy loam site, however, productivity is highest in the less wet period (July–September) at approximately 1.1 Mg C ha^{-1} mo^{-1}, and is generally consistent at approximately 0.9 Mg C ha^{-1} mo^{-1} in other months over the year (Figure 5.8c). In addition, anisohydric plants in Lambir have higher productivity under moist conditions (Kumagai and Porporato, 2012). This supports our findings that higher moisture availability increases productivity, with a potential lag in response to a wetter period.

On the clay plot, the largest allocation is to leaf production, with the highest allocation at almost 40% during the wetter period (Figure 5.8b). It later progressively declined to a lowest point of about 10% between October and December. Similar patterns with smaller proportions are allocated for twigs, reproductive materials, fine roots and branch. Productivity tends to decline in the drier period and this reduces the allocation to leaves but increases allocation to reproductive materials and fine roots. The proportions of above- and below-ground wood are fairly consistent, with slightly larger proportions allocated to above-ground coarse wood in the second half of the year.

In the sandy loam plot, the seasonal allocation varies over time (Figure 5.8d). Contrary to clay, productivity is at its highest of about 1.1 Mg C ha^{-1} mo^{-1} towards the end of the drier period between July and September. Lower productivity occurs during the wetter period at approximately 0.9 Mg C ha^{-1} mo^{-1}. When productivity is highest, a larger allocation is invested in the production of leaves. However, when productivity is low during the wetter period the allocation is mostly to above-ground coarse wood and fine roots. Similarly, on the sandy loam the proportion of reproductive materials is larger during the drier period.

These contrasting patterns suggest the seasonal allocation of NPP is different on clay and sandy loam sites. During the wetter period the proportion of leaves is larger on clay, but more allocation is in the above-ground coarse wood and fine root on sandy loam (Figure 5.8b and 5.8d). In the drier period, there is a shift of allocation from leaves to above-ground coarse wood and reproductive materials on clay, while on the sandy loam site a large proportion is allocated to leaves, reproductive materials and above-ground coarse wood. Because spatial distributions of tree species in Lambir are edaphically biased (Palmiotto, 1998; Potts *et al*., 2002; Davies *et al*., 2005) and show contrasting growth and mortality rates on different soil types (Russo *et al*., 2005; Itoh *et al*., 2012), the seasonal allocation of NPP is likely to be affected by nutrient availability in the soil coupled with different demographic trade-offs.

. The allocation of NPP below-ground to fine roots shows strong effects in the wetter period. On the less nutrient-poor clay soil, where soil retains more water, the allocation to fine root is significantly higher (t = 31.7, $p < 0.001$) (Figure 5.8b). Green *et al*. (2005) found that fine root biomass is positively correlated with precipitation, but they found no relationship with soil nutrients. While the above-ground NPP may be linked to soil fertility, the below-ground productivity is strongly explained by the availability of water (Sánchez-Gallén and Alvarez-Sánchez, 1996; Cavelier *et al*., 1999; Green *et al*., 2005). In contrast, higher fine root production on sandy loam soil during the drier period may be explained by the lower water-holding capacity that may have increased root productivity to maintain soil water access (Aragão *et al*., 2009). Although there is no difference in fine root production between clay and sandy loam soils (Table 5.2), the allocation to fine roots appears to be slightly higher on sandy loam (Figure 5.8). However, the allocation is not significantly different between plots (t = 0.37, p > 0.05). Moreover, any observed seasonal patterns should be interpreted with a high degree of caution as data were only collected over one annual cycle, and there is evidence of strong inter-annual variability. In addition, our measurements were conducted during one of the driest period between 2000 and 2010 and also incorporated a mass flowering event.

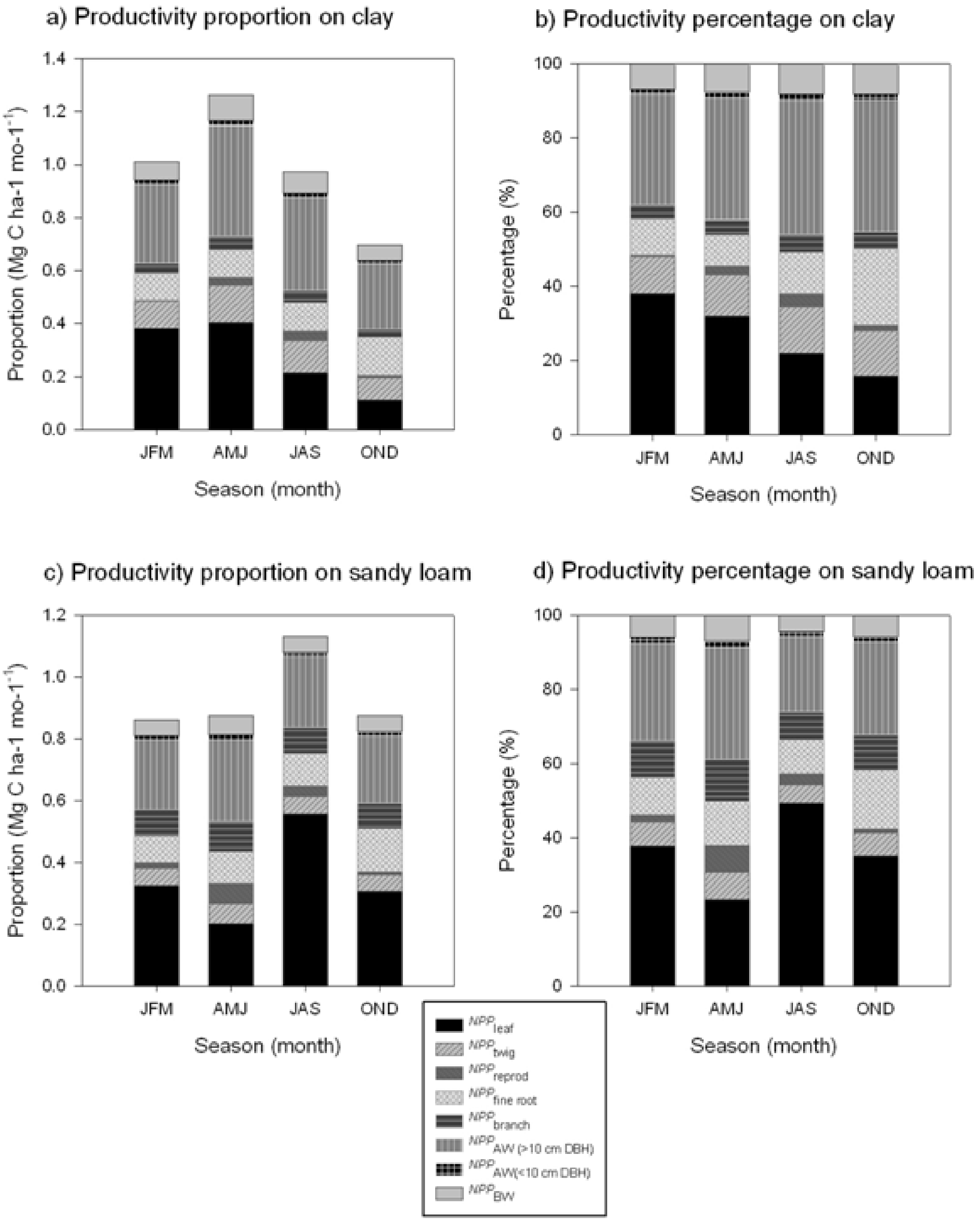


Figure 5.8: The seasonal allocation of NPP and its components on clay in a) absolute value of proportion and b) percentage, and on sandy loam in c) absolute value of proportion and d) percentage.

5.2.2. Overall Allocation of NPP

Total NPP is consistent with results from several sites in the Southeast Asian region (Table 5.3) (Kira *et al*., 1967; Kira, 1978; Kira, 1987). Our estimation is, however, relatively higher than the average total NPP across several Amazonian sites (Table 5.3) and the montane forests (Hertel *et al*., 2009). This higher estimation in our study is partly due to an extensive measurement of NPP components (e.g. coarse roots, lost to leaf herbivory), such as have not been measured in previous studies. The average ratio of above-ground and below-ground NPP was 0.81 and 0.17 on clay and sandy loam respectively.

The allocation of above-ground NPP between stem and canopy shows a substantial difference between clay and sandy loam. The allocation pattern on clay is similar to that reported in Kalimantan, suggesting a saturating function between $NPP_{\text{fine roots}}$ and NPP_{ACW} at high NPP sites (Paoli and Curran, 2007), as observed in our study on the clay soil. The allocation pattern on sandy loam is quite similar to that in the Neotropics (Malhi *et al*., 2011). Hence, there is substantial variation in the patterns of allocation in lowland dipterocarp forest, with no fixed ratio (Malhi *et al*., 2011). Furthermore, the allocation between three major components of NPP is partitioned into (canopy : wood : fine root) 8:4:2 on clay and 6:3:2 on sandy loam. Overall, the highest fraction of NPP is allocated to woody material and the least to fine roots (Malhi *et al*., 2011).

Herbivory loss is usually unaccounted for because it is often a small and negligible contribution (Clark *et al*., 2001b). Kira (1978) showed that grazing by caterpillars may consume approximately 0.15 Mg C ha^{-1} yr^{-1}. The rate of consumption derived from the rate of faecal droppings by caterpillars was estimated based on the efficiency of assimilation given as 13%. However, we show higher rates using herbivory rates measured from the canopy in Lambir (Kurokawa and Nakashizuka, 2008).

Table 5.3: The mean (± standard error) total NPP of tropical forests in Asia and the Amazon.

Site	Forest type	Total NPP (Mg C $ha^{-1} yr^{-1}$)	Reference
Asia			
Malaysia: Lambir	Lowland dipterocarp	15.9 ± 0.9[1]	This study
Malaysia: Lambir	Lowland dipterocarp	13.0 ± 0.7[2]	This study
Malaysia: Pasoh	Lowland dipterocarp	13.7 ± 1.4*	Kira (1978)
Malaysia: Pasoh	Lowland dipterocarp	12.8 ± 1.3*	Kira (1987)
Thailand: Khao Chong	Seasonal evergreen	14.3 ± 1.4*	Kira *et al.* (1967)
Thailand: Central Thailand	Deciduous dipterocarp/ Dry evergreen	6.1 ± 0.6*	Ogino *et al.* (1967)
Indonesia: Sulawesi	Pre-montane	6.7 ± 0.3	Hertel et al. (2009)
China	Tropical forest	7.2 ± 1.6	Ni *et al.* (2001)
China: Fujian	Sub-tropical forest	11.2 ± 0.6	Yang *et al.* (2003)
China: Xishuangbanna	Tropical seasonal	8.8 ± 0.9*	Tan *et al.* (2010)
India: Western Ghats	Wet evergreen	11.9 ± 2.0	Swamy *et al.* (2010)
	Estimated Mean	**11.0 ± 0.3**	
Amazonia			
Brazil: Caxiuanã	Moist old-growth	11.6 ± 0.7	Aragão et al. (2009) Malhi et al. (2009)
Brazil: Tapajós	Moist old-growth	14.4 ± 0.9	Aragão et al. (2009) Malhi et al. (2009)
Brazil: Manaus	Moist old-growth	10.8 ± 1.0	Aragão et al. (2009) Malhi et al. (2009)
Colombia: Agua Pudre	Moist lowland	11.5 ± 0.5	Aragão *et al.* (2009)
Colombia: Zafire	Moist lowland	9.3 ± 1.3	Aragão *et al.* (2009)
	Estimated Mean	**11.5 ± 0.4**	

[1] Clay soil site
[2] Sandy loam soil site
* 10% standard error assigned (Aragão *et al.*, 2009; Malhi *et al.*, 2009)

In fact, herbivory damage in the canopy is generally lower (Coley and Barone, 1996; Kurokawa and Nakashizuka, 2008), suggesting a higher level of damage if measured in the understory. Our estimates are within the range between two mature tropical forest sites in Amazonia, namely Tambopata (0.65–0.74 Mg C ha^{-1} yr^{-1}) (Farfan-Amezquita *et al.*, *submitted* 2012) and Caxiuana (0.20 Mg C ha^{-1} yr^{-1}) (Doughty et al., *submitted* 2012). The proportion of $NPP_{\mathrm{herbivory}}$ to NPP_{Total} is still small, at less than 2%.

5.3. Conclusion

Our study provides a detailed description of the NPP budget and its seasonal allocation in a lowland dipterocarp forest. We find that the NPP in a dipterocarp forest is large and that considerable production is allocated to above-ground NPP. Productivity and the seasonal allocation of NPP are relatively different on clay and sandy loam. There is evidence that the dry–wet seasonality may shift the allocation of NPP on clay and sandy loam, even though this forest does not experience a significant water stress season. It is important to note, however, that these results are taken from two geographically close plots and that further similar studies are needed before we can generalise about the productivity and carbon cycle of the tropical forests in the old world .

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Chapter 6

Chapter 6: Comprehensive Assessment of the Carbon Budget of a Bornean Lowland Dipterocarp Forest

Overview

The classic pioneering study conducted during the International Biological Programme (IBP) programme in Pasoh has been the fundamental reference point in the understanding of carbon cycles in tropical forests (Kira, 1978). Since then, there has not yet been any study illustrating or improving on such a complete carbon budget for an Asian tropical forest. In this study, I present the first comprehensive carbon budget for a lowland dipterocarp forest in Borneo. I focus on the autotrophic respiration and integrate the heterotrophic respiration resulting from the soil CO_2 efflux partitioning study previously described in Chapter 4. Combining all the net primary productivity (NPP) estimates from Chapter 5, the comprehensive carbon budget is synthesised and illustrated in a tree diagram. Finally, I compare this new result to estimates from Pasoh and several established sites in the Amazon. Ultimately, this study will provide a detailed description of the carbon cycle of lowland dipterocarp forest.

Various collaborators[*] contributed to this study providing data that I was unable to measure during the course of my D.Phil. and measurement campaign. Tomo'omi Kumagai and Tomonori Kume provided the meteorological data; Hiroko Kurokawa provided herbivory data; Stuart Davies provided the census data; Sylvester Tan provided assistance in experimental design; and Mohd. Haniff Harun provided various instruments for measurements. The study overall and this chapter were supervised by Yadvinder Malhi.

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[*] Contribution Statement: experimental design: KLK, YM, ST, MHH; data gathering: KLK, ST; data analysis: KLK; interpretation of results: KLK, YM; paper writing: KLK.

6.1. Abstract

Carbon allocation is an important but poorly understood component of the cycling of carbon in a tropical forest ecosystem. In this study, we quantify above- and below-ground NPP and the autotrophic and heterotrophic respiratory fluxes in a lowland dipterocarp forest at Lambir Hills, Borneo. The total annual NPP (NPP_{Total}) was 15.9 ± 0.9 Mg C ha^{-1} yr^{-1} on clay and 13.0 ± 0.7 Mg C ha^{-1} yr^{-1} on sandy loam. A larger proportion of production was allocated to above-ground NPP, at approximately 81.8 ± 6.0% on clay and 80.0 ± 6.4% on sand of NPP_{Total}. Total annual below-ground production was approximately 20% of NPP_{Total} on both clay and sandy loam. Scaling respiration to the ecosystem, we estimated an average annual total ecosystem respiration (R_{Total}) of 32.2 ± 4.0 Mg C ha^{-1} yr^{-1} on clay and 33.9 ± 3.6 Mg C ha^{-1} yr^{-1} on sandy loam. Autotrophic respiration contributed 66.2 ± 14.8% of R_{Total} on clay and 60.8 ± 12.5% on sandy loam of R_{Total}. Carbon use efficiency (CUE) was relatively similar on both substrates: 0.43 ± 0.05 and 0.39 ± 0.05 on clay and sandy loam respectively, which indicated that approximately 40% of photosynthate was allocated to NPP for production of new organic material. The estimated gross primary productivity (GPP) was 37.2 ± 4.1 Mg C ha^{-1} yr^{-1} on clay and 33.6 ± 3.7 Mg C ha^{-1} yr^{-1} on sandy loam, and in good agreement with independent modelled estimates of GPP. The lowland dipterocarp forest in Lambir showed a similar level of GPP compared to tropical forests in Amazonia, but higher levels of NPP and CUE.

6.2. Introduction

One of the main areas of interest in global climatic changes is to understand the exchange of carbon dioxide (CO_2) between the biosphere and the atmosphere. Tropical forest accounts for approximately one-third of the global terrestrial NPP (Field *et al.*, 1998; Grace *et al.*, 2001; Grace, 2004), and thus plays a key role in the global carbon cycle. In addition, about 25% of the world's terrestrial biomass and soil carbon is stored in tropical forest (Jobbágy and Jackson, 2000). As a result, a small shift in the interaction between tropical forest and the atmosphere could have important consequences for tropical forests' carbon dynamics and the global carbon budget. Given the dominant role of tropical forests in regulating global terrestrial–atmospheric CO_2 exchange and climate, it is important to quantify and understand a comprehensive carbon budget and the dynamics of this ecosystem.

Plants take up CO_2 through photosynthesis or GPP, and at the same time release it to the atmosphere through respiration. The balance of these two large fluxes is NPP, defined as the rate of the production of biomass and organic matter produced by the plant over a specified time interval. Tropical forests have been estimated to contribute approximately 34% of the total global terrestrial GPP (Beer *et al.*, 2010). In addition to photosynthesis, an equally important large flux is respiration involving autotrophic (R_a; leaf, stem, root) and heterotrophic (R_h; litter, soil organic matter (SOM) decomposition) processes. However, there have been very few studies, particularly in tropical forests, aimed at quantifying and understanding these respiration components, NPP and GPP at ecosystem level (Kira, 1978; Yoda, 1983; Chambers *et al.*, 2004; Cavaleri *et al.*, 2008; Malhi *et al.*, 2009; Metcalfe *et al.*, 2010b; Tan *et al.*, 2010).

The first carbon cycle description in a Southeast Asian tropical forest was the pioneering study in the Pasoh Forest Reserve (Kira, 1978; Kira, 1987), but since then similar studies have been limited (Hertel *et al.*, 2009; Tan *et al.*, 2010; Saner *et al.*, 2012).

Alternatively, the focus have recently shifted to the micrometeorological approach intended to quantify the net carbon budget (e.g. Saitoh *et al*., 2005b; Kato and Tang, 2008; Kosugi *et al*., 2008; Mizoguchi *et al*., 2008). In complex tropical forest environments, however, uncertainties surround these micrometeorological approaches (Saitoh *et al*., 2005a; Araújo *et al*., 2008). Recently, there have been significant advances towards developing an accurate carbon budget by directly measuring and quantifying components of NPP and respiration (autotrophic and heterotrophic), particularly in the Amazonian forests (Chambers *et al*., 2004; Luyssaert *et al*., 2007; Malhi *et al*., 2009; Malhi, 2012). This recent effort has yet to be extended to Paleotropical sites.

In this study, we aim to quantify each component of NPP (above-ground wood, canopy, herbivory loss, branch turnover, coarse roots and fine roots), and the respiratory sources (stem, leaf, roots and the soil) to understand its relative contribution to the overall carbon budget in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysian Borneo. Specifically, we aim to address the following scientific questions:

1. What is the overall allocation of NPP components and respiration rates (autotrophic and heterotrophic) in Lambir, and how do they vary between clay and sandy loam sites?
2. What is the total budget of carbon productivity, CUE, and NPP in Lambir, and how do they differ between these sites and tropical forest elsewhere?

6.3. Materials and Methods

6.3.1. Site Characteristics

This study was carried out in the Lambir Hills National Park, Sarawak, Malaysia (4° 12' N, 114° 2' E). Lambir is an exceptionally diverse lowland mixed dipterocarp forest, with the highest recorded tree diversity in the Paleotropics (Ashton, 1964; Davies and Becker, 1996; Lee *et al*., 2002; Ashton, 2005). Basal area (trees ≥ 8.9 cm diameter at breast height (DBH)) is between 43 and 53 m^2 ha^{-1} (Yamakura *et al*., 1986; Phillips *et al*., 1994), whilst above-ground biomass is between 249 and 260 Mg C ha^{-1} (Yamakura *et al*., 1986; Chave *et al*., 2008). Although there is little seasonality in climate, Lambir experiences strong *El-Niño*-associated droughts about once per decade (Harrison, 2005). The mean annual rainfall was approximately 2,630 mm for the period 2000–2010 (recorded from an 80 m tall canopy crane approximately 3 km away from our study site). The drier season has mean monthly rainfall of around 150 mm mo^{-1}, well above the 100 mm mo^{-1} that typically transpires from forest canopies (Fisher *et al*., 2007). The mean annual temperature in Lambir for the period 2000–2010 was 25.9°C with little seasonal variation.

Investigations were carried out in the 52-ha forest dynamics plot in the Lambir Hills National Park, which is part of the Center for Tropical Forest Science (CTFS) global network of large plots (Condit, 1995; Lee *et al*., 2004). In the 52-ha plot, we established two one-hectare research plots (100 m x 100 m), one each on clay and sandy loam sites. The one-hectare plot was further divided into 25 subplots measuring 20 m x 20 m. The clay-rich udult Ultisols (Soil Survey Staff, 2006) are shale-derived soils (typically 40% sand), with a thin litter layer on the soil surface, relatively higher fertility, and high water-holding capacity (Davies *et al*., 1998; Davies *et al*., 2005). The sandy loam humult Ultisols (Soil Survey Staff, 2006) are sandstone-derived soils, with densely matted fine roots on the surface horizon, high sand content (typically 68% sand), low levels of nutrients and low water-holding capacity

(Ashton and Hall, 1992; Davies *et al*., 1998). Shale-derived soils typically occur in low-lying gullies, while the sandstone-derived soils occur mostly on slopes and ridges (Davies *et al*., 1998). The altitude difference (highest and the lowest points) between these two contrasting soil types is approximately 150 m, with steep slopes, undulating terrain, and complex bisected topography (Yamakura *et al*., 1995). The soils and geomorphology of Lambir have been previously described in detail (Ishizuka *et al*., 1998; Baillie *et al*., 2006; Tan *et al*., 2009).

In addition, we established two smaller research plots (20 m x 20 m) located outside of the 52-ha plot, on clay and sandy loam soils. These sites were chosen according to soil types, species and elevation that were similar to and representative of the one-hectare plot. These smaller plots were dedicated to an intensive soil partitioning study using the Detritus Input and Removal Treatment (DIRT) experimental approach (Sulzman *et al*., 2005; Nadelhoffer *et al*., 2006). Each of the DIRT plots was divided into three 11 m x 5 m subplots as replicates, and further divided into eight 2 m x 2 m treatment plots (see section 4.3.2, Chapter 4; Kho et al., *submitted* 2012a; Kho et al., *submitted* 2012b). Treatment plots for soil CO_2 efflux partitioning are summarised as follows:

a) Control (T_C) – Undisturbed condition with normal above-ground inputs of litterfall, defined as total soil CO_2 efflux (R_s)

b) No Litter (T_{NL}) – Aboveground inputs of litterfall and woody materials excluded

c) Double Litter (T_{DL}) – Enriched with additional litter inputs (i.e. litter from the T_{NL} treatment) and exposed to normal aboveground litter inputs thereafter

d) No Input (T_{NI}) – Above-ground litter inputs and roots excluded to retain only SOM, defined as SOM respiration (R_{SOM})

e) Mycorrhizae (T_{Myc}) – Excluded ingrowth of roots, but allowed ingrowth of mycorrhizae hyphae

6.3.2. Estimating Components of NPP and Respiration

The main components of NPP and respiration were measured using the protocols developed by the RAINFOR-GEM network (gem.tropicalforests.ox.ac.uk) to facilitate direct comparison with new NPP data emerging from the African and Amazonian tropics. Measurements of NPP components and soil respiration have been previously described in detail (see Chapter 4 and 5; Kho et al., *submitted* 2012a; Kho et al., *submitted* 2012b) and so are only summarised here. The ultimate aim here is to estimate the overall NPP, GPP and CUE of a lowland dipterocarp forest.

Measuring CO_2 Efflux

Stem CO_2 *efflux* (R_{stem})

We measured stem CO_2 efflux (R_{stem}) using a portable Infra-Red Gas Analysis (IRGA) system (EGM-4 and SRC-1 soil chamber, PP Systems, UK) with a custom-made adaptor to fit on soil collars. A PVC collar measuring 11 cm diameter and 10 cm length was sealed to each stem at 1.3 m above ground using non-setting sealant and glue. Collars were shaped according to the curve on the stem surface in order to provide a good seal on the stem area. Prior to installation, mosses and epiphytes were removed to provide the optimal surface areas for sealing. Collar depth on each stem was recorded to estimate the volume of CO_2 flux calculation. The field methods and equipment were adapted from Fenn et al. (2010).

Measurements were conducted on a fixed collar for 18 randomly selected trees, with DBH in the range of 13.7–150.7 cm on clay and 15.6–69.4 cm on sandy loam sites. The trees selected had DBH representing our study sites. Monthly CO_2 efflux was measured for 120 seconds on each tree during the day, with repetition if measurements were incomplete (less than 14 seconds). For each measurement, a linear fit to the CO_2 concentration data proved to be adequate in all cases (typical $r^2 \geq 0.80$), with the first nine seconds of data removed due to the potential for initial disturbance associated with chamber placement on the collar. Subsequent concentration data were sometimes also removed, to a maximum of 43 seconds, if found to deviate from the linear fit. Estimated stem CO_2 efflux was carefully checked. Stem CO_2 efflux measurements began in September 2008 and lasted until September 2009.

To scale the measured stem CO_2 efflux to whole trees, we estimated the total sum of stem surface area and branch surface area for the entire tree. Stem surface area is calculated as a truncated cone (Yoneda, 1993) using the following equation:

$$A_{stem} = \pi\,(r_b+r_{min})\sqrt{h_b^2 + (r_b-r_{min})^2} \qquad \text{(Eq. 6.1)}$$

where r_b is DBH in metres, r_{min} is the radii at the top of the stem in metres, and h_b is the height of the stem in metres. The r_{min} was calculated based on the taper equation pioneered by Chambers *et al*. (2000).

The surface area for branches was based on the pipe-model theory (Shinozaki *et al*., 1964) and verified for trees in Pasoh Forest Reserve, Peninsular Malaysia (Yoneda, 1993) by using the following equation:

$$A_b = \pi\,K\,\ln\,(d_{max}/d_{min}) \qquad \text{(Eq. 6.2)}$$

where A_b is the surface area of branches in metres, d_{max} and d_{min} are the maximum and minimum diameters of branches. D_{max} was estimated to be 40% of DBH, and d_{min} was assumed to be 0.002 metres (Shinozaki *et al*., 1964; Yoneda, 1993). *K* is the characteristics of each tree derived from the pipe-model theory (Shinozaki *et al*., 1964).

The total surface stem area is simply the sum of Equation 6.1 and 6.2. We applied these equations to all trees (≥ 1 cm DBH) on clay and sandy loam sites and calculated the stem area index (SAI) over the one-hectare plot. The estimated SAI was 2.39 and 3.07 on clay and sandy loam respectively. The average stem CO_2 efflux per unit stem area was then multiplied by the SAI. Finally, we aimed to explore the relationship between the average monthly stem CO_2 efflux and NPP_{ACW}. We assigned a 40% uncertainty to account for errors associated with variation between the stem area and measurement uncertainty. Given that stem CO_2 efflux is significantly related to surface area and volume, the measured stem CO_2 efflux was regressed against these variables to explore the relationship (Levy and Jarvis, 1998; Meir and Grace, 2002).

Leaf CO_2 Efflux (R_{leaf})

In this study, we did not directly measure leaf respiration. Alternatively, we used the nighttime leaf respiration estimated from nine dipterocarp species in Lambir (Kenzo *et al*., 2003). We attempted to accurately assess leaf respiration (R_{leaf}) by estimating daytime photoinhibition in order to obtain the total leaf dark respiration that incorporates mitochondrial activity. Hence, we estimated R_{leaf} by using a photoinhibition reduction factor of 67% (as in the study by Malhi *et al*., 2009). To scale across the one-hectare plot, we multiplied R_{leaf} by the mean LAI derived from section 5.3.2 in Chapter 5 (Kho et al., *submitted* 2012). The uncertainty in the multiplier was assigned as ± 0.15 to account for uncertainty in the amount of photorespiration and the variation between sites (Doughty et al., *submitted* 2012; Farfan-Amezquita et al., *submitted* 2012).

Coarse Root CO_2 *Efflux (*$R_{\text{coarse root}}$*)*

Although coarse root may contribute to substantial respiration, it is rarely quantified. Using a mass-based approach, we multiplied NPP_{ACW} by the ratio of coarse root biomass to above-ground wood biomass, estimated at 0.22 on both clay and sandy loam (see section 5.3.3., Chapter 5 Kho et al., *submitted* 2012b). Here, we assigned an uncertainty of 40% to the variation between sites and the sources of error due to the allometric model.

Soil CO_2 *Efflux*

The soil CO_2 efflux and partitioning data were derived from section 4.4.3 in Chapter 4 (Kho et al., *submitted* 2012a). Measurement of soil CO_2 efflux was conducted in the DIRT experimental plot and one-hectare plot, both for clay and sandy loam soils. Measurements were recorded using the aforementioned portable IRGA system, with a custom-made adaptor to fit on soil collars.

In the DIRT experimental plot, soil CO_2 efflux measurements were recorded from each treatment plot from May 2009 to October 2010. Based on these measurements, the total soil CO_2 efflux (Rs) was partitioned into litter (R_{litter}), root (R_{root}), SOM (R_{SOM}), and mycorrhizae (R_{myc}), with the following expression:

$$R_s = R_{\text{litter}} + R_{\text{SOM}} + R_{\text{root}} + R_{\text{myc}} \quad \text{(Eq. 6.3)}$$

where each component of the soil CO_2 efflux was calculated by taking the differences of the soil CO_2 efflux between treatments in each subplot based on additional equations as follows:

Litter respiration, $R_{\text{litter}} = T_{\text{DL}} - T_{\text{C}}$ (Eq. 6.4)

Root respiration, $R_{\mathrm{root}} = T_{\mathrm{NL}} - T_{\mathrm{Myc}}$ (Eq. 6.5)

Mycorrhizae respiration, $R_{\mathrm{myc}} = T_{\mathrm{Myc}} - T_{\mathrm{NI}}$ (Eq. 6.6)

SOM respiration, $R_{\mathrm{SOM}} = T_{\mathrm{NI}}$ (Eq. 6.7)

In the one-hectare plot, R_s was directly measured from a designated measurement point (microsite) near the centre of each subplot (20 m x 20 m). Measurements were conducted over two years from October 2008 to October 2010. Monthly R_s over the one-hectare plot was calculated based on the average CO_2 efflux measured on each microsite. To accurately estimate respiration from the soil components in the DIRT plot, we scaled the mean annual respiration for soil components across one-hectare based on the ratio of total annual R_s over the DIRT plot to total annual R_s over one-hectare.

Measuring NPP

Above-ground Coarse Wood NPP (NPP_{ACW})

Above-ground coarse wood production data were derived from section 5.4.3 in Chapter 5 (Kho et al., *submitted* 2012b). We used multiple tree censuses from sandy loam and clay sites to determine plot-level above-ground woody biomass and NPP (NPP_{ACW}). Above-ground woody biomass was estimated as a function of DBH and wood-specific gravity for each tree (≥ 1 cm DBH) using an allometric equation for moist tropical forest stands (Chave *et al.*, 2005). The above-ground wood productivity (NPP_{ACW}) was then estimated based on the change in woody biomass between census intervals plus the biomass of recruitment. Biomass values were converted into carbon based on a dry stem biomass of 47.4% (Martin and Thomas, 2011).

Litterfall NPP (*NPP*$_{\text{litterfall}}$)

Litterfall data were derived from section 5.4.4 in Chapter 5 (Kho et al., *submitted* 2012b). We collected litterfall including dead organic material (woody material < 2 cm diameter) from litter traps measuring 0.25 m^2 (0.5 m x 0.5 m). Collection began in July 2008 and continued until August 2009. Litterfall was collected every 14 days to minimise in-trap decomposition, oven-dried at 80°C to constant weight, and weighed immediately after removal from the oven. The litter was separated into i) leaves; ii) branches, twigs and woody tissue; iii) fruits, flowers and seeds; and iv) undefined fine debris. The sum of all these components was determined as canopy production. Biomass values were converted by assuming that litter biomass has a carbon content of 50% (Kenzo *et al*., 2003).

Branch Turnover NPP (NPP$_{\text{branch turnover}}$*)*

Branch turnover production data were derived from section 5.4.6 in Chapter 5 (Kho et al., *submitted* 2012b). Fallen coarse woody materials (woody material > 2 cm diameter, including bark) were collected at three-monthly intervals from four 100 m x 1 m transects established along the boundary within the one-hectare plot between August 2009 and July 2010. Branches that were easily lifted were cut to only include the transect-crossing components, removed and weighed directly. Heavier and larger branches that could not be removed were recorded for dimensions (diameter, height, and length), and were allocated a wood density value based on their decomposition stage.

Coarse Root NPP (NPP$_{\text{coarse roots}}$*)*

NPP$_{\text{coarse root}}$ was derived from section 5.1.2 in Chapter 5 (Kho et al., *submitted* 2012b). We used an allometric equation for coarse root biomass developed from a large-scale root excavation study conducted at Pasoh (Niiyama *et al*., 2010), which is a similar lowland dipterocarp forest to our study site. $NPP_{\text{coarse root}}$ is calculated by taking the difference between census intervals, analogous to NPP_{ACW}.

NPP Lost to Leaf Herbivory ($NPP_{\text{herbivory}}$)

The production lost to leaf herbivory was derived from section 5.1.1 in Chapter 5 (Kho et al., *submitted* 2012b). In this study, we adopted the mean herbivory rate of 0.0135% per day from synchronous and continuous leafing patterns in Lambir reported by Kurokawa and Nakashizuka (2008). $NPP_{\text{herbivory}}$ was estimated by multiplying the herbivory rate by the annual NPP_{leaf}.

Fine Roots NPP ($NPP_{\text{fine roots}}$)

Fine roots production ($NPP_{\text{fine roots}}$) data were derived from section 5.1.3 in Chapter 5 (Kho et al., *submitted* 2012b). Nine ingrowth cores made from mesh nets (mesh size: 1 cm^2) of 14 cm diameter and 40 cm height were systematically installed to 30 cm depth from the soil surface on the clay and sandy loam sites. The mesh nets were extracted every three months from September 2008 to October 2009. Extracted fine roots were predicted following an established approach (Metcalfe *et al.*, 2007). Fine roots production was estimated by scaling to one-hectare. Next, we applied a correction factor of 1.125 to soil depth between 30 and 100 cm to reduce discrepancies of fine root production from different soil depths (Kho et al., *submitted* 2012b). The depth correction was estimated following a similar approach to that employed by Malhi et al. (2009).

Estimating NPP, GPP, and CUE

The total NPP (NPP_{Total}) is the sum of above-ground production (NPP_{AG}) and below-ground primary production (NPP_{BG}). The total NPP is the sum of NPP_{AG} and NPP_{BG}, and both these terms are calculated with the following equations:

$$NPP_{\text{AG}} = NPP_{\text{ACW (trees} \geq \text{10 cm DBH)}} + NPP_{\text{ACW (trees} < \text{10 cm DBH)}} + NPP_{\text{litterfall}} + NPP_{\text{branch turnover}} + NPP_{\text{herbivory}} \quad \text{(Eq. 6.8)}$$

$$NPP_{\text{BG}} = NPP_{\text{fine roots}} + NPP_{\text{coarse roots}} \quad \text{(Eq. 6.9)}$$

Total respiration (R_{Total}) is the sum of R_{a} and R_{h}, which is given as

$$R_{\text{a}} = R_{\text{leaf}} + R_{\text{stem}} + R_{\text{rhizosphere}} \quad \text{(Eq. 6.10)}$$

$$R_{\text{h}} = R_{\text{litter}} + R_{\text{SOM}} + R_{\text{CWD}} \quad \text{(Eq. 6.11)}$$

where $R_{\text{rhizosphere}}$ is fine roots respiration plus rhizomicrobial (including mycorrhizae and rhizodeposits).

A large fraction, approximately 76% of the decomposing coarse woody debris (CWD) is respired *in situ*, and the remaining fraction (24%) is transferred into the soil (Chambers *et al*., 2001). Hence, R_{CWD} can be estimated from the inputs of CWD, multiplying them by a factor of 0.76 ± 0.15 (see Malhi *et al*., 2009). NPP loss of volatile organic emissions is not included here as this term is a small component and thus negligible (Malhi *et al*., 2009).

Under the quasi-equilibrium state when carbon inputs equal outputs, the sum of total net carbon produced (NPP_{Total}) and the R_a in plants is given with the following expression:

$$\mathrm{GPP} = NPP_{\mathrm{Total}} + R_a \qquad \text{(Eq. 6.12)}$$

Finally, CUE is the proportion of NPP_{Total} to GPP, and thus given as:

$$\mathrm{CUE} = NPP_{\mathrm{Total}} / \mathrm{GPP} \qquad \text{(Eq. 6.13)}$$

6.4. Results

6.4.1. Total Respiration (R_{Total})

R_{Total} was 32.2 ± 4.0 Mg C ha^{-1} yr^{-1} on clay and 33.9 ± 3.6 Mg C ha^{-1} yr^{-1} on sandy loam (Table 6.1). R_{Total} was largely attributed to R_a on both clay and sandy loam sites, estimated at 21.3 ± 4.0 Mg C ha^{-1} yr^{-1} on clay and 20.6 ± 3.6 Mg C ha^{-1} yr^{-1} on sandy loam during the period of measurement. R_h was 10.9 ± 0.7 Mg C ha^{-1} yr^{-1} on clay and 13.3 ± 0.3 Mg C ha^{-1} yr^{-1} on sandy loam.

R_a was quite similar between clay and sandy loam. The stem CO_2 efflux (R_{stem}) per unit surface area ranged from 0.35 to 1.28 µmol CO_2 m^{-2} s^{-1} (n = 158 measurements) on clay and sandy loam. Using SAI to scale R_{stem} across the plots, the total annual R_{stem} on clay and sandy loam was similar at 7.3 ± 2.9 Mg C ha^{-1} yr^{-1} and 5.8 ± 2.3 Mg C ha^{-1} yr^{-1} respectively. Leaf respiration (R_{leaf}) contributed the largest flux of approximately 26.4 ± 8.6/26.6 ± 8.5% of the total R_{Total} on clay and sandy loam (clay/sandy loam) (Figure 6.1a, Table 6.1). The estimated R_{leaf} corrected for photorespiration was comparable to other similar studies in tropical forests elsewhere (Chambers *et al.*, 2004; Malhi *et al.*, 2009; Metcalfe *et al.*, 2010b; Tan *et al.*, 2010). Based on the soil CO_2 efflux partitioning study, the fraction of $R_{\mathrm{fine\ root}}$ was

7.8 ± 1.5% on clay and 8.8 ± 1.1% on sandy loam of the total R_{Total} (Figure 6.1a, Table 6.1). $R_{\mathrm{coarse\ root}}$ contributed the smallest proportion of 3.0 ± 1.3% on clay and 2.0 ± 0.8% on sandy loam (Figure 6.1a, Table 6.1). R_{myc} contributed approximately 4.3 ± 0.9% on clay and 4.5 ± 0.7% on sandy loam (Figure 6.1b, Table 6.1).

For the components of R_{h}, the clay site showed significantly lower respiration rates than the sandy loam site (Figure 6.1b). This can be explained by litter respiration on clay, which is approximately 53% lower than on sandy loam soil (Figure 6.1b, Table 6.1). SOM was the largest component with fractions of 17.7 ± 2.6% on clay and 19.3 ± 2.1% on sandy loam (Figure 6.1b, Table 6.1). The proportion of R_{CWD} was estimated at 11.2 ± 1.7% on clay and 9.4 ± 1.2% on sandy loam (Table 6.1), proportions comparable to a previous study using a similar approach (2.2–4.5 Mg C ha^{-1} yr^{-1}) (Malhi *et al.*, 2009).

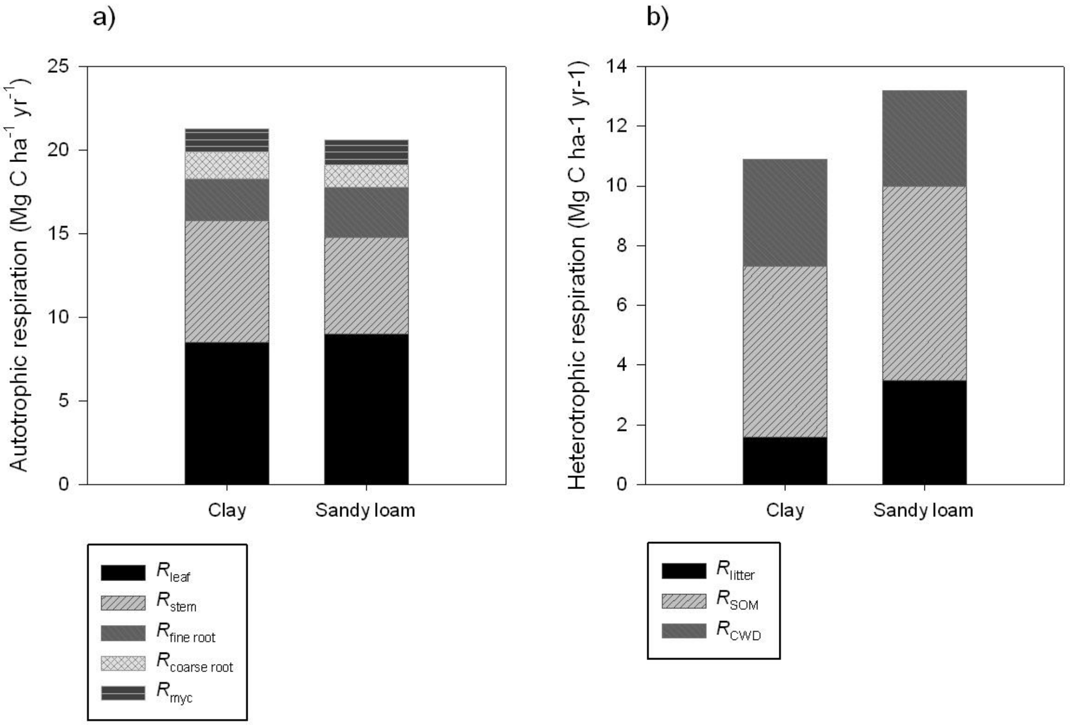


Figure 6.1: a) Autotrophic respiration (R_{a}) and b) heterotrophic respiration (R_{h}) on clay and sandy loam. All data are presented in Table 6.1.

Table 6.1: Synthesis of carbon fluxes estimate

	Clay		Sandy loam	
	Mean	SE	Mean	SE
NPP (Mg C ha^{-1} yr^{-1})				
Leaves	5.5	0.4	4.4	0.3
Twigs (< 2 cm diameter)	1.4	0.2	0.7	0.1
Reproductive materials	0.3	0.1	0.5	0.1
Undefined fine debris	0.7	0.1	0.5	0.1
Herbivory	0.3	0.1	0.2	0.1
Branch turnover (> 2 cm diameter)	0.5	0.1	1.1	0.1
Aboveground coarse wood (trees ≥ 10 cm DBH)	4.1	0.4	2.9	0.3
Aboveground coarse wood (trees < 10 cm DBH)	0.2	0.02	0.2	0.02
CWD[1]	4.8	0.4	4.2	0.3
Coarse root	0.9	0.4	0.7	0.3
Fine root	2.0	0.6	1.9	0.3
Respiration (Mg C ha^{-1} yr^{-1})				
Leaf	8.5	2.6	9.0	2.7
Stem (> 10 cm DBH)	7.3	2.9	5.8	2.3
Coarse root	1.6	0.6	1.3	0.5
Fine root	2.5	0.4	3.0	0.2
CWD	3.6	0.3	3.2	0.2
Litter	1.6	0.3	3.5	0.2
SOM	5.7	0.5	6.5	0.1
Mycorrhizae	1.4	0.2	1.5	0.2
Measured soil heterotrophic respiration[2]	7.3	0.6	10.1	0.3
Predicted soil heterotrophic respiration[3]	10.8	0.8	8.6	0.6
Measured soil respiration[4]	11.2	0.7	14.6	0.4
Predicted soil respiration[5]	15.9	1.0	14.1	0.8
Ecosystem Fluxes (Mg C ha^{-1} yr^{-1})				
Total NPP (NPP_{Total})	15.9	0.9	13.0	0.7
Measured total respiration (R_{Total})	32.2	4.0	33.9	3.6
Predicted total ecosystem respiration (R_{Total})	35.7	4.0	32.4	3.7
Autotrophic respiration (R_{a})	21.3	4.0	20.6	3.6
Measured heterotrophic respiration (R_{h})[6]	10.9	0.7	13.3	0.3
Predicted heterotrophic respiration (R_{h})[7]	14.4	0.9	11.8	0.7
GPP	37.2	4.1	33.6	3.7
CUE				
Ecosystem	0.43	0.05	0.39	0.05
Leaf	0.39	0.14	0.33	0.12
Stem	0.37	0.24	0.35	0.32
Fine root	0.64	0.17	0.53	0.09

[1] Estimated as the sum of above-ground coarse woody (trees > 1 cm DBH) NPP and branch turnover NPP
[2] Estimated as the sum of litter and SOM respiration
[3] Estimated as the sum of litterfall NPP and below-ground NPP
[4] Direct soil respiration measurements (see Chapter 4)
[5] Estimated as the sum of soil heterotrophic respiration, fine root respiration and mycorrhizae respiration
[6] Sum of measured soil heterotrophic and coarse woody debris respiration
[7] Sum of predicted soil heterotrophic and coarse woody debris respiration

6.4.2. Total NPP (NPP_{Total})

NPP_{Total} was 15.9 ± 0.9 Mg C ha^{-1} yr^{-1} on clay and 13.0 ± 0.7 Mg C ha^{-1} yr^{-1} on sandy loam (Table 6.1). Above-ground NPP was 13.0 ± 0.6 Mg C ha^{-1} yr^{-1} on clay and 10.4 ± 0.6 Mg C ha^{-1} yr^{-1} on sandy loam. Across clay and sandy loam soils, litterfall production (leaves, twigs, reproductive materials, and undefined debris) contributed the largest component to NPP_{Total} on clay (7.9 ± 0.4 Mg C ha^{-1} yr^{-1}) and sandy loam (6.0 ± 0.5 Mg C ha^{-1} yr^{-1}) (Figure 6.2a, Table 6.1). Above-ground coarse wood production (NPP_{ACW}) for all trees greater than 1 cm DBH was 4.3 ± 0.4 Mg C ha^{-1} yr^{-1} on clay and 3.1 ± 0.3 Mg C ha^{-1} yr^{-1} on sandy loam. The production lost to leaf herbivory was quite similar on both clay and sandy loam, with an average of 1.8 ± 0.5% of NPP_{Total} (Figure 6.2a, Table 6.1). The proportion of branch turnover NPP was significantly lower on clay (3.1 ± 0.7%) than on sandy loam (8.5 ± 0.9%). Below-ground NPP was quite similar at 2.9 ± 0.7 Mg C ha^{-1} yr^{-1} on clay and 2.6 ± 0.4 Mg C ha^{-1} yr^{-1} on sandy loam. The largest component in the NPP_{BG} was fine roots, with an average NPP of 2.0 ± 0.3 Mg C ha^{-1} yr^{-1} on both plots (Figure 6.2b, Table 6.1). The above-ground NPP was significantly higher on clay than on sandy loam, suggesting that soil fertility may influence NPP.

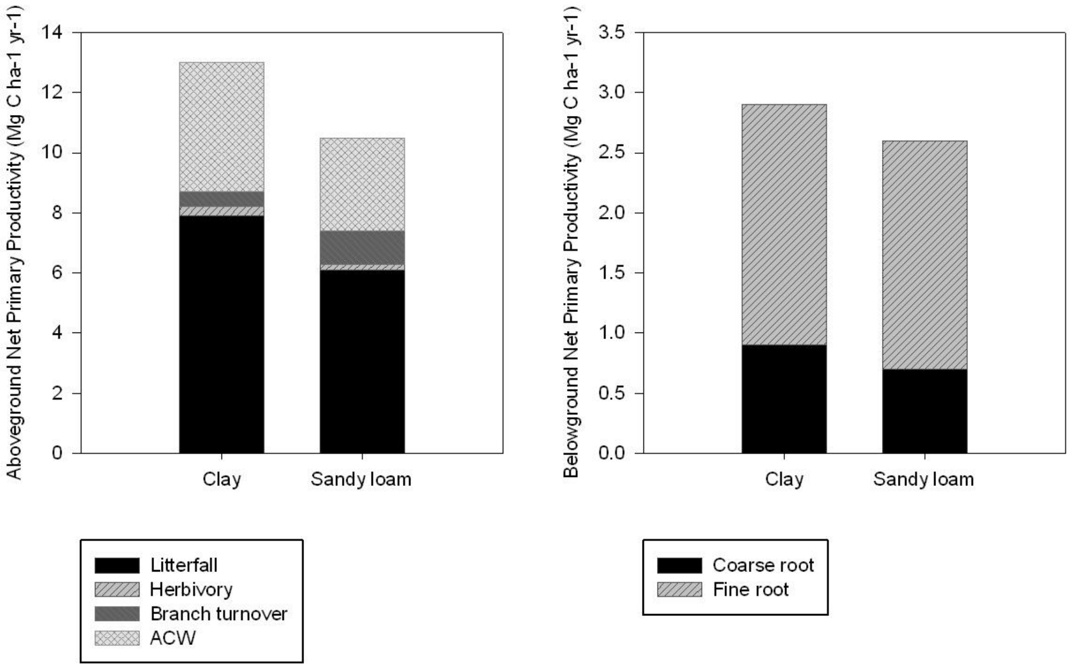


Figure 6.2: The a) above-ground and b) below-ground components of NPP on clay and sandy loam. The litterfall NPP includes leaves, twigs, reproductive materials, and undefined fine debris. ACW, above-ground coarse wood for all tree (≥ 1 cm DBH).

6.5. Discussion

6.5.1. NPP and Respiration

In this study, we have quantified the main components of NPP and respiration. The total NPP in this lowland dipterocarp forest is substantially higher than the average value of about 10.0 Mg C ha^{-1} yr^{-1} for several sites in the Amazonian forests (Clark *et al.*, 2001; Giardina *et al.*, 2003; Chambers *et al.*, 2004; Aragão *et al.*, 2009; Metcalfe *et al.*, 2010b), with the exception of the 14.4 Mg C ha^{-1} yr^{-1} recorded at the Tapajos site (Aragão *et al.*, 2009; Malhi *et al.*, 2009). In fact, our higher estimate on clay soil seem to show a similar magnitude to the Tapajos site, which is also characterised as a clay soil site (Silver *et al.*, 2000). Our estimates are broadly consistent with previous estimates (6.7–14.3 Mg C ha^{-1} yr^{-1}) in Southeast Asia (Kira, 1978; Kira, 1987; Paoli and Curran, 2007; Hertel *et al.*, 2009), as well as being within the range expected for a typical lowland dipterocarp forest (10–19 Mg C ha^{-1} yr^{-1}) (Clark *et al*., 2001; Malhi *et al*., 2011).

This higher total NPP is mainly attributed to higher allocation of NPP to above-ground components. This implies that lowland dipterocarp forests, such as the one in our study, allocate a larger amount of production to above-ground productivity. Therefore, it is evident that the forest in our study site has greater stature and constitutes a larger biomass (Ashton and Hall, 1992). This is evident from our tree-height data (section 5.4.2., Chapter 5), which shows the Lambir trees to be substantially higher than tropical forest elsewhere. Furthermore, we have shown that the productivity of a forest plot on the clay site is significantly higher than the forest plot on the sandy loam site. Clearly, this is attributed to soil nutrient availability (Paoli and Curran, 2007; Cleveland *et al*., 2011). At our study site, clay soil is typically more fertile, with higher soil phosphorus content, than on the sandy loam soil (Baillie *et al*., 2006; Tan *et al*., 2009). A recent study has shown that above-ground productivity increases with soil nutrients, particularly soil phosphorus (Paoli and Curran, 2007). Considering all this, we can see that soil nutrient levels are the primary driver of the spatial pattern of above-ground productivity.

For below-ground production, however, our estimates are generally lower than those at several sites in the Amazonian forest (Giardina *et al*., 2003; Aragão *et al*., 2009; Malhi *et al*., 2009; Metcalfe *et al*., 2010b). This is mainly attributed to a lower level of fine root production, which contributes significantly to NPP_{BG}. Our estimates are comparable to previously reported $NPP_{\text{fine roots}}$ of 2.0 Mg C ha^{-1} yr^{-1} (Kira, 1978), predicted from an extensive root biomass study in Pasoh (Yoda, 1978). In addition, a recent study suggested that fine root biomass in northern Borneo is relatively low when compared to tropical forests elsewhere (Green *et al*., 2005).

Table 6.2: Summary of autotrophic (R_a), heterotrophic (R_h), and total (R_{Total}) respiration in tropical forests. All flux data are in Mg C ha^{-1} yr^{-1}

	Soil type	$\boldsymbol{R_a}$	$\boldsymbol{R_h}$	$\boldsymbol{R_{Total}}$	**Source**
Lambir, Malaysia	Clay	21.3 ± 4.0	10.9 ± 0.7	32.2 ± 4.0	This study
Lambir, Malaysia	Sandy loam	20.6 ± 3.6	13.3 ± 0.3	33.9 ± 3.6	This study
Pasoh, Malaysia	Sandy	37.6	-	-	Yoda (1983)
Pasoh, Malaysia	Sandy	31.9*	12.4*	43.0*	Kira (1987)
Pasoh, Malaysia	Sandy	-	14.3	-	Nakane (1980)
Khao Chong, Thailand	Sandy	57.8	-	-	Yoda 1967
Xishuangbanna, China	Sandy	17.2	5.2	22.4	Tan et al. (2010)
Manaus, Brazil	Clay	19.8 ± 4.6	9.6 ± 1.2	29.3 ± 4.7	Malhi et al. (2009)
Manaus, Brazil	Clay	21.0	8.5	29.5	Chambers et al. (2004)
Tapajós, Brazil	Clay	14.9 ± 4.2	14.9 ± 1.4	29.8 ± 4.4	Malhi et al. (2009)
Caxiuanã, Brazil	Clay	21.4 ± 4.1	9.4 ± 0.8	30.1 ± 4.2	Malhi et al. (2009)
Caxiuanã, Brazil	Clay	22.4 ± 2.8	10.2 ± 1.0	32.6 ± 2.9	Metcalfe et al. (2010)

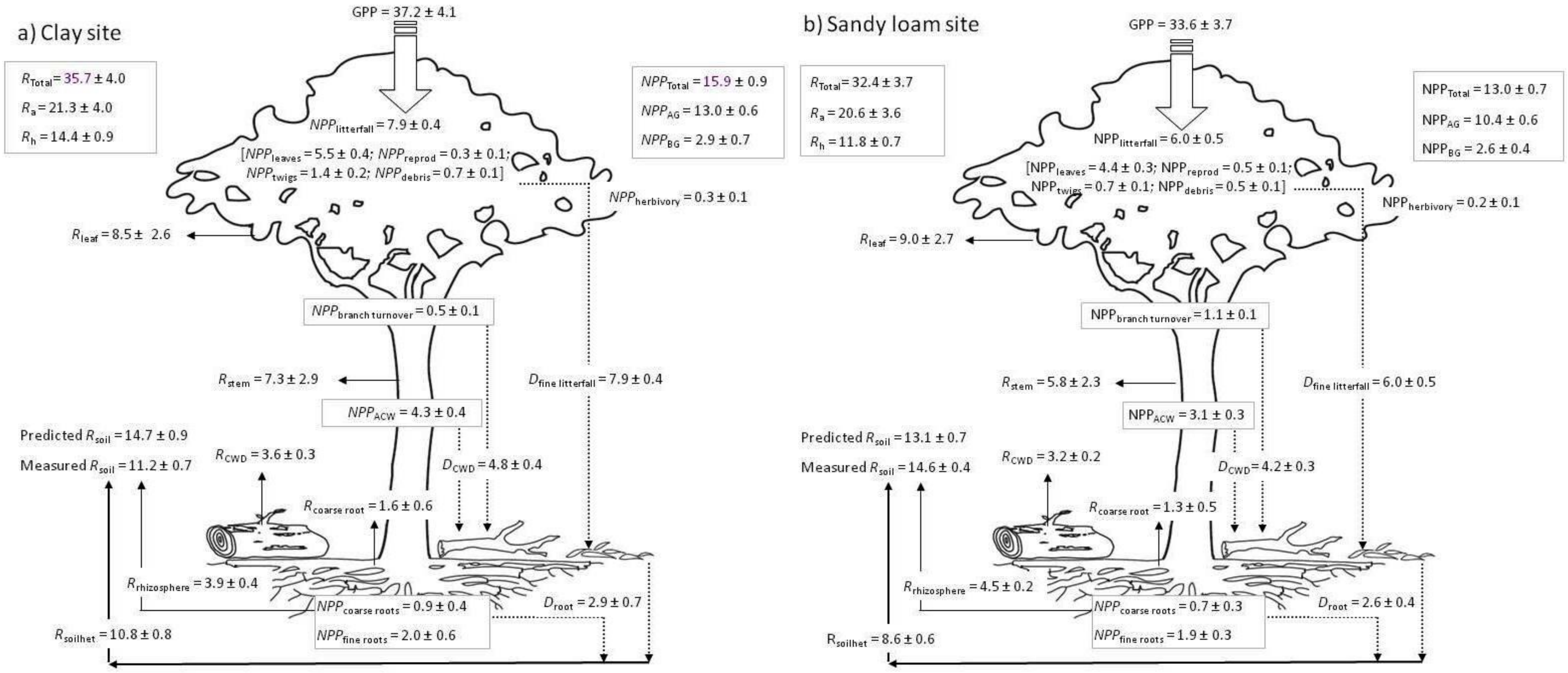
* Estimated based on data from Kira (1987)

Scaling our flux estimates to the ecosystem-level, our estimates of R_a and R_h are generally in good agreement with recent studies using a similar approach (see Table 6.2). In the Southeast Asia region, our R_a estimate is substantially lower than the previous studies conducted in Pasoh. The differences may be attributed to methodological issues. There appears to be a substantial respiration rate being measured from the leaf and fine roots. The Pasoh R_{leaf} was not corrected for light inhibition of dark respiration. A recent study suggested a 67% reduction in total leaf respiration when the photoinhibition factor is applied to leaf dark respiration (Lloyd *et al.*, 2009; Malhi *et al.*, 2009). Our revised R_{leaf}, based on the data from Yoda (1983), is a more conservative estimate and in good agreement with values reported from several sites in Amazonian forests (Malhi *et al.*, 2009). In addition, leaf respiration in Pasoh was measured instantaneously, which may potentially increase the rate of respiration in the leaf during the first few minutes after darkening (Azcón-Bieto and Osmond, 1983; Atkin *et al*., 1998). Severing parts of plants (i.e. branches, stems, and leaves) and the time taken to measure respiration for all these part may affect the rate of respiration (Yoda, 1983).

6.5.2. Ecosystem Fluxes

This is the first attempt to quantify all components of NPP and respiration and to determine a comprehensive carbon budget for a lowland dipterocarp forest, particularly in Lambir (Figure 6.3). Assuming that the lowland dipterocarp forest in Lambir is in a steady-state condition, GPP was slightly greater on clay (37.2 ± 4.1 Mg C ha^{-1} yr^{-1}) than on sandy loam (33.6 ± 3.7 Mg C ha^{-1} yr^{-1}) during the period of our measurement (Figure 6.3, Table 6.1). Considering the similar bottom-up approach, our GPP estimates are quite similar to several sites in the Amazonian forests, with values in the range 29.3–34.4 (Malhi *et al*., 2009; Metcalfe *et al*., 2010b). Furthermore, the estimates are comparable to previously modelled GPP based on the eddy covariance method from the flux tower. The estimated GPP from these flux towers have been reported in the range of 32.3 to 33.7 Mg C ha^{-1} yr^{-1} for the period 1968–2002 in Lambir, and 30.0–34.0 Mg C ha^{-1} yr^{-1} for the period between 2003 and 2009 (Kumagai *et al*., 2004; Saitoh *et al*., 2005b; Kosugi *et al*., 2012). Our GPP estimates on clay and sandy loam sites, however, show slightly higher GPP than the average modelled GPP (32.2 Mg C ha^{-1} yr^{-1}) in Lambir. Given that plant carbon expenditure (PCE) is approximately equal to GPP in a steady-state condition, the balance between carbon input and output is the net tree production (Metcalfe *et al*., 2010b). Subtracting the average modelled GPP from the estimated PCE, the carbon expenditure is higher on clay (5.0 ± 4.7 Mg C ha^{-1} yr^{-1}) than on the sandy loam site (1.4 ± 4.3 Mg C ha^{-1} yr^{-1}). If our estimates are plausible, this implies that production is slightly higher than assimilation on clay.

We calculated CUE to determine the fraction of GPP allocated to NPP. The ecosystem CUE was 0.43 ± 0.05 on clay and 0.39 ± 0.05 on sandy loam (Table 6.1; Figure 6.4). Hence, almost 40% is allocated above-ground for production of new tissue, with the remainder being respired. This agrees with a recent study suggesting low CUE in old-growth tropical forests (Vicca *et al*., 2012). Nevertheless, our estimates are relatively higher than the CUE previously estimated in Pasoh (Kira, 1987) and several sites in the Amazonian forests (Chambers *et al*., 2004; Malhi *et al*., 2009). Explicitly, CUE for stem was 0.37 ± 0.24/0.35 ± 0.32 and leaf was 0.39 ± 0.14/0.33 ± 0.12 on clay and sandy loam (clay/sandy loam) (Table 6.1; Figure 6.4). For the below-ground components, CUE for root (coarse and fine root) was 0.64 ± 0.17 on clay and 0.53 ± 0.09 on sandy loam. The forest plot on clay consistently shows greater CUE at ecosystem-level than the sandy loam site (Figure 6.4).



Key: GPP, gross primary productivity; R_{Total}, total ecosystem respiration; R_{a}, autotrophic respiration; R_{h}, heterotrophic respiration; NPP_{Total}, total net primary productivity; NPP_{AG}, above-ground NPP; NPP_{BG}, below-ground NPP; $NPP_{\text{litterfall}}$, litterfall NPP; NPP_{leaves}, leaf NPP; NPP_{reprod}, reproductive materials NPP; NPP_{twigs}, twig NPP; NPP_{debris}, fine undefined debris NPP; $NPP_{\text{herbivory}}$, lost to leaf herbivory NPP; $NPP_{\text{branch turnover}}$, branch turnover NPP, NPP_{ACW}, above-ground coarse wood NPP, D_{CWD}, coarse wood debris detritus, $NPP_{\text{coarse roots}}$, coarse roots NPP; $NPP_{\text{fine roots}}$, fine roots NPP; D_{root}, root detritus; $D_{\text{litterfall}}$, litterfall detritus; R_{soilhet}, soil heterotrophic respiration; $R_{\text{rhizosphere}}$, root respiration; $R_{\text{coarse root}}$, coarse root respiration; R_{CWD}, coarse woody debris respiration; R_{stem}, stem respiration; R_{soil}, total soil respiration; R_{leaf}, leaf respiration.

Figure 6.3: The complete carbon cycle for lowland dipterocarp forests on a) clay and b) sandy loam soils in Lambir. All data are estimated and measured in this study (Table 6.1). All units are in Mg C ha^{-1} yr^{-1}.

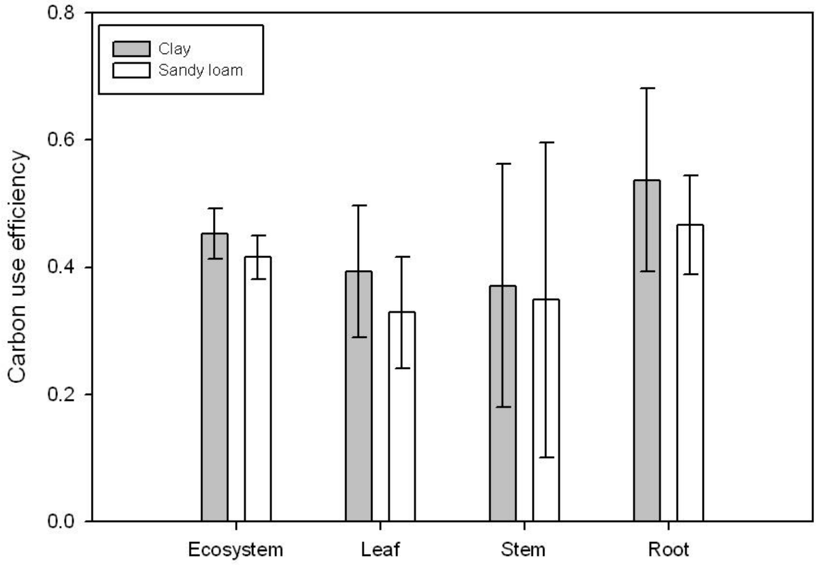


Figure 6.4: Ecosystem CUE for above- and below-ground components on clay (grey bars) and sandy loam (white bars). Data are presented in Table 6.1. Error bar denotes standard error of the mean.

The allocation of carbon to below-ground (TBCA) is mainly for the production and maintenance of roots, while at the same time being released as root exudates or from biomass turnover. We calculated the balance between aboveground input and measured R_s following the method introduced by Raich and Nadelhoffer (1989). TBCA was 3.3 ± 0.8 Mg C ha^{-1} yr^{-1} on clay and 8.6 ± 0.6 Mg C ha^{-1} yr^{-1} on sandy loam. However, modifying TBCA following Metcalfe *et al*. (2010b) to include all below-ground components estimated in this study, we found quite similar TBCA between clay (4.5 ± 0.9 Mg C ha^{-1} yr^{-1}) and sandy loam (3.9 ± 0.7 Mg C ha^{-1} yr^{-1}). This is about 12% of the total assimilated carbon from GPP being transferred below-ground.

In this study, we validated our carbon budget estimation using predicted R_s against measured R_s. Assuming a steady-state condition, the predicted R_s is 14.7 ± 0.9 Mg C ha^{-1} yr^{-1} on clay and 13.1 ± 0.7 Mg C ha^{-1} yr^{-1} on sandy loam (Figure 6.3, Table 6.1). The predicted R_s is very close to the measured R_s on sandy loam (Figure 6.3, Table 6.1). As such, this gives us greater confidence in our bottom-up approach and soil respiration partitioning approaches in predicting total ecosystem R_h (Figure 6.3, Table 6.1). However, the difference, particularly on clay soil, suggests that there may be less respiration being measured or insufficient field sampling to obtain a reasonably accurate carbon budget (Malhi *et al*., 2009; Metcalfe *et al*., 2010b).

6.6. Conclusion

Our study has shown that the total NPP in a lowland dipterocarp forest is higher than has been seen in tropical forests elsewhere. Approximately 40% is allocated to NPP and the remaining proportion is respired. Our calculated GPP, which suggests is in good agreement with the modelled GPP suggesting greater confidence in our bottom-up approach. This present study suggests that higher productivity is closely associated with higher nutrient availability. Future work, involving extensive and refined respiration methods, should be extended to develop and improve our current understanding of the carbon budget of tropical forests.

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Chapter 7

Chapter 7: Discussion

This section synthesises and reviews key findings from the work carried out during the course of my D.Phil. In the introduction, the scarcity of data on the carbon cycle of lowland dipterocarp forests was emphasised. This issue arises because of difficulties in conducting well-designed and reliable field studies, together with lack of measurements over longer timescales. Therefore, the key findings from this thesis contribute to understanding of: i) temporal variation in soil respiration and soil components; ii) seasonal allocation of carbon productivity and metabolism in above- and below-ground components; iii) contrasting responses to environmental factors between two contrasting soil types; and iv) the comprehensive carbon budget and carbon cycling processes in a lowland dipterocarp forest. Here, the research questions established in Chapter 1 are revisited.

7.1. Key Research Findings

7.1.1. How does respiration from soil and its components vary on seasonal and diurnal timescales across the clay and sandy loam soils?

This thesis presented the first study in a tropical forest where the soil CO_2 efflux from various components of the soil (litter, soil organic matter, mycorrhizae, and root) has been tracked over a full diurnal cycle. Over the diurnal cycle, soil CO_2 efflux showed a distinct and surprising pattern over approximately six months of observation on clay sites (see Figure 3.3a, Chapter 3). Nighttime levels of soil CO_2 efflux were significantly higher than daytime levels by approximately 12%. This daytime depression is entirely driven by litter respiration, indicating the potential influence of litter moisture content, which was not recorded. Furthermore, it is possible that daytime plant uptake of dissolved CO_2 via transpiration streams from roots may explain the daytime depression (see section 3.5.1., Chapter 3), although it is unclear why this effect would dominate litter layer respiration. This unexpected diurnal pattern has important implications for understanding the biological (e.g. Tang *et al.*, 2005) and physical (e.g. Phillips *et al.*, 2011) soil mechanisms driving diurnal soil respiration. Monthly soil CO_2 efflux showed a notable seasonal pattern over the two years of the observation on both the clay and sandy loam sites. Soil CO_2 efflux increased approximately two-fold following the wetter period (see Figure 4.2a, Chapter 4), and was negatively correlated with soil moisture.

Replicating and extending the measurement across a larger spatial area would be useful to determine if the effect of the daytime depression persists beyond the unusually dry period during the course of these measurements.

7.1.2. What is the mean rate of soil CO_2 efflux in a Bornean lowland dipterocarp forest? How much do litter, root, mycorrhizae and SOM contribute to soil respiration?

Using the monthly measured soil respiration across the one-hectare plot, I recorded significantly higher mean annual soil respiration on clay (11.2 ± 0.2 Mg C ha^{-1} yr^{-1}) than sandy loam (14.6 ± 0.2 Mg C ha^{-1} yr^{-1}) soil. Although relatively lower than previous soil CO_2 efflux recorded in Lambir (15.8–22.7 Mg C ha^{-1} yr^{-1}), mean annual soil respiration agrees with previously published estimates in the tropics (12.73 ± 0.35 Mg C ha^{-1} yr^{-1}, n = 365) and across Amazonia (13.84 ± 0.50 Mg C ha^{-1} yr^{-1}, n = 128) (Bond-Lamberty and Thomson, 2010).

This thesis represents the first attempt at partitioning the sources of soil CO_2 efflux for a lowland dipterocarp forest. Across clay and sandy loam soils, litter, SOM and mycorrhizae contributed approximately 20%, 50% and 12% of soil respiration respectively. As such, almost 80% of soil respiration is attributable to soil heterotrophic respiration. Litter appears to be the main component driving diurnal variation and some of the seasonal variation in soil CO_2 efflux. For example, there appears to be an increase in soil respiration (Figure 4.2a, Chapter 4) that coincides with a rapid increase in litterfall between July and August 2009 (Figure 5.4a, Chapter 5). This is an important result, because enhanced soil respiration as a result of an increase in above-ground inputs provides favourable conditions to microorganisms and may potentially accelerate carbon cycling (Kuzyakov, 2011).

7.1.3. What is the response of soil respiration and its soil components to environmental drivers on clay and sandy loam soils?

Soil respiration was negatively correlated with soil moisture content on clay and sandy loam. The measurements were conducted during an unusually dry period (mean soil moisture was in the range of 23.0 to 24.3%). This implies that there may be a threshold for the effect of moisture on soil respiration (Davidson *et al*., 1998; Schwendenmann *et al*., 2003; Sotta *et al*., 2006). This has profound implications for drought-associated sites such as in Lambir. For example, when soil moisture drops to a threshold value and microbial and root metabolisms shut, soil respiration will progressively decline with soil moisture. Additionally, litter respiration was found to be significantly correlated with soil moisture on both clay and sandy loam. This implies that litter respiration again is also controlled by soil moisture.

Over the diurnal cycle, however, soil temperature shows a strong effect to total soil respiration. Given that litter respiration drives total respiration, the response of R_{litter} to soil temperature indicates that short-term variation of soil CO_2 efflux strongly influenced by the diurnal variation of temperature and biotic factor drivers. In addition, heat and CO_2 transport processes may be an important driver controlling litter and the response of diurnal soil respiration (Phillips *et al*., 2011).

7.1.4. How is total above- and below-ground NPP partitioned into wood material, canopy, fine roots and coarse roots? How do these values vary between clay and sandy loam sites and compare to observations from tropical forests elsewhere?

Across both clay and sandy loam sites, above-ground NPP contributed approximately 81% of total NPP. This proportion is relatively higher than the average above-ground proportion (64 ± 3%) across ten sites, such as in the Amazonian forests (Aragão *et al.*, 2009). In contrast, below-ground productivity in this study is substantially lower than the average below-ground proportion (36 ± 3%) across the ten sites in the Amazon (Aragão *et al.*, 2009). This implies that lowland dipterocarp forests tend to allocate greater production to the above-ground components.

Total NPP was significantly higher for the forest plot on clay than for the forest plot on the sandy loam site. This can be explained by a strong link between soil nutrients and above-ground productivity, particularly the availability of phosphorus that essentially limits above-ground productivity (Palmiotto *et al.*, 2004; Baillie *et al.*, 2006; Tan *et al.*, 2009). In addition, the higher-productivity forest plot on the clay site had lower above-ground biomass and shorter carbon residence time (51 years). This suggests an inverse relationship between carbon residence time and woody productivity, as was suggested by Malhi et al. (2006) for old-growth Amazonian forests. Hence, greater above-ground biomass may not indicate higher productivity in this old-growth forest, instead suggesting that there is no relationship between above-ground woody biomass and productivity (Malhi *et al.*, 2006; Malhi, 2012).

7.1.5. What is the response of above- and below-ground NPP to environmental factors?

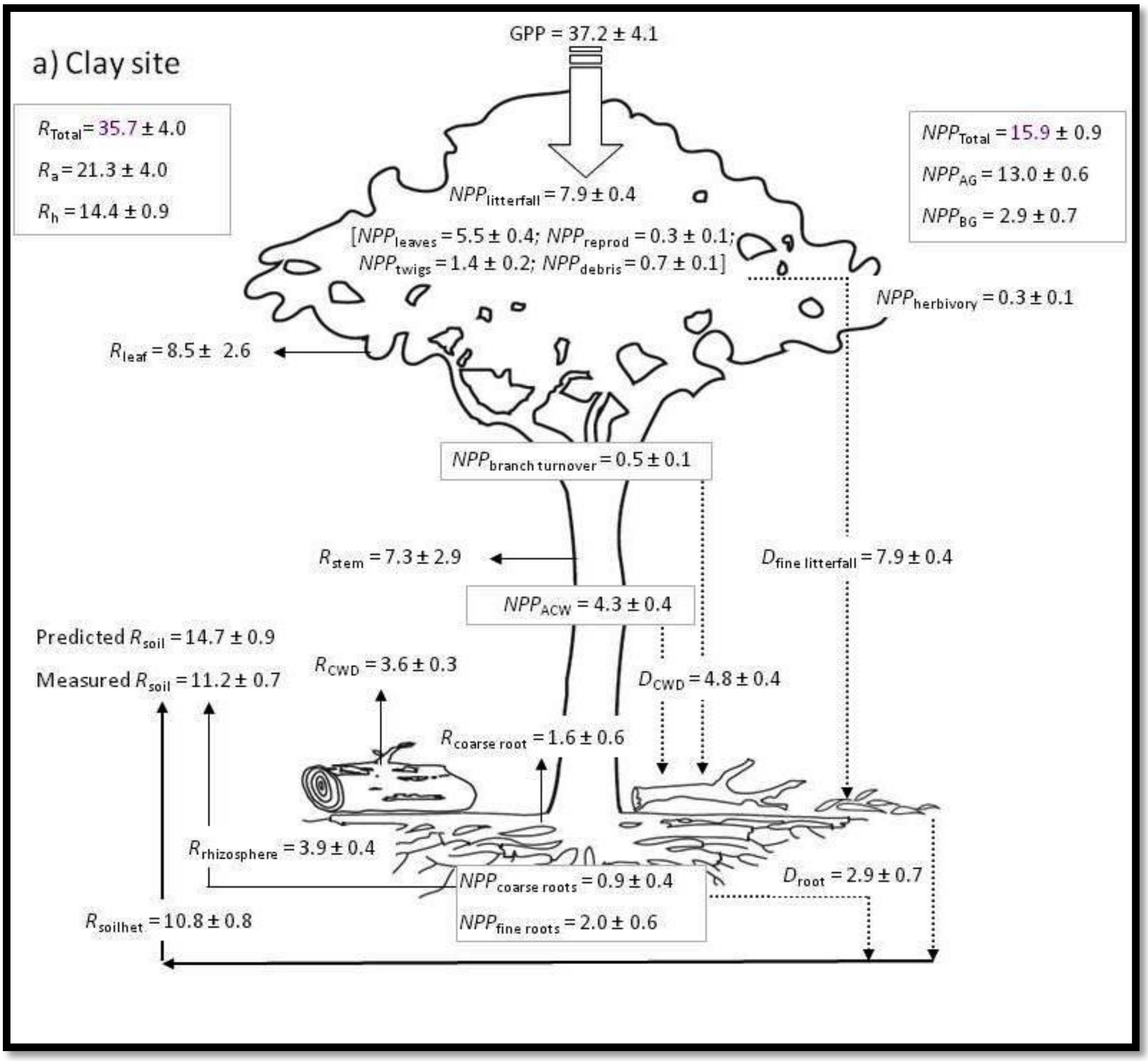
In line with the fact that the climate in Lambir is typically defined as aseasonal, the above- and below-ground components of NPP showed little seasonality over the measurement period. However, there was some evidence suggesting inter-annual variability. For example, production of fine roots shows strong seasonal and some inter-annual variability, typically during the wetter period (Sánchez-Gallén and Alvarez-Sánchez, 1996; see also Cavelier *et al.*, 1999; Green *et al.*, 2005). Additionally, this thesis has shown that an increase in litterfall and above-ground woody materials as a result of a large tree mortality in a forest plot on clay can substantially increase above-ground productivity (Chapter 5). In fact, such enhancement in regard to the below-ground carbon pool has also been reported to increase soil respiration, although such an effect may not be discernible during the period of my measurement.

The overall allocation of NPP showed an interesting shift between the forest plots on clay and sandy loam. The allocation of NPP increased at the onset of the wetter period in the forest plot on clay, while this effect is only discernible following the less wet period for the forest plot on sandy loam. A recent study found that anisohydric plants in Lambir have higher productivity under moist conditions (Kumagai and Porporato, 2012). While a larger allocation of NPP is invested in above-ground coarse wood on the clay site, there appears to be a higher proportion of NPP allocated to the production of leaves. Although there is no clear seasonal above- and below-ground productivity, the seasonal allocation of NPP shows marked seasonality in this lowland dipterocarp forest, which is primarily driven by moisture.

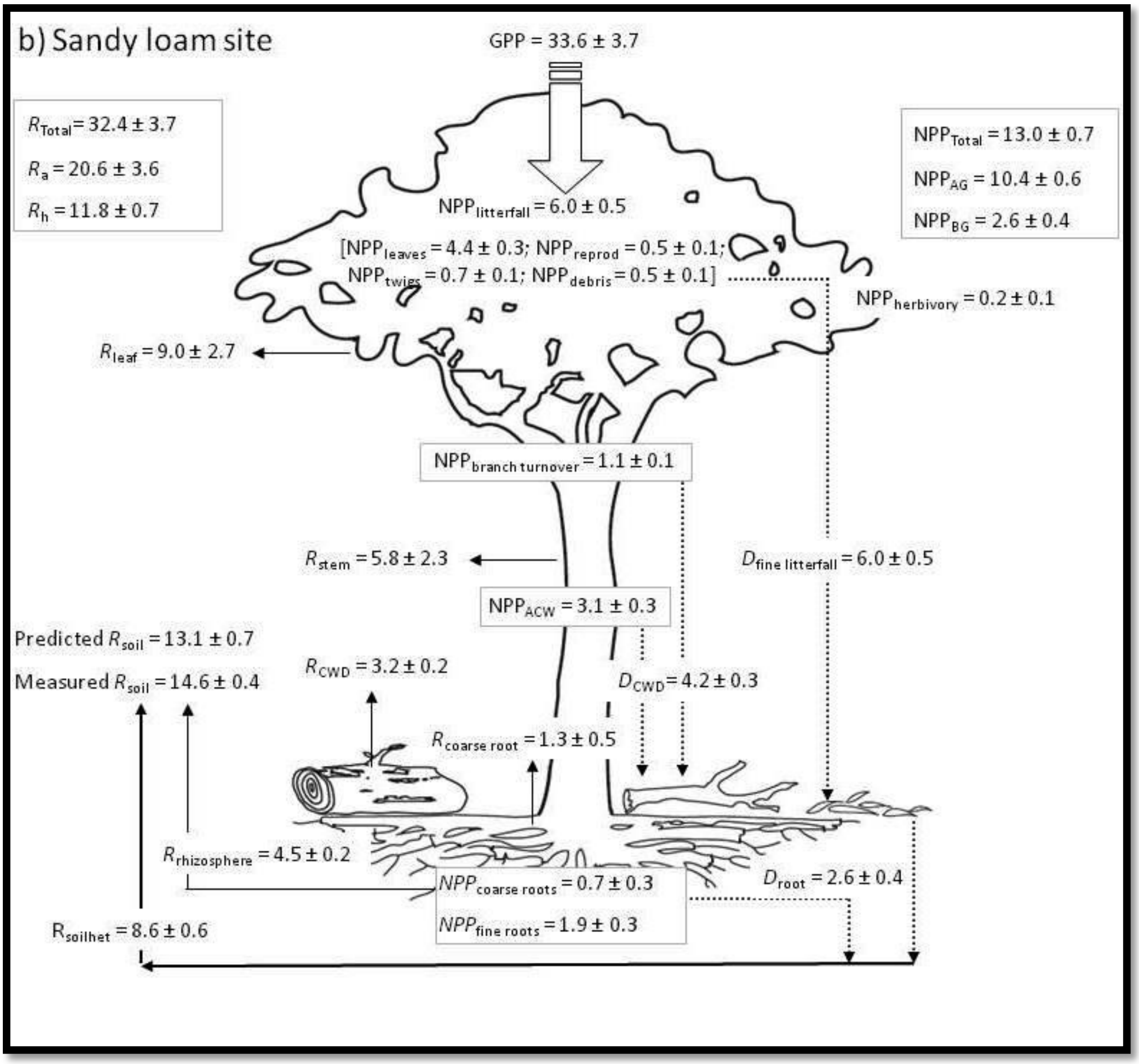
7.1.6. What is the overall carbon budget for the forest plots on clay and sandy loam in Lambir?

I have estimated that heterotrophic respiration contributes approximately 35.7 ± 3.1% of R_{Total}, while the remainder is attributed to plant respiration or R_{a}. Total productivity is slightly higher in lowland dipterocarp forest, as observed in Lambir, compared to tropical forests elsewhere. There appears to be a higher rate of above-ground productivity in Lambir (11.7 ± 0.4 Mg C ha^{-1} yr^{-1}) relative to previously reviewed estimates (5.8 ± 0.3 Mg C ha^{-1} yr^{-1}) across 74 tropical forest sites (Clark *et al.*, 2001; Malhi *et al.*, 2011). Although CUE is typically low for old-growth tropical forest, such as the case in this study, biomass production is relatively higher than several forest sites in Amazonia.

The close agreement between estimates from this study and data observed from the eddy covariance study in Lambir suggests that greater confidence can be had in regard to both approaches to estimating GPP. Validating below-ground fluxes, good agreement was also found between predicted and measured soil respiration (see Figure 7.1a and 7.1b). However, the slight difference suggests that there may be less respiration being measured or insufficient field sampling to obtain a reasonably accurate carbon budget (Malhi *et al*., 2009; Metcalfe *et al*., 2010). Further work is needed to close the gap between these terms. For example, measurements over a longer timescale and across a larger spatial area are useful to quantify respiration from soil and its underlying components with greater confidence. Although soil respiration in this study exhibits plausible values, measurement across different periods of time in a year and the effect of soil disturbance may not capture a consistent soil respiration pattern.



Key: GPP, gross primary productivity; R_{Total}, total ecosystem respiration; R_{a}, autotrophic respiration; R_{h}, heterotrophic respiration; NPP_{Total}, total net primary productivity; NPP_{AG}, above-ground NPP; NPP_{BG}, below-ground NPP; $NPP_{\mathrm{litterfall}}$, litterfall NPP; NPP_{leaves}, leaves NPP; NPP_{reprod}, reproductive materials NPP; NPP_{twigs}, twigs NPP; NPP_{debris}, fine undefined debris NPP; $NPP_{\mathrm{herbivory}}$, lost to leaf herbivory NPP; $NPP_{\mathrm{branch\ turnover}}$, branch turnover NPP, NPP_{ACW}, above-ground coarse wood NPP, D_{CWD}, coarse wood debris detritus, $NPP_{\mathrm{coarse\ roots}}$, coarse roots NPP; $NPP_{\mathrm{fine\ roots}}$, fine roots NPP; D_{root}, root detritus; $D_{\mathrm{litterfall}}$, litterfall detritus; R_{soilhet}, soil heterotrophic respiration; $R_{\mathrm{rhizosphere}}$, rhizosphere respiration; $R_{\mathrm{coarse\ root}}$, coarse root respiration; R_{CWD}, coarse woody debris respiration; R_{stem}, stem respiration; R_{soil}, total soil respiration; R_{leaf}, leaf respiration.



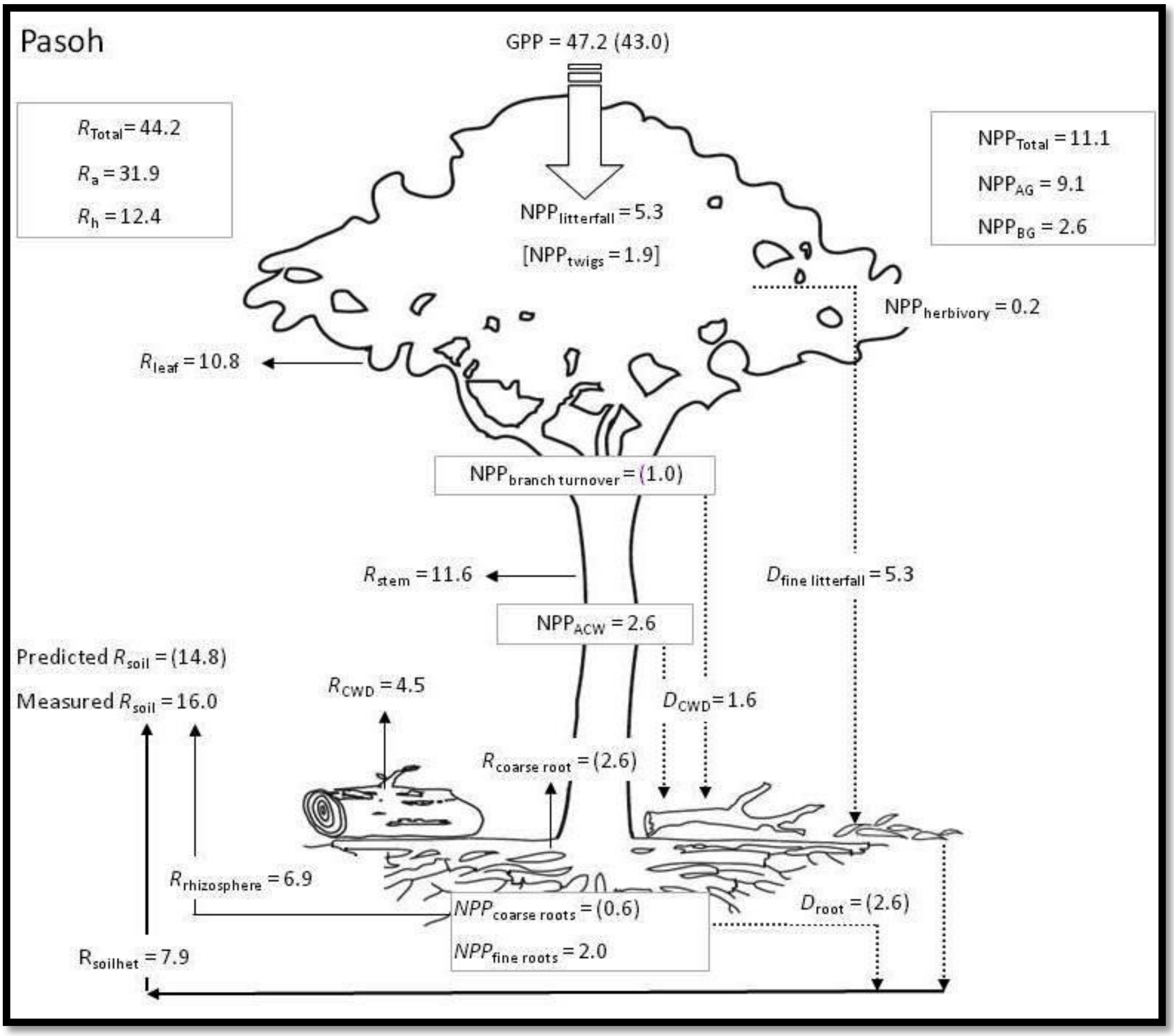
Key: GPP, gross primary productivity; R_{Total}, total ecosystem respiration; R_{a}, autotrophic respiration; R_{h}, heterotrophic respiration; NPP_{Total}, total net primary productivity; NPP_{AG}, above-ground NPP; NPP_{BG}, below-ground NPP; $NPP_{\text{litterfall}}$, litterfall NPP; NPP_{leaves}, leaves NPP; NPP_{reprod}, reproductive materials NPP; NPP_{twigs}, twigs NPP; NPP_{debris}, fine undefined debris NPP; $NPP_{\text{herbivory}}$, lost to leaf herbivory NPP; $NPP_{\text{branch turnover}}$, branch turnover NPP, NPP_{ACW}, above-ground coarse wood NPP, D_{CWD}, coarse wood debris detritus, $NPP_{\text{coarse roots}}$, coarse roots NPP; $NPP_{\text{fine roots}}$, fine roots NPP; D_{root}, root detritus; $D_{\text{litterfall}}$, litterfall detritus; R_{soilhet}, soil heterotrophic respiration; $R_{\text{rhizosphere}}$, rhizosphere respiration; $R_{\text{coarse root}}$, coarse root respiration; R_{CWD}, coarse woody debris respiration; R_{stem}, stem respiration; R_{soil}, total soil respiration; R_{leaf}, leaf respiration.

Figure 7.1: The complete carbon cycle for lowland dipterocarp forests on a) clay and b) sandy loam soils. All data are estimated and measured in this study (Table 6.1). All units are in Mg C ha^{-1} yr^{-1}.

7.1.7. How does carbon cycling in Lambir compare to observations from Pasoh and Amazonian forests?

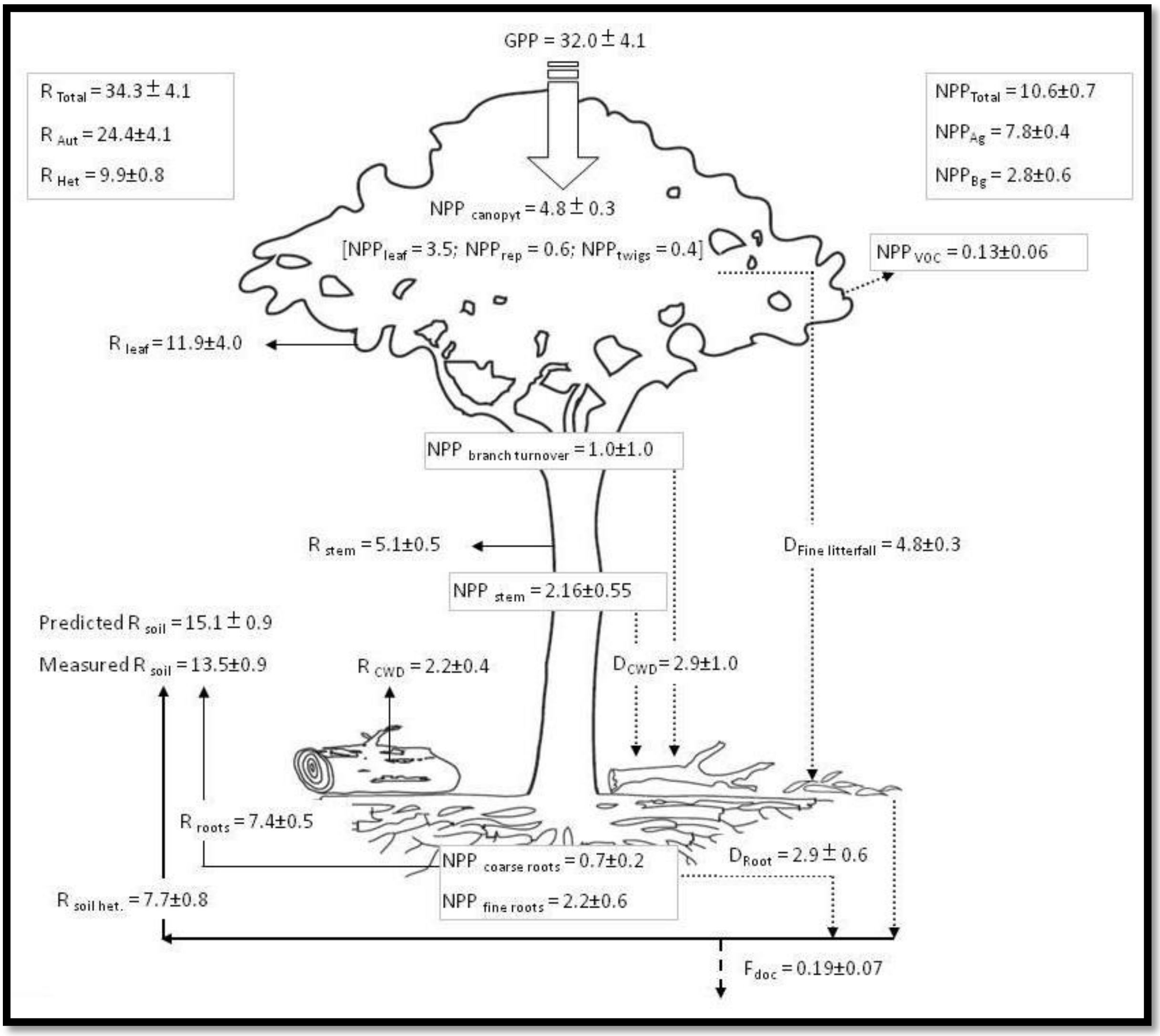
To compare and assess the overall carbon cycling in Lambir, all estimates were compiled in Figure 7.1a and 7.1b, and compared it to a similar dipterocarp forest in Pasoh (Figure 7.2), which was extensively studied in the 1970s and has been one of the iconic sites in tropical ecosystems ecology (Kira, 1978; Yoda, 1983; Kira, 1987), and also to a primary forest on clay oxisol (USDA soil taxonomy) site in Caxiuanã, Brazil (Figure 7.3). Table 7.1 provides the summary of NPP and respiration for the three forest sites.

The NPP at Pasoh is comparable in some aspects to that of the sandy loam site in this study (Figure 7.2). However, the values of leaf and wood autotrophic respiration reported at Pasoh are much greater than what has been found or estimated at Lambir. The differences may be methodological. The Pasoh leaf respiration values do not allow for light inhibition of dark respiration (Yoda, 1983), which was not recognised as an issue until more recently. Applying the 33% reduction that has been applied in the Amazonian sites (Malhi *et al* 2009), the daytime leaf respiration would reduce to 10.8 and the bottom-up estimate of GPP to 43.0 Mg C ha^{-1} yr^{-1}. The stem respiration was partially estimated from cut branches – the associated tissue damage and exposure of CO_2-rich xylem vessels may also have led to an overestimate of wood respiration. Moreover, the 1970s estimates of respiration at Pasoh employed by early chemical absorption approaches may exhibit substantial systematic errors compared to modern infra-red gas analysers.



Key: GPP, gross primary productivity; R_{Total}, total ecosystem respiration; R_{a}, autotrophic respiration; R_{h}, heterotrophic respiration; NPP_{Total}, total net primary productivity; NPP_{AG}, above-ground NPP; NPP_{BG}, below-ground NPP; $NPP_{\mathrm{litterfall}}$, litterfall NPP; NPP_{twigs}, twigs NPP; $NPP_{\mathrm{herbivory}}$, lost to leaf herbivory NPP; $NPP_{\mathrm{branch\ turnover}}$, branch turnover NPP, NPP_{ACW}, above-ground coarse wood NPP, D_{CWD}, coarse wood debris detritus, $NPP_{\mathrm{coarse\ roots}}$, coarse roots NPP; $NPP_{\mathrm{fine\ roots}}$, fine roots NPP; D_{root}, root detritus; $D_{\mathrm{litterfall}}$, litterfall detritus; R_{soilhet}, soil heterotrophic respiration; $R_{\mathrm{rhizosphere}}$, rhizosphere respiration; $R_{\mathrm{coarse\ root}}$, coarse root respiration; R_{CWD}, coarse woody debris respiration; R_{stem}, stem respiration; R_{soil}, total soil respiration; R_{leaf}, leaf respiration.

Figure 7.2: A full carbon cycle for a primary lowland dipterocarp forest in Pasoh Forest Reserve, in Peninsular Malaysia. All data derived from Yoneda *et al* (1977), Kira (1978), Yoda (1983), and Kira (1987). Figures in parentheses denote estimated value in this study. All units are in Mg C $\mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$.



Key: GPP, gross primary productivity; R_{Total}, total ecosystem respiration; R_{Aut}, autotrophic respiration; R_{Het}, heterotrophic respiration; NPP_{Total}, total net primary productivity; NPP_{Ag}, above-ground NPP; NPP_{Bg}, below-ground NPP; NPP_{canopy}, canopy NPP; NPP_{rep}, reproductive materials NPP; NPP_{twigs}, twigs NPP; NPP_{VOC}, volatile organic compound NPP; $NPP_{\mathrm{branch\ turnover}}$, branch turnover NPP, NPP_{stem}, stem NPP, D_{CWD}, coarse wood debris detritus, $NPP_{\mathrm{coarse\ roots}}$, coarse roots NPP; $NPP_{\mathrm{fine\ roots}}$, fine roots NPP; D_{root}, root detritus; F_{doc}, outflow of dissolved organic compound; $D_{Fine\ \mathrm{litterfall}}$, litterfall detritus; $R_{\mathrm{soil\ het}}$, soil heterotrophic respiration; R_{roots}, rhizosphere respiration; R_{CWD}, coarse woody debris respiration; R_{stem}, stem respiration; R_{soil}, total soil respiration; R_{leaf}, leaf respiration.

Figure 7.3: The complete carbon cycle for a mature primary forest on a typical clay Oxisol site in Caxiuanã, Brazil (adapted from Malhi, 2012). All units are in Mg C ha^{-1} yr^{-1}.

Table 7.1: Summary of carbon productivity and respiration for forest plots in Lambir (Borneo Malaysia), Pasoh (Peninsular Malaysia), and Caxiuanã (Brazil). Figures in parentheses are estimated in this study. All fluxes are reported in Mg C ha^{-1} yr^{-1}.

	Lambir	**Lambir**	**Pasoh**	**Caxiuanã**
Source	This study	This study	Kira (1978); Yoda (1983); Kira (1987)	Malhi (2012)
Soil type	Humult Ultisols (clay)	Udult Ultisols (sandy loam)	Durian series (clay)	Geric Acric ferralsol (clay)
Vegetation	Lowland dipterocarp	Lowland dipterocarp	Lowland dipterocarp	Lowland moist
MAT (^{o}C)	27	27	24.8	26.9
Rainfall (mm)	2630	2630	2054	2314
NPP (Mg C ha^{-1} yr^{-1})				
$NPP_{\text{litterfall}}$	7.9 ± 0.4	6.0 ± 0.5	5.3	4.8 ± 0.3
$NPP_{\text{herbivory}}$	0.3 ± 0.1	0.2 ± 0.1	0.2	-
NPP_{ACW}	4.3 ± 0.4	3.1 ± 0.3	2.6	2.2 ± 0.6
$NPP_{\text{branch turnover}}$	0.5 ± 0.1	1.1 ± 0.1	(1.0)[1]	1.0 ± 1.0
$NPP_{\text{coarse root}}$	0.9 ± 0.4	0.7 ± 0.3	(0.6)[2]	0.7 ± 0.2
$NPP_{\text{fine root}}$	2.0 ± 0.6	1.9 ± 0.3	2.0	2.2 ± 0.6
NPP_{AG}	13.0 ± 0.6	10.4 ± 0.6	(9.1)	7.8 ± 0.4
NPP_{BG}	2.9 ± 0.7	2.6 ± 0.4	(2.0)	2.8 ± 0.6
NPP_{Total}	15.9 ± 0.9	13.0 ± 0.7	(11.1)	10.6 ± 0.7
Respiration (Mg C ha^{-1} yr^{-1})				
R_{leaf}	8.5 ± 2.6	9.0 ± 2.7	(10.8)[3]	11.9 ± 4.0
R_{stem}	7.3 ± 2.9	5.8 ± 2.3	11.6	5.1 ± 0.5
$R_{\text{coarse root}}$	1.6 ± 0.6	0.7 ± 0.3	(2.6)[2]	-
$R_{\text{rhizosphere}}$	3.9 ± 0.4	4.5 ± 0.2	6.9	7.4 ± 0.5
R_{CWD}	3.6 ± 0.3	3.2 ± 0.2	4.5	2.2 ± 0.4
R_{soil}	11.2 ± 0.7	14.6 ± 0.4	16.0	13.5 ± 0.9
R_{a}	21.3 ± 4.0	20.6 ± 3.6	(31.9)	24.4 ± 4.1
R_{h}	14.4 ± 0.9	11.8 ± 0.7	(12.4)	9.9 ± 0.8
R_{Total}	35.7 ± 4.0	32.4 ± 3.7	(44.2)	34.4 ± 4.1
GPP	37.2 ± 4.1	33.6 ± 3.7	47.2 (43.0)	32.0 ± 4.1
CUE	0.44 ± 0.05	0.39 ± 0.05	0.23 (0.29)	0.33 ± 0.05

[1] Estimated as the balance between NPP_{ACW} and large wood detritus (Yoneda *et al.*, 1977; Kira, 1987)

[2] Estimated by multiplying NPP_{ACW} by the ratio of coarse root over above-ground coarse wood biomass (0.22) calculated for Lambir (see Chapter 5; Kho et al., *submitted* 2012)

[3] Corrected based on a 33% reduction for photoinhibition (see Malhi *et al.*, 2009)

Key: MAT, mean annual temperature; $NPP_{\text{litterfall}}$, litterfall net primary productivity; $NPP_{\text{herbivory}}$, production lost to leaf herbivory; NPP_{ACW}, above-ground coarse wood NPP; $NPP_{\text{branch turnover}}$, branch turnover NPP; $NPP_{\text{coarse root}}$, coarse root NPP; $NPP_{\text{fine root}}$, fine root NPP; NPP_{AG}, above-ground NPP; NPP_{BG}, below-ground NPP; NPP_{Total}, total NPP; R_{leaf}, leaf respiration; R_{stem}, stem respiration; $R_{\text{coarse root}}$, coarse root respiration; $R_{\text{rhizosphere}}$, rhizosphere respiration; R_{soil}, soil respiration; R_{a}, autotrophic respiration; R_{h}, heterotrophic respiration; R_{Total}, total respiration; GPP, gross primary productivity; CUE, carbon use efficiency.

The bottom-up approach at Pasoh estimated GPP to be 47.2 Mg C ha^{-1} yr^{-1} (Kira, 1987). This early estimation contradicts observations from the flux tower in Pasoh, which suggest a GPP in a range of 30.0 to 34.0 Mg C ha^{-1} yr^{-1} (Kosugi *et al.*, 2012). However, GPP is lower and in better agreement (estimated value of 43.0 Mg C ha^{-1} yr^{-1}) when corrected for leaf dark respiration. This further suggests that fluxes from respiration terms should be corrected and scaled up to ecosystem level to improve carbon budget estimation.

The overall total productivity, respiration and GPP are in good agreement between Lambir and Caxiuanã, Brazil (Figure 7.3). However, the total NPP differed by about 20% between these two sites. There appears to be a much higher allocation of NPP to above-ground components and heterotrophic respiration in Lambir as compared to Caxiuanã. In contrast, autotrophic respiration in Caxiuanã is substantially higher than Lambir, resulting in a lower ecosystem CUE. It is interesting to speculate whether the higher CUE at Lambir is associated with the more fertile soils (ultisols vs. oxisols) or with certain characteristics of the dominant, fast-growth dipterocarps.

7.2. Bornean Lowland Dipterocarp Forest and Climate Change

The aseasonal climate in large parts of Borneo experiences occasional drought, often associated with a strong ENSO event (Brunig, 1969; Walsh, 1996; Walsh and Newbery, 1999). Over recent decades, the intensity and frequency of ENSO events have increased (Salafsky, 1998; Malhi and Wright, 2004). Recently, terrestrial tropics have been experiencing new and significant climate change, with frequent and more adverse moisture deficits (Williams *et al.*, 2007). I have shown that moisture is the essential key driver in carbon cycling processes such as productivity, the allocation of carbon and respiration, and these responses vary between two contrasting soil types. In addition, higher productivity occurred on soil with higher nutrients and moisture content. For example, when soil moisture declines there may be a concomitant decline in above- and below-ground production, with an increase in the rate of soil respiration. Hence, more carbon would be respired rather than allocated for plant biomass production.

In Borneo, frequent adverse drought events can substantially affect forest structure (Becker *et al*., 1998; Curran *et al*., 1999; Nakagawa *et al*., 2000; Harrison, 2001; Potts, 2003; Van Nieuwstadt and Sheil, 2005), floristic composition (Wright, 1992; Becker and Wong, 1993; Davies and Becker, 1996; Corlett and Lafrankie, 1998; Harrison, 2000; Delissio and Primack, 2003), and the overall functional composition of tropical forests (Phillips *et al*., 2010). Such extreme and prolonged drought events have caused widespread tree mortality events in both Amazonia and Borneo, with greater vulnerability found for trees in Borneo (Phillips *et al*., 2010). In the dipterocarp family, the mortality rate can be 12 – 30 times higher during the drought period (Nakagawa *et al*., 2000). The frequency of such events has increased in recent decades (Allen *et al*., 2010). In addition, a recent study in Lambir has shown that mortality drastically increased when precipitation and moisture decreased (Kumagai and Porporato, 2012). In fact, I have shown in my study that the increase in mortality and decrease in biomass may be the effect of severe drought, and there may be a lag in the response on the sandy loam soil (Chapter 5). In Borneo, extreme moisture deficits have also been attributed not only to drought but also to the consequences of large fires (Leighton and Wirawan, 1986; Woods, 1989; Siegert *et al*., 2001; Cochrane, 2003; Slik and Eichhorn, 2003). Such catastrophic fires would result in tropical forests collapsing and could create potentially dangerous positive feedback (Lewis, 2006). Thus, the evidence shows that lowland dipterocarp forests are potentially vulnerable to climatic drying.

Extreme climate conditions, particularly drought in lowland dipterocarp forests would have a large impact on the terrestrial carbon cycle and on land–atmosphere energy exchange. Clearly, should the intensity of drought increase and become protracted, there would be considerable shifts in the processes of the carbon cycle. This would have a significant effect on the global carbon budget and on climate change more generally.

7.3. Future Research

7.3.1. Long-term Spatial and Temporal Measurement Extrapolation

Throughout this thesis, I have noted that the results and interpretation presented here should be treated with caution. During my measurement campaign, several measurements were conducted over different periods of the year and on smaller plots. In addition, my measurement coincided with particularly strong seasonality when there was a notable dry period, which was then followed by the mass flowering event. Clearly, incomplete and short-term measurements may miss some important patterns and episodic events. For example, I have shown that the mean soil respiration over the full diurnal cycle may be higher by more than half when compared to measurements conducted during daytime (Section 7.2 and Chapter 3). Although this inference may be tentative, should the result turn out to be a realistic estimate, this difference would have a significant impact on our understanding of the terrestrial carbon cycle. Hence, continuous measurement is imperative, particularly on the same study site so as to closely monitor changes over time. In addition, measurements can be expanded across larger study sites to capture the strong spatial variability across several study sites and soil types in Lambir. In the Amazon, several dedicated plots have continuously been monitored and results recorded over time (Phillips *et al.*, 1998; Malhi *et al.*, 2009). These studies have produced consistent and comparable results necessary to aid our understanding of the carbon cycle in tropical forests.

7.3.2. Data Integration and Modelling

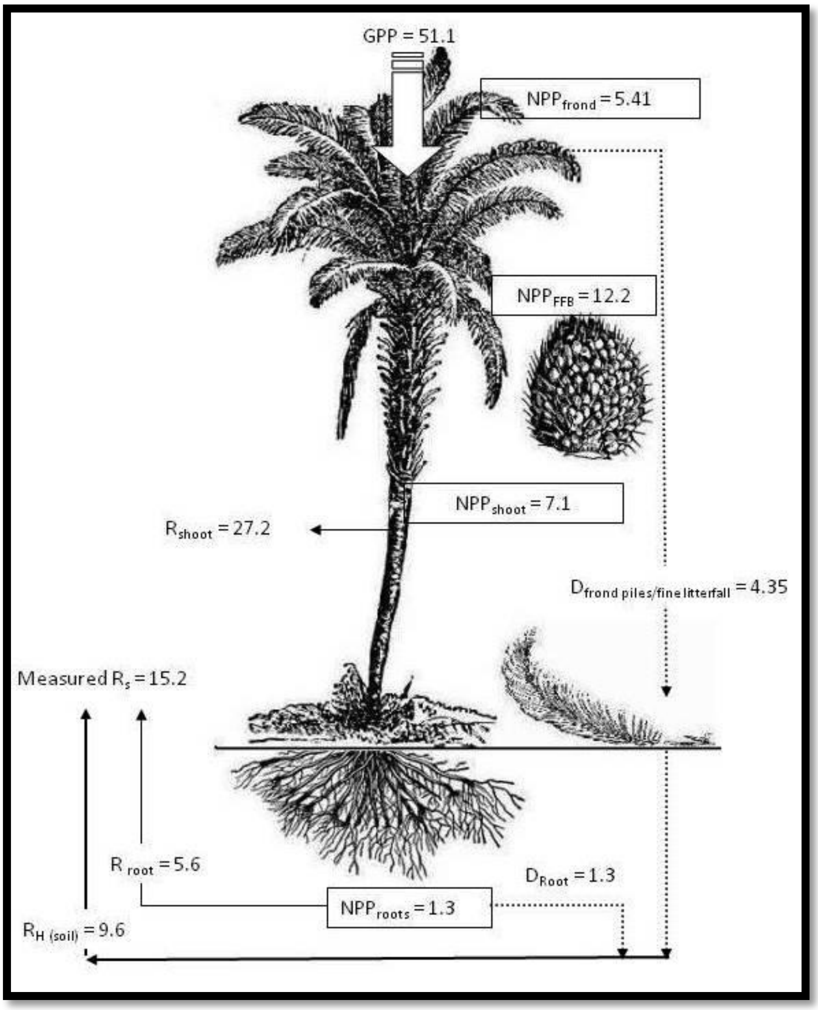
The lowland dipterocarp forest in Lambir provides the ideal laboratory for understanding the mechanisms and interactions between forest ecosystems and the atmosphere. Recently, there have been considerable advances aiding our efforts to account for the carbon budget using the flux tower eddy covariance technique (e.g. Kumagai *et al*., 2004; Saitoh *et al*., 2005). However, different approaches will have different sources of errors. Hence, it is imperative to integrate and cross-check the studies to quantify an accurate and reliable carbon balance and components across an ecosystem (Luyssaert *et al*., 2009; Malhi, 2012). The results presented in this D.Phil. thesis have shown a good agreement with those produced using the flux tower measurements (Kumagai *et al*., 2004). However, there are differences between the two contrasting soil types (see section 7.6 and Chapter 6), and the measurements are time-specific. Hence, extensive plot replications and concurrent measurements can improve these estimations and provide plausible estimates for terrestrial models (Adachi *et al*., 2011).

7.3.3. Land Use and Changing Ecosystems

In the Southeast Asia region, the rates of deforestation and forest loss have recently accelerated (Hansen *et al*., 2010; Miettinen *et al*., 2011). Tropical deforestation accounted for 25–50% of carbon emissions across the tropical regions between 2000 and 2005 (Harris *et al*., 2012). The loss of tropical forest in this region is driven by human activities including extensive logging, agricultural expansion, shifting cultivations, and development. While tropical forests provide one of the largest carbon sinks in terrestrial ecosystems, current changes in vegetation and land use by agriculture and agroforestry are continuously feeding into the imbalances of the carbon cycle.

During the past few decades, the oil palm (*Elaeis guineensis*) has become the most extensive and rapidly expanding equatorial crops in the world (Koh and Wilcove, 2008).

However, the historical pathways of land-use change leading to oil palm plantations remain understudied (Danielsen *et al*., 2009; Reynolds *et al*., 2011). Thus, the impact and the functioning of these new biological sinks are poorly understood. There is evidence indicating profound changes in the exchange of trace gases when tropical forests are replaced by oil palm (Fowler *et al*., 2011). In addition, studies have shown that younger forest stands may have a similar rate of production to oil palm (see Figure 7.4) and rubber (Kira, 1987; Henson, 1999). If oil palm continues to rapidly change the landscape and vegetation, there may be changes in biomass (Henson, 2005; Morel *et al*., 2011) and shifts in the carbon dynamics, which may potentially affect the global carbon budget. Hence, it is imperative to understand the differences between the carbon cycle processes of these two contrasting ecosystems and the changes in the transition from forests to oil palm plantations. Such studies are currently being developed in the SAFE (Stability of Altered Forest Ecosystems) Project, a new forest fragmentation experiment in northern Borneo (Ewers *et al*., 2011).



Key: GPP, gross primary productivity; NPP_{frond}, frond net primary productivity; NPP_{FFB}, fresh fruit bunches NPP; NPP_{shoot}, shoot NPP; $NPP_{\text{frond piles/fine litterfall}}$, frond piles and fine litterfall NPP; NPP_{roots}, root NPP; D_{root}, root detritus; R_{root}, root respiration; $R_{\text{H (soil)}}$, soil heterotrophic respiration; R_{s}, soil respiration; R_{shoot}, shoot respiration. All units are in Mg C ha^{-1} yr^{-1}.

Figure 7.4: The carbon cycle in a coastal oil palm plantation 9–10 years after planting. All data derived from (Henson, 1999).

7.4. Concluding Remarks

This thesis has presented an attempt to describe in detail the carbon cycle of two forest plots in Lambir. It has achieved this goal, in doing so has highlighted interesting differences between the two plots and between these sites and other sites in the tropics. It has demonstrated the potential of such detailed and continuous measurements but also the limitations of a relatively short study, which is all that is possible during D.Phil. study. It is clearly important that such studies take place and can continue into long-term monitoring, enabling us to track how the functioning of these sites varies in response to 21st-century atmospheric change. These measurements are ongoing at Lambir, and I hope to obtain a longer-term understanding of the dynamics of this forest, which is amongst the richest forests on Planet Earth.

7.5. References

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